UNIVERSIDADE DO ALGARVE
UNIDADE DE CIÊNCIAS E TECNOLOGIAS DOS RECURSOS AQUÁTICOS

TROPHIC ECOLOGY OF THE NORWAY LOBSTER *Nephrops norvegicus* (L.) (CRUSTACEA: NEPHROPIDAE) IN THE MEDITERRANEAN AND ADJACENT ATLANTIC: DIETS, EVACUATION RATES AND DAILY RATIONS.

Margarida de Lurdes de Jesus Bastos Cristo

Dissertação apresentada à Universidade do Algarve para obtenção do
grau de Doutor em Ecologia, especialidade Ecologia de Comunidades

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PREFACE

This thesis is presented as a collection of papers. The reason for this choice has to do with the variety of themes that, although related to the feeding ecology studies in *Nephrops norvegicus*, could be much easier presented as separate subjects.

From the work presented herein, three papers have already been published and three are submitted:

a) Cristo, M. 1998 - Feeding Ecology of *Nephrops norvegicus* (Decapoda:Nephropidae). *J. Nat. Hist.* **32**: 1493 - 1498, constituting chapter 2;

b) Cristo, M. and J. E. Cartes. 1998 - A comparative study of the feeding ecology of *Nephrops norvegicus* (L.), (Decapoda: Nephropidae) in the bathyal Mediterranean and the adjacent Atlantic. *Scient. Mar.* **62**: 81-90., constituting chapter 3;

c) Cristo, M. and P. Encarnação. 2000 - Laboratory estimates of the daily ration of the Norway lobster *Nephrops norvegicus* (L.) (Decapoda) from the southern coast of Portugal. *Crustacean Issues* **12**: 689-695, constituting chapter 6;

d) Cristo, M. (submitted). Diet of the Norway lobster (*Nephrops norvegicus* (L.)) off the South coast of Portugal, constituting chapter 4;

e) Cristo, M. (submitted). Gut evacuation rates in *Nephrops norvegicus* (L.): laboratory and field estimates, constituting chapter 5;

f) Cristo, M. and M. Castro. (submitted). Field estimation of daily ration of Norway lobster -*Nephrops norvegicus* (L.)- in the south of Portugal, constituting chapter 7.

SUMMARY

The subject of this Ph.D. thesis is the feeding ecology of the Norway lobster - *Nephrops norvegicus* (Linnaeus, 1758), and related aspects.

Stomach content analysis using traditional methods (frequency of occurrence, numerical frequency and frequency by points) showed that Norway lobster is a euryphagous species, an opportunist that feeds on a wide variety of prey, both living and dead. It can, therefore, also be considered a scavenger.

Comparative studies showed that there are no qualitative differences between the diets of male and female animals. There are, however, slight variations among length classes. Although the types of prey are essentially the same for big or small individuals, small lobsters tend to feed on smaller prey items than do larger animals.

After comparing data from lobster populations from different areas in the Mediterranean and adjacent Atlantic, it was concluded that no significant seasonal or geographic differences in diets exist. The small differences found could be attributed to environmental variations and, consequently, prey availability.

An aspect of the lobster's feeding habits relevant to stock conservation is the fact that, irrespective of location, season, sex or size, the dominant prey groups are crustaceans and fish.

Female maturity, and the presence or absence of eggs, influence feeding intensity negatively. Possible reasons for this may be that sexual activity reduces feeding activity, and that large, ripe gonads compress the stomach. During the mating season the feeding activity of males is also reduced.

The necessity to remain in the burrows for longer periods, in order to protect the eggs will also have the effect of reducing the feeding activity of the females.

Several laboratory and field experiments were conducted in order to quantify food intake. Evacuation rates were determined using both captive animals, supplied with food, or lobsters in a semi-natural environment, feeding on natural food. In both cases the “serial slaughter method” was used. The rates obtained were similar (R=0.172-h in laboratory experiments, and R=0.177-h in field experiments).

Daily rations were also determine using both laboratory and field experiments. Food intake in the field was slightly higher than that measured in the laboratory. Expressed as food dry weight percentage of lobsters’ fresh weight, the field and laboratory average rations were calculated to be, respectively 1.4% e 0.8%.

RESUMO

A ideia mestra na base do desenvolvimento desta tese de doutoramento, foi o estudo da alimentação do lagostim - *Nephrops norvegicus* (Linnaeus, 1758), tentando cobrir os diversos aspectos com ele relacionados

Uma vez projectado e efectivado um estudo base de análise de conteúdos estomacais, aplicando metodologias tradicionais neste tipo de estudo (frequência de ocorrência, frequência numérica e frequência por pontos), concluiu-se que o lagostim é uma espécie eurifágica, oportunista, alimentando-se de um leque variadíssimo de presas vivas ou mortas, podendo por isso ser ainda considerado como necrófago.

Da análise comparativa da dieta, foi ainda possível concluir que não existem diferenças qualitativas na dieta de machos e fêmeas, mas no entanto relativamente ao tamanho já parecem existir pequenas variações. Assim, apesar do tipo de presas ser essencialmente o mesmo quer para indivíduos pequenos quer como grandes, e não existirem diferenças qualitativamente significativas, parece haver uma tendência para os indivíduos de menores dimensões se alimentarem essencialmente (em termos quantitativos) de presas mais pequenas e os maiores de presas maiores.

Foi ainda feita a comparação da dieta entre populações de diferentes áreas geográficas da região mediterrânica e atlântica adjacente, em diferentes estações do ano. Deste estudo concluiu-se que não existem diferenças significativas quer geográficas, quer sazonais. Essencialmente, as pequenas variações observadas são apenas reflexo das variações ambientais e portanto da disponibilidade de presas.

No entanto, em termos de grandes grupos de presas dominantes na dieta existe um aspecto conservacionista, pois em todos os locais, estações do ano, qualquer que seja o sexo e tamanho as presas preferidas são crustáceos e peixes.

Outro aspecto importanteanalisado foi o da influência do estado de maturação das fêmeas e do porte de ovos na intensidade alimentar. Verificou-se que ambos influenciam negativamente a alimentação. Próximo da época de postura, por um lado as gónadas encontram-se tão desenvolvidas que comprimem fortemente o estômago, e por outro a actividade reprodutora sobrepõe-se, provavelmente, à necessidade de se alimentarem, notando-se nesta época igual abrandamento da actividade alimentar dos machos. Durante a época em que as fêmeas estão ovadas, estas reduzem também fortemente a sua alimentação, o que se deve provavelmente à necessidade de protecção dos ovos, mantendo-se, por isso, confinadas ao interior das suas tocas.

Relativamente aos estudos que dizem respeito às quantidades de comida ingerida foram realizadas experiências em cativeiro e experiências de campo.

Foi determinada a taxa de evacuação gástrica de lagostins em cativeiro com alimento fornecido e de lagostins em ambiente semi-natural com alimento natural, pelo método das matanças sucessivas. As taxas obtidas pelos dois métodos são muito semelhantes (R=0.172-h nas experiências de laboratório e R=0.177-h nas experiências de campo).

Para a determinação da ração diária foram também ensaiadas duas experiências: em cativeiro e em campo. Os resultados das experiências de campo deram valores ligeiramente superiores aos de laboratório, respectivamente 1.4% e 0.8% de peso seco de comida por peso fresco de lagostim.

GENERAL INTRODUCTION

CONTEXT OF THE STUDY

After finishing the "Provas de Aptidão Pedagógica e Capacidade Científica", where the theoretical models and methodologies used in feeding ecology were discussed, I had the chance of developing the research conducting to the doctorate degree, applying these same concepts. This opportunity came associated with the chance of collaborating in the research project "NEMED" (EC DG XIV. MED92/008, Fishery) (Sardà, 1998) (general co-ordination of Dr. Francisco Sardà, ICM, co-ordination in the University of Algarve by Dr. Margarida Castro).

One of the objectives of this project was the comparative feeding ecology of the Norway lobster (*Nephrops norvegicus* (L.)) among several areas of the Mediterranean and adjacent Atlantic. Similar studies had already been developed for other benthic decapods in the Mediterranean (Cartes, 1991; Cartes, 1993b; Cartes, 1994; Cartes, 1995; Cartes, 1998; Cartes and Abelló, 1992; Cartes and Maynou, 1998; Cartes and Sardà, 1989), in fact the first comprehensive studies ever made around the feeding ecology of deep-water decapods. The participation in this project also allowed the straight collaboration with Dr. Joan Cartes, who became a co-adviser of the research.

In the context of the "NEMED" project, the first part of the study was defined: compared feeding ecology of *Nephrops norvegicus*, having as major objective the general characterisation of *Nephrops* diets in different areas and seasons.

Also using samples from the NEMED project, a second theme was approached, the variability of feeding rates with sex, maturation, ovigerous condition and time of the year. This study was done using samples from the South coast of Portugal and involved a much greater sampling effort. Samples were obtained monthly throughout a period of two years.

Having obtained the general characterisation of diets and feeding needs, the estimation of quantitative rates was done through controlled experiments. Four experiments were planed: two to obtain estimates of gastric evacuation rates (laboratory and field), and two others to estimate daily rations (again laboratory and field estimates). These experiments completed the general study of feeding ecology of the Norway lobster.

STATE OF THE ART AND OBJECTIVES

The decapod crustacean *Nephrops norvegicus* (L.) is a species with a wide geographical distribution, from North-west Atlantic coasts to the East Mediterranean Sea and the Moroccan coast (Figueiredo and Thomas, 1967a; Farmer, 1975; Sardà and Fernández, 1981) with the southern most distribution in the Canary Islands (Barquin et al., 1998). Its bathymetric distribution in the Mediterranean extends from the continental shelf to bathyal grounds, reaching depths of 871 m in the western Mediterranean (Abelló et al., 1988) although maximum densities are found between 245 and 485 m (Cartes et al., 1994). In the Atlantic its bathymetric distribution extends from a mere 10 m to 720 m (Figueiredo and Thomas, 1967b), but in the South coast of Portugal, maximum densities are found between 300 and 600 m (Figueiredo, 1988).

This species has long been a target species for commercial fisheries an, as a consequence it has also been widely studied. Figueiredo and Thomas (1967a), Farmer (1975) and more recently Sardà (1995) published reviews summarizing the state of knowledge on the Norway lobster (*Nephrops norvegicus*).

In the last review (Sardà, 1995), the need for further studies on feeding amongst other things, is emphasised . According to this author feeding in this species is poorly understood. The first published work on the subject dates from 1924, and describs the feeding process (Yonge, 1924 *in* Sardà, 1995), but it was only in 1962 that the diet of *N. norvegicus* was described for the first time (Thomas and Davidson, 1962). The identification of stomach contents was also carried out by Lagardère (1977) and Gual-Frau and Gallardo-Cabello (1988).

Another subject of great importance in the study of feeding is the determination of the feeding rate, maximum daily ration and daily rations in the wild. The first two subjects were studied by Sardà and Valladares (1990), through laboratory experiments.

However, as it was pointed out by Sardà (1995) there was little information on feeding rates and therefore, studies that allows to undersand the ability of *N. norvegicus* to withstand basal metabolism apparently with low quantities of food should be encourage.

Bearing in mind the points raised by the various reviews, it was decided to structure the present work in the following manner:

1) Carry out an initial assessment of diet of the Norway lobster in the south coast of Portugal;

2) A comparative seasonal study on the type of feeding in 7 close geographical regions, covering all the Mediterranean sea, from Greece to the Alboran sea and the adjacent Atlantic;

3) To carry out a detailed study on the diet of the Norway lobster in the south coast of Portugal, comparing the diet between sexes and length classes throughout a year of sampling.

4) To calculate the gastric evacuation rate of *N. norvegicus* through field and laboratory experiments;

5) To calculate the daily ration of *N. norvegicus* through laboratory experiments;

6) To calculate the daily ration of *N. norvegicus* through field experiments.

METHODOGICAL CONSIDERATIONS

Taxonomy

The Norway lobster was first described by Linnaeus (1758 *in* Zariquiey, 1968) as *Cancer norvegicus*. The genus *Nephrops* was later described by Leach (1814 *in* Zariquiey, 1968), and the species assigned to this genus as *Nephrops norvegicus* (L.).This decapod (Table 1) belongs to the family Nephropidae.

Table 1: Taxonomic classification of the Norway lobster

Sistematic position	
Phylum	Arthropoda
Subphylum	Crustacea
Class	Malacostraca
Order	Decapoda
Superfamily	Astacidea
Family	Nephropidae
Genus	*Nephrops* Leach, 1814
Species	*Nephrops norvegicus* (Linnaeus, 1758)

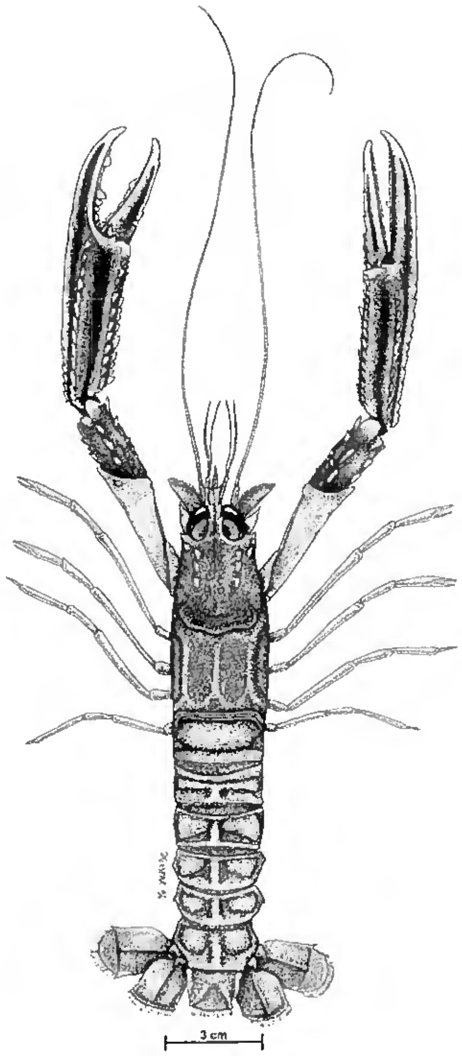

Fig. 1 - *Nephrops norvegicus (L.)*. Male. (Drawn by P. Gaspar)

N. norvegicus (Fig. 1) is easily recognised by it's dark salmon bands intercalated by white bands, its hard and spiny shell and the presence of long and strong quelipods (bigger in males than in females); and for the fortunates that can eat them, for it's unequal taste.

Feeding studies

There are numerous studies on feeding, particularly on fish. Hynes (1950), Pillay (1952), Hyslop (1980), and Herran (1988), systematize and criticise the methods employed. Regarding feeding characterization, many species have been the subject of studies (e. g. Carvalho, 1981; Crozier, 1985; De Silva, 1973; Geistdoerfer, 1978; Lyle, 1983; Macpherson, 1979; Macpherson, 1980; Matallanas, 1980; Mauchline and Gordon, 1984; Mori, 1982; Pereda and Olaso, 1990; Sartor et al., 1992).In contrast, the studies done on invertebrate, and in particular on decapods, are much less numerous. This fact may be partly due to the difficulties encountered in identifying and quantifying the ingested prey.

In general, fish ingest whole prey, making its identification easier. Decapod crustaceans eat in fractions and grind the prey to a greater or lesser degree according to the morphology of their mouth pieces, in partucular their mandibules. Furthermore, some species possess a number of plates or chitinous teeth that cover the anterior part of the stomach which are moved by a complex muscular system usualy named "gastric mill" (Sardà and Fernández, 1981)

This difficulty in identifying and quantifying is reflected on the lack of uniformity of the methods used by the different authors. Regarding crustaceans, it can be emphasised the studies done on penaeids (Chong and Sasekumar, 1981; Cockcroft and McLachlan, 1986; Wassenberg and Hill, 1987), aristeids (Cartes and Sardà, 1989), pandalids (Cartes, 1993a), nephropids (*Metanephrops*, *Nephrops* and *Homarus*) (Cartes, 1993a; Elner and Campbell, 1987; Gual-Frau and Gallardo-Cabello, 1988; Mytilineou et al., 1992) and on a great variety of brachiurids (Abelló and Cartes, 1987; Elner, 1981; Freire, 1996;

Freire and González-Gurriarán, 1995; Orsi and Mori, 1977; Wassenberg and Hill, 1989; Williams, 1982).

In general, crustaceans are opportunistic species with the ability to use any type of food resource. They are able to rapidly locate corpses, to detect filter-feeders or burrowed organisms in the substrate or to use sediment or particulated organic matter as a food source.(Cartes , 1991).

The feeding habits of a species are an essential biotic factor to its distribution and abundance. (Sokolova, 1972). Cartes (1991), suggest that the abundance of certain species, such as *Calocaris macandreae*, coincides with the scarceness of its predators, *Geryon longipes* and *Policheles typhlops*.

Having in mind all these factors, the study on the trophic ecology of decapod crustaceans must be targeted to the following goals:

a) To characterize its diet trying to establish the degree of specialization of a given species in relation to the available resources; b) to determine seasonal differences in diets for the different age groups and sexes; c) to establish the differences in feeding intensity in the daily cicle and in the biological cicle; d) and to establish the overlaping of diets between species or groups.

Diet evaluation methodologies

There are several methods that can be applied in feeding studies which, in general, become more complicated as the goals set become more specific.

These methods have been subject to several revisons (Herran, 1988; Hynes, 1950; Hyslop, 1980; Pillay, 1952) which serve as a reference to the description of three general types of methodologies: those of qualitative type, those of quantitative type, and those of subjective type.

Qualitative methods

Occurrence and dominance methods are included here:

a) Occurrence Frequency (F)

The number of stomachs that contain one (or more) individuals of a certain food category are registered and divided by the total number of stomachs observed (or by the total number of stomachs with food) and then multiplied by 100.

$F = n_i / N \times 100$

ni = number of stomach that contain the prey i

N = total number of stomachs considered in the analisis

b) Dominance frequency

Only the percentage of stomachs that contain the dominant food category is considered (the bulk) expressed in accordance to the total number of stomachs observed (or with some content).

Occurrence frequency is a widely used method, since it is fast and it requires very little equipment. However, it only gives an idea of the type of food used by the predator, desregarding entirely the importance of the several types of prey in the food mass.

The dominance frequency method has the same inconveniences as the previous method besides the problem of choosing which dominance method to use. Some authors have been using the criteria of numeric, volumetric and gravimetric dominance. If direct mass, volume or number is chosen for measurements, there is no point to use the dominance method and, therefore, it is better to use the quantitative methods described as follows. (Hyslop, 1980).

Quantitative methods

Among these , we find numeric methods (a), volumetric (b) and gravimetric (c).

a) Numerical percentage (PN)

The number of individuals from each food category (prey) is registered, expressed in percentage in relation to the total number of individuals from all the categories found in all stomachs examined.

$PN = p_i / P \times 100$

pi = total number of prey from the category i

P = total number of prey

This method is widely used because it is fast and simple but it requires a reliable counting of the prey. It is the most appropriate method when the size of the prey is similar, like in planctonic animals .

If the average prey number per stomach is calculated , we can have an indication of the variations in feeding intensity, which may occur by season, by breeding season or as a result of any other factor of exogenous or endogenous origin.

There are several negative aspects of this method that weigh against its use. (i) It overestimates the value of small size prey. (ii) It is difficult to calculate when there is fragmentation of the food, which happens in crustaceans (iii) It does not account for the prey size. (iv) It is not useful for food categories that do not appear in discrete units, such as algae or detritus.

b) and c) Volumetric or gravimetric methods

These are based on the determination of the prey volume or weight.

Volume can be calculated directly or by water movement on a graduated container or indirectly by comparing with blocks with a pre set volume. Weight can be calculated with the material dry or wet.

Either of these methods have the inconvenience of quantifying the water that is absorbed by the prey, requiring its elimination either by absorption using a filter paper or by drying it in a stove in order to obtain dry weight. A method that overcomes this problem is the determination of the prey volume after drying in a stove, a method used by Carter and Steele (1982) to study the diet of *Homarus americanus*.

Values are usualy expressed in percentage per volume,

$PV = v_i / V X100$

vi = Volume of the food category i

V = Total volume of stomach contents

Or percentage per weight, dry or wet:

$PP = p_i / P X 100$

pi = weight of the food category i

P= total weight of stomach contents

In the particular case of crustaceans, the use of these two last methods becomes very difficult, since the stomach contents are generally of small dimension as a consequence of grinding by the predator`s mouth pieces. The latter makes it exceedingly difficult to separate the different prey.

Therefore, the use of volume determination methods is recommended. This method the stomach contents are spread in a scaled plate, which takes height in consideration, and only the area occupied by each food category is calculated (Chong and Sasekumar, 1981).

The degree of digestion that prey may present is another problem for volume determination. However, it is possible to estimate the size or weight of prey by measuring hard body parts hat resist digestion (jaw bone, telson, otholits) and by linear regression determine the length or weight of intact prey (Macpherson, 1979). Another aspect that may help interpreting the results is previous knowledge of the gastric excretion from the different food categories ingested by a species (Sardà and Valladares, 1990).

Subjective Methods

The previously described methods can sometimes be difficult to use, particulary when analysing a large amount of samples or when the nature of the samples is like the one described in crustaceans, in which, for example, the numeric, volumetric or gravimetric methods are inadequate.

This fact lead to the development of subjective methods of analysis of the different components in the diets of the populations studied, giving rise to various visual estimation methods.

Pillay (1952) establishes a volumetrical percentage calculation method of the different food categories in the stomach. The total volume in the stomach is considered as a unit through visual estimation in a way similar to the percentage method described by Hansson (1980).

A similar method is the points method, initially used by Swynnerton and Worthington (1940) and argued by por Hynes (1950) in which to each food category it is attributed a score in accordance to its proportion in the total stomach content..

This points method can also be used to assess the degree of filling of the stomach. In this case the degree of filling is estimated (between empty and full) and the total of the points attributed are changed proportionally. Finally, regardless of adjustment or not for the degree of repletion of the stomach, the points attributed to each category are added and expressed as a percentage of the total points (PMP).

$$PMP = tpi / Tp \times 100$$

tpi = total points of the food category i

Tp = total points attributed

These methods have been criticised precisely because of their subjectiveness, but, in fact, they have the advantage of being fast and easy to apply. Also the error attributed to the subjectiveness is minimised if working with a large number of samples. .

Besides, there are relatively handy methods to decrease subjectiveness, such as, for example, by placing the stomach contents in a scaled slide or by standardizing the repletion degree by comparing it with the wet weight of the stomach content.

Gastric evacuation

Gut evacuation rates have been largely determined in fish, either during field or laboratory experiments (Amundsen and Klemetsen, 1988; Brodeur, 1984; Brodeur and Pearcy, 1987; Garcia and Adelman, 1985; Héroux and Magnan, 1996; Jobling, 1980; Persson, 1979). However, the methodologies used for fish have rarely been applied to invertebrates such as decapod crustaceans. In fact, only in a few studies, have decapod crustacean gastric evacuation rates of different tipes of food been estimated and all were laboratory experiments (Hill, 1976; Joll, 1982; Sardà and Valladares, 1990).

Several studies have also been carried out on non-decapod crustaceans to determine *in situ* and *in vitro* evacuation rates (Clarke et al., 1988; Dam and Peterson, 1988; Kiorboe and Tiselius, 1987; Murtaugh, 1984; Perissinotto and Pakhomov, 1996). However, no studies have been conducted to date to determine *in situ* gut evacuation rates of deep water decapod crustaceans, mainly due to logistical constraints.

The determination of the evacuation rate of a certain species is important when feeding studies are addressed (Joll, 1982) and it is also a necessary parameter to evaluate daily rations (Maynou and Cartes, 1997; Maynou and Cartes, 1998).

Daily ration

Daily ration estimates can be determined through laboratory or field estimates.

Over the past decades, numerous studies have focused on daily rationestimates in fish, either using field experiments (Amundsen and Klemetsen, 1988; Brodeur and Pearcy, 1987; Héroux and Magnan, 1996; Pakhomov et al., 1996; Tudela and Palomera, 1995; Worobec, 1984) or laboratory experiments (Walh and Stein, 1991). In crustaceans, however, comparatively few experiments on this subject have been carried out in the field (Dam and Peterson, 1988; Maynou and Cartes, 1997; Maynou and Cartes, 1998; Pakhomov and Perissinotto, 1996; Perissinotto and Pakhomov, 1996) or in laboratory (Sardà and Valladares, 1990). All the results derived from these studies have direct application in the field of trophic ecology, for example the determination of predation pressure on prey species, sustainable yields of different habitats, impact of environmental modifications, or even for testing bioenergetic models in different species (Héroux and Magnan, 1996).

The estimation of daily rations can be a source of indirect information on the carrying capacity of the environments to sustain given levels of abundance, biomass and diversity (Maynou and Cartes, 1997).

Daily ration models

Several authors have developed daily ration models based on field experiments (Eggers, 1977; Eggers, 1979; Elliott and Persson, 1978) and they have been applied to studies of fish and decapod crustaceans.

Daily ration models are based on the assumption that gastric evacuation is an exponential decay function (Eggers, 1977; Elliot and Persson, 1978) which includes a constant for gastric evacuation rate (R).

This value of R can be obtained from the results of field experiments under controlled conditions (Héroux and Magnant, 1996; Cristo, submitted), or by laboratory experiments (Sardà and Valladares, 1990, Héroux and Magnan, 1996; Cristo, submitted).

These models can be expressed as:

Eggers model (1977):

$$C_{(24E)} = F_{24}\, R\, 24$$

where F_{24} is the mean stomach fullness index over 24 h, as F_{wet}. This model assumes that the feeding periodicity is such that the fullness index at the beginning and at the end of a 24 h period are equal (Boisclair and Leggett, 1988; Eggers, 1977)

When the previous assumption cannot be met, (Eggers,1979; see also Boisclair and Marchand ,1993) a corrected model proposed by Eggers (1979) exsts:

$$C_{(24EC)} = C_{(24E)} + (F_{t=24} - F_{t=0})$$

where $F_{t=24}$ and $F_{t=0}$ are the values of stomach fullness index as F_{wet} at the end and the beginning of the 24 h sampling period.

Elliot and Persson model (1978): The food consumed during the time interval t_i is:

$$Ct_i = \frac{(Ft_i - Ft_0\, e^{-Rt_i})Rt_i}{1 - e^{-Rt_i}}$$

and the daily ration is the summation, over 24 h, of the K time intervals considered:

$$C_{(24E\&P)} = \sum_{i=1}^{K} Ct_i$$

This model assumes, as do the others, that food evacuation is exponential and that the rate of food consumption within each sampling interval is constant. It does, however, have an important limitation, namely, that time intervals should not be greater then 3 hours.

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FEEDING ECOLOGY OF *Nephrops norvegicus* (DECAPODA: NEPHROPIDAE)

ABSTRACTS

The stomach contents of 248 Norway lobster were analysed. Prey specimens were identified to the lowest taxonomical level possible. The frequency of occurrence method was used to analyse the data and the results are presented considering only major groups.

The results obtained indicate great diversity in terms of prey in the stomachs of *N. norvegicus*, with a clear preference for decapods, followed by other crustaceans and fish. Seasonal changes in the diet were not significant; particularly for the major groups.

Key words: Diet analysis; Feeding ecology; *Nephrops norvegicus*

INTRODUCTION

Norway lobster presents a wide geographical distribution, extending from the northern part of the west coast of Africa to Iceland, into the North Sea and into the East Mediterranean Sea (Figueiredo and Thomas, 1967; Zariquiey-Alvarez, 1968). Its bathymetric distribution extends from the continental shelf, in depths of 10 m, to bathyal grounds, reaching depths of 871 m in the western Mediterranean (Abelló et al., 1988). In Portuguese waters the bathymetric distribution ranges from 200 to 720 m with maximum concentrations between 300 and 600 m (Figueiredo, 1988). *N. norvegicus* is always one of the dominant species in the bathyal crustacean decapod assemblages both in the Mediterranean (Abelló et al., 1989; Cartes et al., 1994; Froglia and Gramitto, 1995), and the Atlantic coast (Figueiredo, 1988; 1989).

Due to its great ecological and commercial importance in Portuguese waters, *Nephrops norvegicus* has been a target species for a great number of biological studies (Figueiredo and Barraca, 1963; Figueiredo,1965; Figueiredo and Nunes, 1965; Figueiredo and Thomas, 1965, 1967). These studies focused mainly on growth, reproduction and moulting. In contrast, to date there have not been any feeding studies in these populations of such a commercially important resource. Even in other areas studies on Norway lobster diet and food consumption are not very common (Thomas and Davidson, 1962; Lagardére, 1977; Gual-Frau and Gallardo-Cabello, 1988; Sardà and Valladares, 1990; Mytilineou *et al*, 1992), compared to other biological studies. The results drawn from these studies, indicate that *N. norvegicus* is a euryphagous and non-selective species, consuming a great variety of crustaceans, fish and molluscs, either as an active predator or as a scavenger. The diet of *N. norvegicus* is influenced by size (Mytilineou *et al.*, 1992), which is a general characteristic in several other decapod crustaceans (Elner and Cambell, 1987; Cartes and Sardà, 1989), and does not differ between sexes (Mytilineou *et al.*, 1992).

The objective of this paper is to present the first results of a study of the diet of *N. norvegicus* from the south coast of Portugal, carried out from 1993 to 1995.

MATERIAL AND METHODS

The results presented here represent the first analysis of a series of 21 samples collected monthly during a period of two years (from November 1993 to October 1995); part of the sampling program for the project "*Nephrops norvegicus* - Compared biology and fisheries - NEMED". For this preliminary study 248 stomachs were analysed. The specimens were fixed immediately after collection in 10% formalin, and preserved in 70% alcohol. For each individual, sex and carapace length was registered to the nearest 1 mm (measurements rounded to the millimetre below), after which stomachs were removed and preserved in 70% alcohol. Only stomachs with contents were analysed, considering those with a repletion equal or superior to 20%,

estimated visually. Stomach contents were quantified using a compound microscope (6.4 - 40X). Individual prey items were identified with my own reference collection, and also using several identification keys, for the different *taxa*.

The results are presented seasonally, since the total number of stomachs observed is too low to permit a finer analysis. Thus, for Spring we considered the samples from March to May, for Summer from June to August, for Autumn from September to November and for Winter from December to February.

The diet analysis was done independently of sex , since there are apparently no differences in feeding between males and females (Mytilineou *et al*, 1992). Differences in the diet in different size classes can not be drown from these preliminary results, due to an unequal number of specimens analysed in different size classes. The analysis was carried out, using the frequency of occurrence method (% F) (Hyslop, 1980), and considering only major groups.

In the diet of Norway lobster, for prey classification purposes, we considered preferential groups those that are present in every season with a high F, and secondary groups those with a high F in at least one season.

RESULTS

A total of 662 food-items, belonging to 78 prey-categories (Table 1), were counted in 248 stomach contents analysed. The stomach contents are composed mainly of small and hard pieces of crustacean carapace, gastropod and bivalve shells, echinoderm exoskeleton, fish vertebra and otoliths, and soft parts of prey. This bulk, makes identification very difficult. From the analysis of the diet we decided to use 15 prey-groups, including non-identified material, which was mainly composed of amorphous soft portions that could not be assigned to any taxon.

The results obtained in terms of percentage of occurrence (%F), indicate a clear preference for decapods, followed by other crustaceans (euphausides,

Table 1 - Lists of prey-categories found in the stomachs of *N. norvegicus* (n. i. - not identified)

- FORAMINIFERA
  - Foraminifera n.i.
  - *Bolivina* sp
  - *Globigerina* sp
  - *Ubigerina* sp
- PORIFERA
  - Porifera n.i.
- CNIDARIA
  - Hydroida
  - Siphonophora
  - *Chelophyes appendiculata*
- SCAPHOPODA
  - *Dentalium* sp
- GASTROPODA
  - Gastropoda n. i.
  - Rissoidae
  - Thecosomata
  - *Cavolinia* sp
  - *Cymbulia* sp
- BIVALVIA
  - Amodonta
  - Taxodonta
  - Nucularidae
  - *Yoldiella striolata*
- CEPHALOPODA
  - Cephalopoda n. i.
  - Teuthida
- POLYCHAETA
  - Polychaeta n. i.
  - Afroditidae
  - *Phanthalis* sp
  - Eunicidae
  - *Glycera* sp
- CRUSTACEA (OTHER)
  - Crustacea (other) n. i.
  - Ostracoda
  - Copepoda
  - Euphausiacea
  - *Meganyctiphanes norvegica*
  - Mysidacea
  - Cumacea
  - *Diastylis* sp
  - Tanaidacea
  - Apseudidae
  - Isopoda
  - Desmosomatidae
  - *Cirolana borealis*
  - Cymothoinae
  - Amphipoda
  - Lysianassidae
  - *Scopelocheirus hopey*
  - Phoxocephalidae
  - *Harpinia* sp
  - Hyperiidea
  - Caprellidea
  - *Phtisica marina*
- DECAPODA
  - Natantia
  - Penaeidae
  - *Aristeus antennatus*
  - *Pasiphaea sivado*
  - *Plesionika cf. martia*
  - *Solenocera membranacea*
  - Crangonidae
  - *Pontophilus* sp
  - Reptantia
  - *Nephrops norvegicus*
  - Anomura
  - Brachiura
  - *Ebalia* sp
  - Portunidae
  - Xanthidae
  - *Monodeus couchi*
  - *Gonoplax rombhoides*
- SIPUNCULA
  - Sipuncula n. i.
  - *Aspidosiphon mulleri*
- ECHINODERMATA
  - Echinoidea
  - Asteroidea
  - Ophiuroidea
  - Holothuroidea
  - *Stichopus regalis*
  - Crinoidea
  - *Antedon cf.bifida*
- CHAETOGNATA
  - Chaetognata n. i.
- FISH
  - Condrychthyes
  - Osteychthyes
  - Mictophidae
  - Macruridae

peracarids) and fish (Fig. 1). However, there was a great diversity of preys in the stomachs of *N. norvegicus* (Table 1).The results also suggest great

heterogeneity in the diet of *Nephrops norvegicus*, with representatives of *taxa* of several origins; benthic, supra benthic and planctonic; siphonophores being an important group, especially during Spring (Table 2).

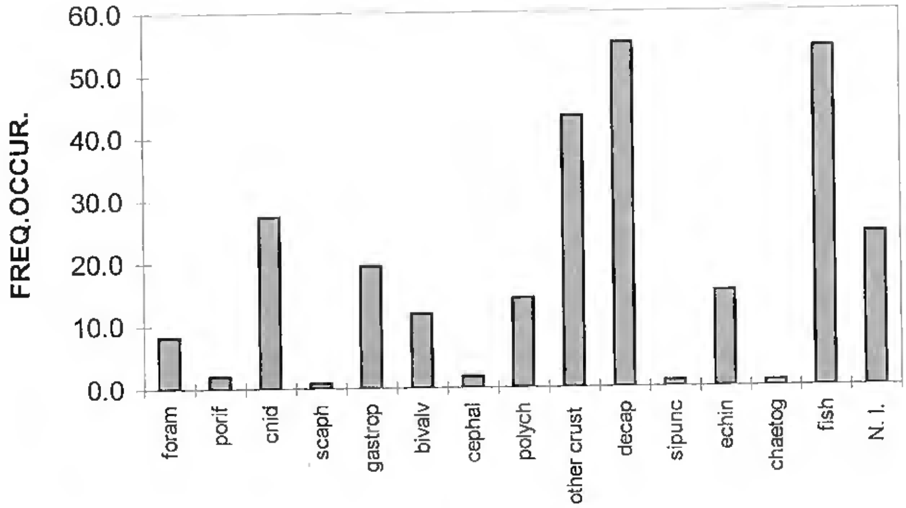

Fig. 1 - Composition of the diet of *Nephrops norvegicus* expressed as frequencies of occurrence for the different groups, for the whole period covered. Abbreviations refer to *taxa* in Table 2.

DISCUSSION

From our preliminary results of the diet study, we can deduce that *Nephrops norvegicus* is not selective in terms of the food resources it exploits; results which are consistent with previously published work (Lagardère, 1977; Gual-Frau and Gallardo-Cabello, 1988; Mytilineou *et al.*, 1992). In our observations, we found fish remains as well as remains of other big prey (crabs), together with small prey such as amphipods or isopods, among which several necrophage Lysianacids and Cirolanids. This suggests that this species can capture live prey; implying an active feeding behaviour, as well as scavenging activity, habits which were observed by Thomas and Davidson (1962), in their aquarium observations. Foraminiferans were the smallest whole

ingested particles, with a minimum size of 1 mm. In the present study we did not find any smaller particles, which could suggest suspension feeding behaviour (Loo *et al.*, 1993). When compared to *Metanephrops* species, which are quite similar both in size and morphologically to Norway lobster and seem to occupy a similar habitat, those present a feeding behaviour which seems to be less selective, since *Metanephrops spp.* capture bigger prey (or parts of it) such as fishes, decapods and squids (Wassenberg and Hill, 1989).

Table 2 - Frequency of Occurrence by season and annual total. italic numbers represent values greater than the mean for all groups

	spring	summer	autumn	winter	annual
Foraminifera	8	*16.7*	8.2	2.5	8.2
Porifera	0	0	8	1	1.9
Cnidaria	*62*	*23.3*	*24*	12.5	*27.3*
Scaphopoda	0	3.3	0	0	0.8
Gastropoda	0	11.2	*56.2*	12.8	*19.4*
Bivalvia	*19*	9.7	*16*	6	11.8
Cephalopoda	0	3.3	0	2.5	1.7
Pplychaeta	12	13.3	*19*	13.5	14.2
Crustacea (other)	*48*	*40*	*52*	*37.5*	*43.3*
Decapoda	*68*	*63.3*	*56*	*40*	*55*
Sipunculida	0	1	0	2.5	0.9
Echinodermata	13	*20*	*21*	8.5	15.2
Chaetognata	0	3.3	0	1	0.8
Fish	*58*	*44.7*	*44*	*66*	*54.5*
Not identified	16.1	33.3	24	23.5	24.4

The basis of the diet of *Nephrops norvegicus* consists mainly of decapod crustaceans, euphausids, peracarids, and fishes, and does not differ seasonally. The preferred prey groups are those which are usually dominant, either in the megabenthic communities (Figueiredo, 1989; Cartes and Sardà, 1992; Froglia and Gramitto, 1995) or in suprabenthic-zooplankton communities (Franqueville, 1971). Seasonally there are some differences in secondary groups, especially in pelagic taxa such as Siphonophora and Gastropoda.

These pelagic resources are particularly dependent on seasonal plankton blooms that occur in the area, in different periods (Cunha, 1993).

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COMPARATIVE STUDY OF THE FEEDING ECOLOGY OF *Nephrops norvegicus* (L.) (DECAPODA : NEPHROPIDAE) IN THE BATHYAL MEDITERRANEAN AND ADJACENT ATLANTIC

ABSTRACTS

A comparative study of the feeding ecology of *Nephrops norvegicus* was carried out on a seasonal basis simultaneously in seven locations in the eastern and western Mediterranean and the adjacent Atlantic: the south coast of Portugal, Faro; the Alboran Sea, Malaga; the Catalan Sea, Barcelona; the Ligurian Sea, Genova; theTyrrheanian Sea, Pisa; the Adriatic Sea, Ancona and the Aegean Sea, Gulf of Euboikos. The principal major groups observed (frequency of occurrence method) in the stomachs of *Nephrops norvegicus* were decapod crustaceans, other crustaceans (euphausids and peracarids) and fish. The results obtained showed no significant differences between sites or seasons, and can be considered very consistent. All major *taxa* were present in the diet at all sites and for all seasons, a fact that can be explained by the great similarity of the bathyal fauna in all sites, which provide a major trophic resource for *N. norvegicus*. The percentage of fullness was also estimated per site and season, and we registered a clear decrease of this value during the summer period for all sites, except the Tyrrheanian Sea, where the lowest value was found in autumn. PCA - analysis did not clearly separate the regions (sites). The Shannon-Weaver (H'), index of diversity, was also determined per site and season, and we found a significant difference between the values of the Atlantic coast and the Western Mediterranean when compared with those of the Eastern Mediterranean.

Key words: Feeding, diet, *Nephrops norvegicus*.

INTRODUCTION

Nephrops norvegicus (L. 1758) (Decapoda: Nephropidae) is a species with a wide geographical distribution, from North-west Atlantic coasts to the East Mediterranean Sea (Zariquiey-Alvarez, 1968). Its bathymetric distribution in the Mediterranean extends from the continental shelf to bathyal grounds, reaching depths of 871 m in the western Mediterranean (Abelló et al., 1988), although maximum densities are found between 245 and 485 m (Cartes et al., 1994). In the Atlantic its bathymetric distribution extends from a mere 10 m to 720 m, but in the south coast of Portugal, maximum densities are found between 300 and 600 m (Figueiredo, 1988). The closely related genus *Metanephrops* (Holthuis, 1974) has a predominantly Indo-Pacific distribution, with a similar bathymetric range on the continental slope to that of *N. norvegicus* (Berry, 1969; Holthuis, 1974; Wassenberg and Hill, 1989). *N. norvegicus* is always one of the dominant species in the bathyal crustacean decapod assemblages in the western Mediterranean (Abelló et al., 1988; Cartes et al., 1994), the eastern Mediterranean (Froglia and Gramitto, 1995), and the eastern Atlantic coast (Figueiredo, 1988; 1989).

Due to its great ecological and commercial importance, *Nephrops norvegicus* has been a target species for a number of biological studies (Figueiredo,1965; Figueiredo and Nunes, 1965; Figueiredo and Thomas, 1967a, b; Sardà, 1983; 1985; 1991; Sardà, 1995), which have focused mainly on growth, reproduction and moulting, which are aspects of major importance for stock assessment and management. In contrast, there have been few studies on its diet and food consumption (Thomas and Davidson, 1962; Lagardére, 1977; Gual-Frau and Gallardo-Cabello, 1988; Sardà and Valladares, 1990; Mytilineou *et al*, 1992), and feeding behaviour (Thomas and Davidson, 1962; Loo *et al.*, 1993). These results indicate that *N. norvegicus* is a euryphagous and non-selective species, consuming a great variety of crustaceans, fish, and molluscs, either as an active predator or scavenger. In contrast, the closely related *Metanephrops* sp. seem to be more selective in their diet (Berry, 1969; Wassenberg and Hill,

1989). The diet of *N. norvegicus* is influenced by their body size (Mytilineou *et al.*, 1992), which is a general characteristic in several other decapod crustaceans (Cartes and Sardà, 1989; Freire and González-Gurriarán,1995; Freire, 1996).

Table 1. - Sumarised data of stomachs observations per site/season.

Location	Code	Depth (m)	Total number of stomachs analized	Total number of food-items	Total number of prey-categories
Atlantic	P Sp	450	23	86	27
(36° 46' N-07° 50' W)	P Su	450	31	76	35
	P Au	450	26	136	23
	P Wi	450	41	88	21
Alboran	M Su	400	12	22	16
(36° 23' N04° 15 w)	M Au	400	14	35	19
	M Wi	400	20	45	33
Catalan	B Sp	450	14	62	28
(41° 11' N-02° 15' E)	B Su	450	17	21	15
	B Wi	450	16	32	15
Ligurian	L Sp	400	18	38	19
(44°12' N-09° 05' E)	L Su	400	18	36	19
Tyrrheanian	T Sp	400	16	34	15
(42° 14' N-10° 37' E)	T Su	400	18	37	16
	T Au	400	16	47	18
	T Wi	400	16	32	14
Adriatic	A Sp	80-110	15	20	12
(43° 35' N-14° 11' E)	A Su	80-110	16	34	21
	A Au	80-110	16	38	18
	A Wi	80-110	15	26	19
Euboikos Gulf	G Sp	150-200	17	56	21
(38° 48' N-22° 59' E)	G Su	150-200	17	27	17
(38° 41' N-23° 21' E)	G Au	150-200	20	43	23
Mean n° of food-items/stomach					
WestMediterranean	2.6				
EastMediterranean	2.1				
Mean n° of food-items/categories					
WestMediterranean	51.7				
EastMediterranean	34.9				

The above studies, refer to populations of Norway lobster from the Bay of Biscay (East Atlantic), Catalan Sea (Northwest Mediterranean) and the Aegean Sea (Northeast Mediterranean). To date, studies of the diet of *Nephrops norvegicus* have been carried out only in specific geographic areas.

The main objective in the present study, beyond the description of the diet *of N. norvegicus*, is to compare the diet in different seasons in seven locations in the Mediterranean and the adjacent Atlantic.

MATERIAL AND METHODS

During 1994-1995, seasonal samples (Spring, Summer, Autumn and Winter) were collected simultaneously, in 7 different sampling sites: the south coast of Portugal, Faro (P), the Alboran Sea, Malaga (M), the Catalan Sea, Barcelona (B), the Ligurian Sea, Genova (L), Tyrrheanian Sea, Pisa (T), and Adriatic Sea , Ancona (A) in the Italian Peninsula, and the Aegean Sea, Euboikos Gulf, Greece (G) (Table 1). All this work was carried out whithin the framework of the CEC Project - NEMED (MED92/008 DG XIV). Each team was responsible for the sampling, fixating and preserving of samples, in its own area, with a standard methodology for all areas. Due to technical problems it was not possible to obtain samples for all seasons in all the areas.

Approximately seventy individuals of *Nephrops norvegicus* were collected in each sample for the present study. From these a subsample of 1/3 was taken for stomach content analysis (Table 1). A total of 1294 individuals were dissected for the estimation of stomach fullness, while a total of 432 stomach contents were studied for the analysis of diet composition. To avoid potential bias of the effect of body size upon diet (Mytilineou *et al.*, 1992) we selected as target individuals those with carapace lengths between 30 and 40 mm, for each site and for each season. For each individual, sex and carapace length were registered with a minimum precision of 1 mm (measurements rounded to the millimeter below). The Norway lobsters were fixed in 10% formalin or 70% alcohol, immedeately after collection, except for Barcelona and Málaga samples, that were fixed after landing. All were preserved in 70% alcohol.

Fullness was determined visually using a scale of 11 points between empty stomach (0=0%; 1=1%-10%...) and full stomach (10=91%-100%). For the diet analyses we observed approximately 20 stomachs independently of

sex, since there are no major differences in feeding between males and females (Mytilineou *et al*, 1992; own unp. data). To correct for the possible underestimation of soft prey items (Sardà and Valladares, 1990) we chose for the analysis of feeding only stomachs with contents, considered by visual estimation to be those with a gut volume equal to or greater than 20%. Stomach contents were identified to the lowest possible taxonomical level. For the comparative study of the diet between site and season, we considered the frequency of occurrence (%F), and number of food-items (N), according to traditional methods in dietary studies (Hyslop, 1980).

For the statistical treatment of data we used a multivariate analysis, since it helps to : i) enhance the data structure; and ii) synthesize the data, thereby permitting a better understanding and a better representation of results (Gauch, 1982). We used a PCA - Principal Component Analysis (Pielou, 1984). The program used was NTSYS 1.8 (Rohlf, 1993).

The PCA was carried out on the matrix of %F (frequency of occurrence per site and season), the Shannon-Weaver (Poole, 1974) diversity index (H') was calculated from nunbers (N). For both calculations we used 17 prey-groups, per site and season, excluding non-identified material, and foraminifera, since their presence in the stomach contents was considered to be the result of accidental ingestion with sand when preying or scavenging on larger prey.

RESULTS

The mean fullness was calculated separately for females and males (Table 2). Percentage of empty stomachs (0% and 10%) was also determined per site/season for females and males (Table 3).

A total of 1071 food-items belonging to 119 prey-categories (Table 4) were identified in the 432 stomach contents analyzed. Stomach contents were composed mainly of small pieces of crustacean carapace, bivalve and gastropod shells, fish vertebrae and otoliths, and other hard and soft parts of prey. From the analysis of the diet we identified 19 prey-groups, including non-

identified material. We have considered as non-identified material several amorphous soft portions that we could not assign with certainty to any taxon (in some cases it could have belonged to gelatinous plankton or molluscs, and was always in an advanced state of digestion). Percentage frequency of occurrence results were based on these 19 major groups (Table 5), including non-identified material.

Table 2. - Percentage of fullness per site/season in females and males. (-) Seasons where samples were not collected.

Sites	Sex	Spring	Summer	Autumn	Winter
Atlantic	F	43,4	40,0	66,5	46,0
	M	52,1	40,0	53,4	42,5
Alboran	F	-	25,6	47,9	67,3
	M	-	40,6	48,7	50,0
Catalan	F	80,9	19,7	-	62,7
	M	-	20,7	-	69,7
Ligurian	F	60,3	22,4	-	-
	M	55,8	19,1	-	-
Tyrrhenian	F	31,6	26,3	26,7	51,5
	M	40,9	42,3	26,1	46,3
Adriatic	F	59,8	38,8	74,5	44,4
	M	61,7	44,5	79,7	49,2
Euboikos	F	41,8	20,4	35,7	-
	M	46,0	30,0	40,0	-

Table 3. - Percentage of empty stomachs. (-) Seasons where samples were not collected.

Site	Sex	Spring	Summer	Autumn	Winter
Atlantic	F	19,5	12,0	0,0	19,0
	M	16,7	16,7	15,8	22,7
Alboran	F	-	40,7	10,3	0,0
	M	-	31,4	30,8	0,0
Catalan	F	0,0	62,5	-	9,1
	M	-	48,6	-	2,9
Ligurian	F	13,9	50,0	-	-
	M	8,3	4,3	-	-
Tyrrhenian	F	42,1	38,1	33,3	20,6
	M	25,0	43,3	35,5	17,1
Adriatic	F	0,0	26,7	0,0	12,8
	M	0,0	12,5	0,0	22,2
Euboikos Gulf	F	15,2	59,3	32,1	-
	M	14,3	38,9	18,8	-

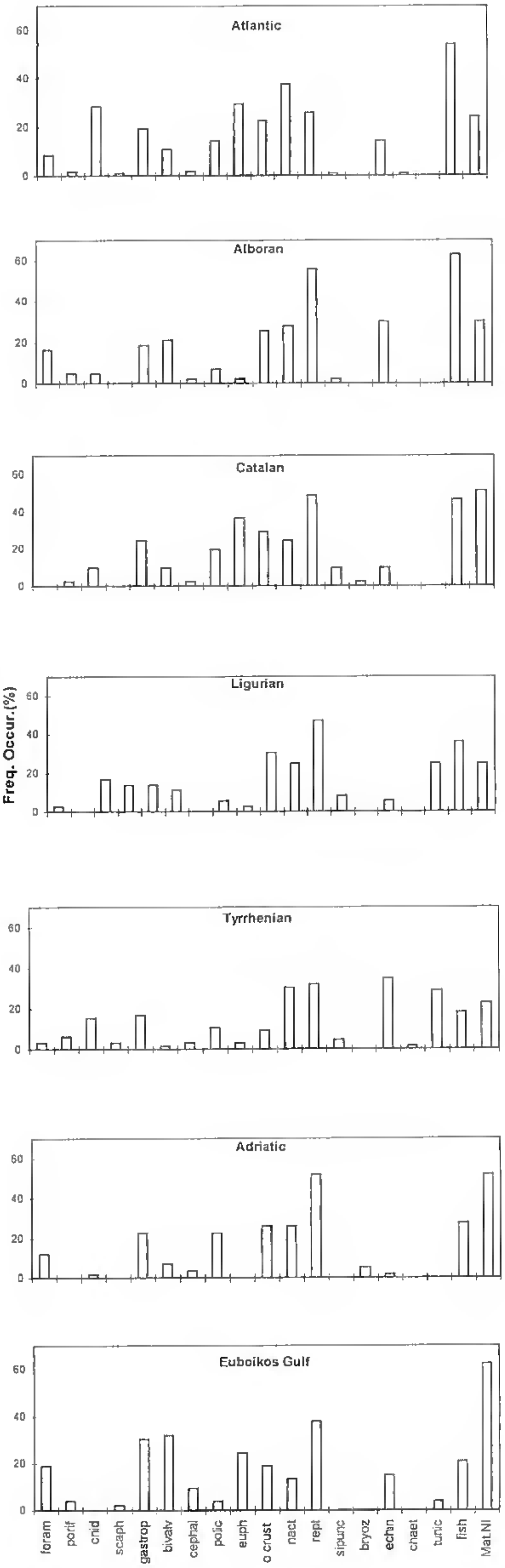

Fig.1 - Frequency of Occurrence of different prey groups in the diet of *Nephrops norvegicus* for all sites and for the entire study. Abbreviations: Foraminifera - Foram; Porifera - PORIF; Cnidaria - CNID; Scaphopoda - SCAPH; Gastropoda - GASTROP; Bivalvia - BIVALV; Cephalopoda - CEPHAL; Polichaeta - POLIC; Euphausiacea - EUFH; Non Decapod Crustaceans - O-CRUST; Nactantia - NACTAN; Reptantia - REPTAN; Sipunculida - SIPUNC; Bryozoa - BRYOZ; Echinodermata - ECHIN; Chaetognatha - CHAET; Tunicata - TUNIC; FISH; Non Identified Material - Mat NI.

Table 4. -Prey categories found in the stomach contents

- FORAMINIFERA
  - *Bolivina* sp.
  - *Globigerina* sp.
  - *Uvigerina* sp.
  - *Quinqueloculina seminulum*

- PORIFERA

- CNIDARIA
- Hydroidea
- Siphonophora
  - *Chelophyes appendiculata*
  - *Stephanoscyphus* spp.

- SCAPHOPODA
  - *Dentalium* sp.

- GASTROPODA
- Rissoidae
  - *Alvania* sp.
- Turritelidae
  - *Caecum* sp.
- Naticidae
  - *Eulimella* sp.
  - *Chrysallida* sp.
- Thecosomata
  - *Cavolinia inflexa*
  - *Cymbulia peroni*

- BIVALVIA
- Amodonta
  - *Abra nitida*
  - *Abra longicallus*
  - *Kellyella miliaris*
  - *Parvicardium* cf. *scabrum*
  - *Pavicardium* sp.
- Taxodonta
- Nuculacea
- Nuculidae
- Nucularidae
  - *Yoldiella striolata*

- CEPHALOPODA
- Teuthida
- Sepiida

- POLYCHAETA
- Aphroditidae
  - *Phanthalis* sp.
- Eunicidae
  - *Lumbrineris* sp.
  - *Glycera* sp.
  - *Nephtys* sp.

- Pantopoda

- CRUSTACEA
- Ostracoda
  - *Cypridina* sp.
- Copepoda
- Mysidacea
  - *Pseudomma* sp.
- Cumacea
  - *Diastylis* sp.
  - *Iphinoe tenella*
- Tanaidacea
- Apseudidae
- Isopoda
- Desmosomatidae
  - *Eugerda* sp.
  - *Cirolana borealis*
- Cymothoidae
- Amphipoda
- Gammaridea
  - *Leucothoe* .sp.
  - *Ampelisca* sp.
  - *Westwoodilla retirostris*
- Lysianassidae
  - *Orchomenella nana*
  - *Scopelocheirus hopei*
- Phoxocephalidae
  - *Harpinia* sp.
- Hyperiidea
  - *Vibilia armata*
  - *Phrosina* sp.
  - *Caprella* sp.
  - *Phtisica marina*
- Euphausiacea
  - *Euphausia krohni*
  - *Meganyctiphanes norvegica*
- Decapoda
- Natantia
  - *Aristeus antennatus*
- Penaeidae
  - *Solenocera membranacea*
  - *Sergestes arcticus*
  - *Pasiphaea sivado*
  - *Plesionika martia*
  - *Processa* sp.
- Reptantia
  - *Nephrops norvegicus*
  - *Calocaris macandrae*
  - *Callianassa* sp.
- Atelecyclidae
  - *Ebalia* sp.
  - *Monodeus couchi*
  - *Goneplax rhomboides*

- BRYOZOA

- SIPUNCULIDA
  - *Aspidosiphon mulleri*

- ECHINODERMATA
- Echinoidea
  - *Echinocardium* sp.
- Asteroidea
- Ophiuroidea
- Holothuroidea
  - *Leptosynapta* sp.
  - *Stichopus regalis*
  - *Molpadia musculus*
- Crinoidea
  - *Antedon* cf. *bifida*

- CHAETOGNATA

- TUNICATA
  - *Pyrosoma atlanticum*

- Chondrychthyes
- Osteychthyes
- Myctophidae
- Macrouridae

Table 5. - Frequency of occurrence (%) by site/season. Abbreviations as in Fig. 1.

		foram	porif	cnid	scaph	gastrop	bivalv	cephal	polic	euph	o crust	nact	rept	sipunc	bryoz	echin	chaet	tunic	fish	Mat.NI
Atlantic	Spring	8.0	0.0	64.0	0.0	0.0	20.0	0.0	12.0	36.0	20.0	48.0	24.0	0.0	0.0	12.0	0.0	0.0	56.0	16.0
	Summer	16.7	0.0	23.3	3.3	13.3	6.7	3.3	13.3	30.0	20.0	43.3	33.3	0.0	0.0	20.0	3.3	0.0	46.7	33.3
	Autumn	8.0	8.0	24.0	0.0	56.0	16.0	0.0	20.0	40.0	20.0	36.0	28.0	0.0	0.0	20.0	0.0	0.0	44.0	24.0
	Winter	2.5	0.0	12.5	0.0	12.5	5.0	2.5	12.5	17.5	27.5	27.5	20.0	2.5	0.0	7.5	0.0	0.0	65.0	22.5
	Annual	8.3	1.7	28.3	0.8	19.2	10.8	1.7	14.2	29.2	22.5	37.5	25.8	0.8	0.0	14.2	0.8	0.0	54.2	24.2
Alboran	Spring																			
	Summer	18.2	0.0	0.0	0.0	9.1	27.3	9.1	9.1	0.0	18.2	18.2	36.4	0.0	0.0	27.3	0.0	0.0	63.6	45.5
	Autumn	8.3	0.0	0.0	0.0	16.7	41.7	0.0	0.0	0.0	33.3	25.0	66.7	0.0	0.0	58.3	0.0	0.0	58.3	25.0
	Winter	20.0	10.0	10.0	0.0	25.0	5.0	0.0	10.0	5.0	25.0	35.0	60.0	5.0	0.0	15.0	0.0	0.0	65.0	25.0
	Annual	16.3	4.7	4.7	0.0	18.6	20.9	2.3	7.0	2.3	25.6	27.9	55.8	2.3	0.0	30.2	0.0	0.0	62.8	30.2
Catalan	Spring	0.0	0.0	20.0	0.0	60.0	30.0	0.0	40.0	60.0	80.0	30.0	50.0	20.0	0.0	40.0	0.0	0.0	60.0	90.0
	Summer	0.0	6.7	6.7	0.0	6.7	6.7	0.0	20.0	13.3	13.3	13.3	46.7	0.0	6.7	0.0	0.0	0.0	53.3	26.7
	Autumn																			
	Winter	0.0	0.0	6.3	0.0	18.8	0.0	6.3	6.3	43.8	12.5	31.3	50.0	12.5	0.0	0.0	0.0	0.0	31.3	50.0
	Annual	0.0	2.4	9.8	0.0	24.4	9.8	2.4	19.5	36.6	29.3	24.4	48.8	9.8	2.4	9.8	0.0	0.0	46.3	51.2
Ligurian	Spring	0.0	0.0	0.0	0.0	22.2	5.6	0.0	5.6	5.6	27.8	22.2	50.0	5.6	0.0	5.6	0.0	50.0	16.7	27.8
	Summer	5.6	0.0	33.3	27.8	5.6	16.7	0.0	5.6	0.0	33.3	27.8	44.4	11.1	0.0	5.6	0.0	0.0	55.6	22.2
	Autumn																			
	Winter																			
	Annual	2.8	0.0	16.7	13.9	13.9	11.1	0.0	5.6	2.8	30.6	25.0	47.2	8.3	0.0	5.6	0.0	25.0	36.1	25.0
Tyrrhenian	Spring	0.0	18.8	6.3	0.0	0.0	0.0	0.0	12.5	6.3	0.0	25.0	31.3	12.5	0.0	31.3	0.0	37.5	6.3	12.5
	Summer	0.0	0.0	16.7	0.0	5.6	0.0	0.0	11.1	5.6	5.6	50.0	33.3	5.6	0.0	22.2	5.6	38.9	11.1	16.7
	Autumn	6.3	6.3	18.8	12.5	50.0	0.0	0.0	18.8	0.0	12.5	31.3	31.3	0.0	0.0	56.3	0.0	6.3	25.0	50.0
	Winter	6.3	0.0	18.8	0.0	12.5	6.3	12.5	0.0	0.0	18.8	12.5	31.3	0.0	0.0	31.3	0.0	31.3	31.3	12.5
	Annual	3.0	6.1	15.2	3.0	16.7	1.5	3.0	10.6	3.0	9.1	30.3	31.8	4.5	0.0	34.8	1.5	28.8	18.2	22.7
Adriatic	Spring	7.7	0.0	0.0	0.0	30.8	0.0	0.0	7.7	0.0	15.4	15.4	46.2	0.0	7.7	0.0	0.0	0.0	15.4	61.5
	Summer	28.6	0.0	0.0	0.0	28.6	7.1	0.0	42.9	0.0	42.9	28.6	50.0	0.0	7.1	0.0	0.0	0.0	28.6	71.4
	Autumn	12.5	0.0	6.3	0.0	25.0	6.3	0.0	25.0	0.0	12.5	37.5	56.3	0.0	0.0	6.3	0.0	0.0	12.5	31.3
	Winter	0.0	0.0	0.0	0.0	6.7	13.3	6.7	6.7	0.0	33.3	20.0	53.3	0.0	6.7	0.0	0.0	0.0	53.3	46.7
	Annual	12.1	0.0	1.7	0.0	22.4	6.9	3.4	22.4	0.0	25.9	25.9	51.7	0.0	5.2	1.7	0.0	0.0	27.6	51.7
Euboikos	Spring	37.5	0.0	0.0	6.3	62.5	43.8	12.5	0.0	25.0	6.3	6.3	43.8	0.0	0.0	31.3	0.0	6.3	25.0	50.0
	Summer	23.5	5.9	0.0	0.0	0.0	41.2	5.9	5.9	5.9	11.8	23.5	58.8	0.0	0.0	0.0	0.0	0.0	11.8	47.1
	Autumn	0.0	5.0	0.0	0.0	30.0	15.0	10.0	5.0	40.0	35.0	10.0	15.0	0.0	0.0	15.0	0.0	5.0	25.0	85.0
	Winter																			
	Annual	18.9	3.8	0.0	1.9	30.2	32.1	9.4	3.8	24.5	18.9	13.2	37.7	0.0	0.0	15.1	0.0	3.8	20.8	62.3

In terms of percentage of occurrence (%F) decapod crustaceans were always the main prey-group followed by other crustaceans (euphausids and peracarids) and fish (Fig. 1). Although the composition of the diet was similar in all sites studied, some minor local and seasonal variations were observed in secondary prey groups. Tunicates were very frequent in stomach contents from the Tyrrhenian Sea almost year-round. Cnidarians (mainly siphonophora) were also frequently found in stomach contents throughout the year, while Gastropods were more frequent in the Adriatic and in Greece than in other areas.

The Principal Component Analysis (PCA) results were based on the values of frequency of occurrence per site and season (Figs 2, 3). No clear OTUs (Operational Taxonomic Units: site per season) distribution structure can be seen on axes 1, 2, which explain only 36.2 % of the total variability (Table 6).

Table 6 - Principal Component Analysis; Vector matrix

Variable	Principal Components		
	1st	2nd	3rd
Porifera - PORIF	0.169	0.265	0.031
Cnidaria - CNID	-0.562	0.477	0.195
Scaphopoda - SCAPH	-0.175	0.056	0.177
Gastropoda - GASTROP	-0.3905	-0.351	0.178
Bivalvia - BIVALV	-0.169	-0.612	0.423
Cephalopoda - CEPHAL	0.388	-0.447	0.575
Polichaeta - POLIC	-0.572	0.045	-0.554
Euphausiacea - EUPH	-0.645	-0.038	0.301
Non Decap Crust O-CRUST	-0.702	-0.404	-0.171
Nactantia - NACTANC	-0.475	0.712	-0.164
Reptantia - REPTAN	0.057	-0.398	-0.428
Sipunculida - SIPUNC	-0.482	0.203	0.024
Bryozoa - BRYOZ	0.232	-0.309	-0.768
Echinodermata - ECHIN	-0.225	0.009	0.581
Chaetognatha - CHAET	0.030	0.644	0.045
Tunicata - TUNIC	0.414	0.534	0.204
FISH	-0.559	-0.316	0.017
EIGENVALUES	3.160	2.988	2.001
PERCENTAGE	18.59	17.58	11.77
CUMULATIVE PERC.	18.59	36.17	47.98

The contribution of the variables to these principal axes (Fig. 2) suggests the presence of a "horse-shoe" effect (Gauch, 1982) which can be the

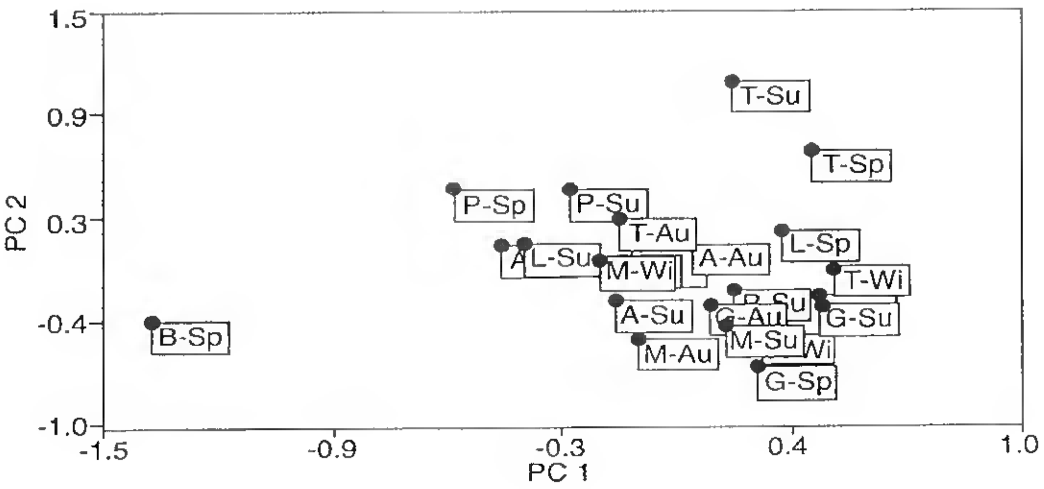

Fig. 2 - PCA on the matrix of the Frequency of Occurrence of different prey groups per site and season; projection of OUT's over axis 1 and 2. Labels: first letter stands for location; P- Portugal, M- Málaga, B- Barcelona, L- Ligurian Sea, T- Tyrrheanian Sea, A- Ancona, G- Greece; the two following letters stand for season: Sp- Spring, Su- Summer, Au- Autumn, Wi- Winter.

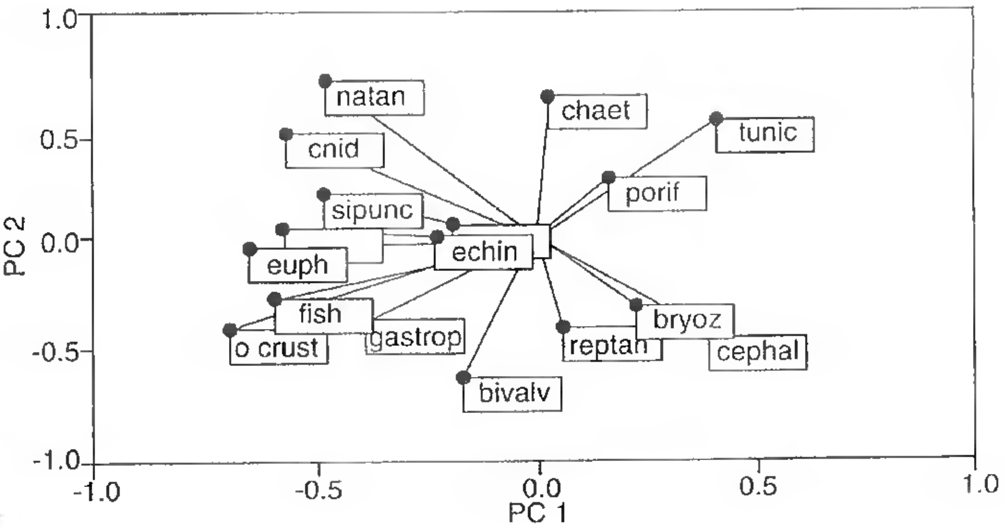

Fig. 3 - PCA on the matrix of different prey groups per site and season; projection of variables over axis 1 and 2. Labels: Porifera - PORIF; Cnidaria - CNID; Scaphopoda - SCAPH; Gastropoda - GASTROP; Bivalvia - BIVALV; Cephalopoda - CEPHAL; Polichaeta - POLIC; Euphausiacea - EUFH; Non Decapod Crustaceans- O-CRUST; Nactantia - NACTAN; Reptantia - REPTAN; Sipunculida - SIPUNC; Bryozoa - BRYOZ; Echinodermata - ECHIN; Chaetognatha - CHAET; Tunicata - TUNIC; FISH

consequence of the gradient of their occurrence, between the low average values on a reduced number of OTU's and high average values for a significant number of OTU's. This would explain both the slow decrease in the extracted eigenvalues and the above mentioned lack of a spatial structure among the OTU's.

Through the examination of Fig.2, we notice one situation, Barcelona in Spring (BSp), that is a clear outlier. The food contents in this sample were clearly dominated by gastropods, euphausids, non decapod crustaceans and fish, which pull BSp to the inferior left quadrant of the graph (Fig 3).

Based on the values of diet diversity (H′), western Mediterranean and Atlantic sites are different from those of the eastern Mediterranean basin (Fig. 4).

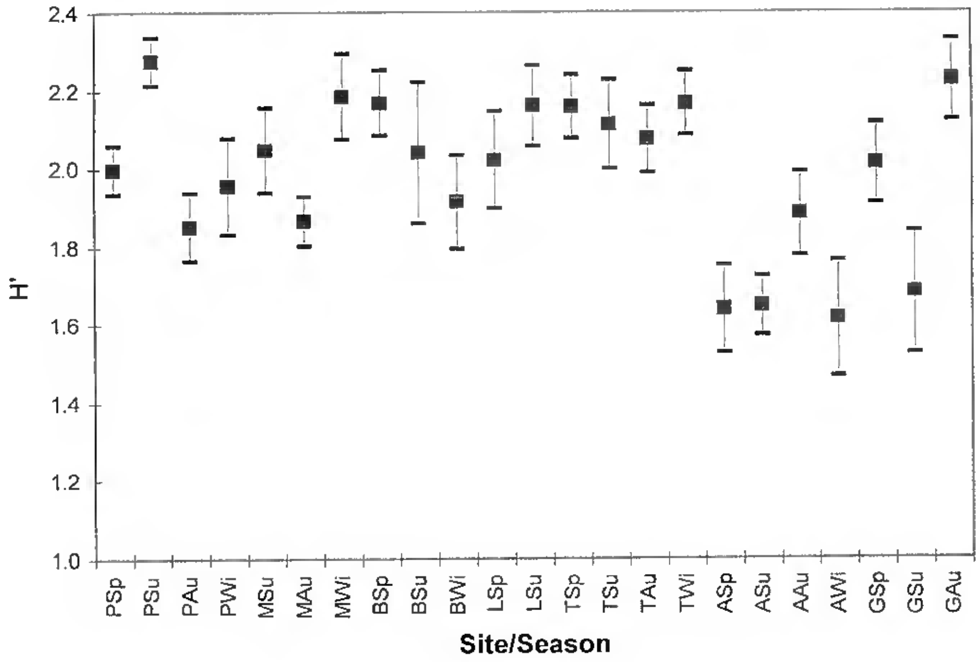

Fig. 4 - Diversity Index (H') per site - Portugal (P), Málaga (M), Barcelona (B), Ligurian Sea (L), Tyrrheanian Sea (T), Ancona (A), Greece (G) - and season - Spring (Sp),Summer (Su), Autumn (Au), Winter (Wi); (e.g. PSp = Portugal in Spring).

The sites of Portugal, Alboran Sea, Catalan Sea, Ligurian Sea, and Tyrrhenian Sea show very homogeneous and significantly higher ($p<0.05$; non-parametric Kruskall-Wallis test) (Siegel and Castellan, 1988) values than those

from the eastern Mediterranean (Adriatic and Aegean Sea). Seasonal variations can be observed among sites. In general, for the western sites, Autumn and Winter were charactrised by a lower diversity, while eastern stations did not follow this pattern.

DISCUSSION

From our general results of the diet composition study, we can deduce that *Nephrops norvegicus* is a generalist species in terms of the food resources it exploits; results which are consistent with previously published work (Lagardère, 1977; Gual-Frau and Gallardo-Cabello, 1988; Mytilineou *et al.*, 1992). According to aquarium observations, their feeding behaviour is based upon active prey capture (Thomas and Davidson, 1962) as well as scavenging activity. In our observations, we found fish remains (chondricthyes), and other large prey (crabs), as well as small prey such as amphipods or isopods, among which were several necrophagous Lysianacids and Cirolanids; a finding also reported by Lagardère (1977). Sand, mud or foraminiferans can be ingested in a passive way from sediment, a fact also reported by the same authors. Foraminiferans were among the smallest whole ingested particles, with a minimum size of 1 mm. In the present study we could not find any smaller particles which could be attributable to ingestion by suspension feeding (Loo *et al.*, 1993). *Metanephrops* sp., which seems to occupy a similar habitat and is quite similar both in size and morphology to Norway lobster, seems to be characterized by a more selective feeding behaviour, capturing larger prey (or parts of it) such as fishes, decapods and squids (Wassenberg and Hill, 1989).

The percentage of empty stomachs in *Metanephrops* spp. is much higher than that observed in the present study, inspite of the fact that in the Summer period our values of percentage of empty stomachs reached 62.5% for females and 48.6% for males. In general the fullness percentage, which can be considered as an indicator of the feeding activity, showed a tendency to be lower in the summer period for all sites, for both sexes. This period corresponds to the peak of gonad maturity, Stage IV (Orsi Relini, 1998),

where the enlargement of the gonad compresses the stomach in the females, thus preventing maximum stomach fullness. In fact the highest percentage of empty stomachs occurred in this period.

According to Mytilineou *et al.*(1992), in the North Aegean Sea percentage of empty stomachs was greater than 50% in September and December for females, a fact that was related to the period of egg bearing. This fact could not be confirmed in the present work, but we found that 59.3% of the female stomachs in the summer period, were empty, corresponding to the peak of mature females.

Our low values of percentage of fullness for males in the same period is still to be explained, since there is no biological factor, such as reproduction or molting (Gramitto, 1998) that showed any synchronicity with the summer period. The low selectivity showed by *Nephrops norvegicus* in its feeding activities, is particularly emphasized by the frequency of occurrence in the stomachs of plastic material (nylon threads, probably from fishing gears), plant remains, wood, and charcoal, etc. These may be ingested by accident while feeding on prey, in or on, the plastic material/plants/wood.

The basis of the diet of *Nephrops norvegicus* consists of decapod crustaceans, euphausiids, peracarids, and fishes, and does not differ geographically or seasonally. The preferred prey groups are those which are dominant, either in the megabenthic communities (Pérès, 1985; Figueiredo, 1989; Froglia and Gramitto, 1995) or in suprabenthic-zooplankton communities (Franqueville, 1971). There are some differences in secondary groups, especially in pelagic taxa such as Siphonophora, Gastropoda, Thecosomata, and Tunicata Pyrosomidae. These kinds of food-resources are particularly dependent on seasonal plankton blooms that occur in the area. These findings support the results of the PCA analysis, since the benthic-bathyal fauna is quite similar in the geographic area studied.

The higher values of diversity (H') observed in the western-Mediterranean sites can be related to: 1) deeper collecting grounds and 2) different biogeographic distributions. The higher number of prey per stomach in the western-Mediterranean could be related to a higher density of the food

resources in the particular environment. There is no data available on macrofaunal densities, that could allow comparison of the two basins, but some comparative data on meiofauna indicates clearly higher biomass values in the western Mediterranean (Thiel, 1983).

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DIET OF THE NORWAY LOBSTER (*Nephrops norvegicus* (L.) OFF THE SOUTH COAST OF PORTUGAL

ABSTRACT

The feeding habits and intraspecific dietary overlap in the Norway lobster *Nephrops norvegicus* (L.) were studied. A comparative analysis of the diet of 3 main size classes was also made. Dietary diversity was evaluated. *N. norvegicus* preys upon benthic, bathypelagic and pelagic organisms, and is also a scavenger. Stomach content analysis indicate that the diet (frequency of occurrence, percentage in number and percentage points) consists mainly of crustaceans (euphausids and decapods), fish, opistobranchia, polychaetes, echinoderms. Differences were found in the diet composition of the various size classes, with overlaps (percentage similarity) between 53.7 and 76.4. No differences were found between sexes, with overlaps of 90.9. Dietary diversity (H') varied between 1.78 and 2.32.

INTRODUCTION

The feeding ecology of *Nephrops norvegicus* from the south coast of Portugal has been the object of several recent studies (Cristo, 1998; Cristo and Cartes, 1998, Cristo and Encarnação, 2000; Cristo, submitted). This species is of great ecological and commercial importance in Portuguese waters and has been the subject of several other biological studies (Figueiredo and Barraca, 1963; Figueiredo,1965; Figueiredo and Nunes, 1965; Figueiredo and Thomas, 1965, 1967), focusing mainly on growth, reproduction and moulting.

Previously published results on the diet of *N. norvegicus*, indicate that it is a euryphagous and poorly selective species, consuming a great variety of crustaceans, fish, and molluscs, either as an active predator or scavenger

(Thomas and Davidson, 1962; Lagardère, 1977; Gual-Frau and Gallardo-Cabello, 1988; Mytilineou *et al*, 1992; Cristo, 1998) . There are no significant differences in the diet between, year season or even different locations in the Mediterranean and adjacent Atlantic considering major prey groups (Cristo and Cartes, 1998), though some variation could be detected in secondary prey, as a reflect of environmental diversity.

However, an important aspect of the feeding ecology deals with the differential analysis of the diet among sexes and size classes, analyses that have been carried out for several other decapod crustaceans, (Cartes and Sardà, 1989; Cartes and Abellò, 1992; Cartes, 1993a; 1993b , Cartes, 1995). For *N. norvegicus* there is only a preliminary study carried out in the North Aegean sea (Mytilineou *et al*, 1992), that states differences among size classes but not among sexes.

The present study of the feeding ecology of *Nephrops norvegicus* off the Portuguese south coast attempts to establish whether the diet of females and males differs, whether the female maturity stages influence feeding intensity or whether there are significant differences in the diet between size classes.

MATERIAL AND METHODS

During 1994-1995, monthly samples were collected off the south coast of Portugal, (36° 46' N-07° 50' W), from depths around 600 m. This work was carried out within the framework of the CEC Project - NEMED (MED92/008 DG XIV).

A total of 1574 individuals were dissected for the estimation of stomach fullness, while a total of 950 stomach contents were studied for the analysis of diet composition. For each individual, sex and carapace length were registered with a minimum precision of 1 mm (measurements rounded to the millimetre below). The Norway lobsters were fixed in 10% formalin for two days and then preserved in 70% alcohol.

Fullness was determined visually using a scale of 11 points between empty stomach (0=0%; 1=1%-10%...) and full stomach (10=91%-100%) (Cristo and

Cartes, 1998). To correct for possible underestimation of soft prey items (Sardà and Valladares, 1990) only stomachs with contents were chosen for analysis of feeding. These were considered by visual estimation to have a gut volume equal to or greater than 20%. Prey categories in stomach contents were identified to the lowest possible taxonomical level.

For the study of the diet the traditional methods in dietary studies were used: frequency of occurrence (%F), the percentage in number (%N) (Hyslop, 1980) and the percentage by points (%P), first employ by Swynnerton and Worthington (1940) and modified by (Frost, 1943) to take the stomach fullness into account .

Quantification of stomach contents was based on the number of pieces of hard parts, most resistant to digestion, such as telsons, jaws, eyes, and otoliths, taking into account the size of these structures, such that they could be assigned to one or several individuals. The following additional criteria were applied in the analyses of results: a) remains of fish, such as skin or vertebra or scales were always counted as a single prey item; b) the same criteria were used for echinoderms, except when it was possible to identify different types of spicula or more than one calyx in the case of crinoids; b) the presence of small fragments of bivalve shells or gastropods, foraminiferans, or other fragments of hard parts of invertebrates was ascribed to passive ingestion when with sand and not considered (Lagardère, 1972 ; Cartes and Sardà, 1989).

The diet composition was analysed by sexes (M and F) and length classes. Three size classes were considered: (LC1) - Carapace length < 30mm; (LC2) - Carapace length [30mm;50 mm[; (LC3) - Carapace length ≥ 50 mm. Quantification and identification was difficult, since *N. norvegicus* have strong mandibles with well-developed cutting incisor and molar process. The mechanical digestion also continues inside the stomach due to the presence of a strong gastric mill. Only small specimens were found whole in the stomach. Individual prey items were identified to species level whenever possible, using a reference collection, and also several identification keys, for the different *taxa*. For this reason, it was decided to present data and perform all data treatments on major taxonomic groups (prey-groups), since identification to

species level was not frequent enough. However a list of all *taxa*identified is presented in Table 1. Foraminiferans were not quantified in this study since their presence in the stomach contents was considered to be the result accidental ingestion with sand when preying or scavenging on larger prey.

The cumulative trophic diversity curve (Hurtubia, 1983; Cartes, 1991) was constructed using the Shannon-Weaver index (H') (Poole, 1974). Asymptotic stabilisation of the curves yields the minimum number of stomachs that need to be analysed to produce reliable results.

In order to establish whether or not the three indexes calculated, %F, %N and %P, give similar information, the Kendall's concordance coefficient was used (Siegel and Castellan,1988; Castro and Guerra, 1990) with the correspondent significance test. The values of this coefficient vary between 0, if there is "perfect disagreement" among rankings, and 1 if there is "perfect agreement" in the rankings in all blocks (Conover, 1980).

The Kolmorov-Smirnov test (Hollander and Wolfe, 1973) was used to determine if differences between % of empty stomachs of males and females, over the months, were significant (H_0: the distribution of % of empty stomachs is equivalent in both groups). In order to assess the significance of differences between % of empty stomach per length classes among sexes the Wilcoxon test was used (Siegel and Castellan, 1988).

In order to establish the influence of egg bearing and the maturity state in the foraging activity, chi-square tests were made on the number of empty stomachs *versus* stomachs with contents, since this parameter that can be considered as an indicator of feeding intensity (Cartes and Abelló, 1992).

For all the statistical tests the 95% confidence interval was considered

The percentage similarity index (Whittaker and Fairbanks, 1958) and a χ^2 test for significance was used to establish dietary affinities between sexes and size classes in terms of %N, since %F is not proportional to the diet (Wallace, 1981). According to Zared and Rand (1971), diets of different species can normally be regarded as significantly different when the overlap index value is below 0.6, however as dietary overlap index under consideration is among

Table 1 - Lists of prey-categories found in the stomachs of *N. norvegicus*. (UN=unidentified)

- FORAMINIFERA
  - Foraminifera UN
    - *Bolivina* sp.
    - *Globigerina* sp.
    - *Uvigerina* sp.
- PORIFERA
  - Porifera UN
- CNIDARIA
  - Hydroidea
  - Siphonophora
    - *Chelophyes appendiculata*
- SCAPHOPODA
    - *Dentalium* sp.
- PROSOBRANCHIA
  - Prosobranchia UN
  - Rissoidae
  - Turritellidae
    - *Trophon cf. echinatus*
    - *Brachystomia albella*
- OPISTOBRANCHIA
  - Thecosomata UN
    - *Cavolinia* sp.
    - *Cymbulia peroni*
- BIVALVIA
  - Amodonta
  - Taxodonta
  - Nuculidae
    - *Nucula* sp.
  - Nuculanidae
    - *Yoldiella striolata*
    - *Pholadidae loscombiana*
- CEPHALOPODA
  - Cephalopoda UN
  - Teuthida
    - *Illex coindetii*
- POLYCHAETA
  - Polychaeta UN
  - Aphroditidae
    - *Afrodite aculeata*
    - *Phanthalis* sp.
  - Eunicidae
  - Glyceridae
    - *Glycera* sp..
    - *Goniada norvegica*
- OSTRACODA
  - Ostracoda UN
- MYSIDACEA
  - Mysidacea UN
    - *Mysidopsis* sp
- CUMACEA
  - Cumacea UN
    - *Diastylis* sp.
- TANAIDACEA
  - Tanaidacea UN
  - Apseudidae
- ISOPODA
  - Isopoda UN
  - Desmosomatidae
    - *Natatolana borealis*
  - Cymothoinae
  - Cymothoidae
- AMPHIPODA
  - Amphipoda UN
  - Lysianassidae
    - *Scopelocheirus hopei*
  - Phoxocephalidae
    - *Harpinia* sp.
    - *Rhachotropis* sp.
  - Hyperiidea
  - Caprellidea
    - *Phtisica marina*
- EUPHAUSIACEA
  - Euphausiacea UN
    - *Meganyctiphanes norvegica*
- NATANTIA
  - Natantia UN
  - Penaeidae
    - *Aristeus antennatus*
    - *Solenocera membranacea*
  - Caridea
    - *Pasiphaea sivado*
    - *Plesionika cf. martia*
  - Crangonidae
    - *Pontophilus* sp.
    - *Philocheras* sp.
- REPTANTIA
  - Reptantia UN
    - *Nephrops norvegicus*
  - Anomura
  - Brachiura
  - Homolidae
    - *Ebalia* sp.
  - Portunidae
    - *Liocarcinus depurator*
    - *Bathynectes maravigna*
  - Xanthidae
    - *Monodeus couchi*
    - *Goneplax rhomboides*
- SIPUNCULIDA
  - Sipunculida UN
    - *Aspidosiphon muelleri*
- ECHINODERMATA
  - Echinoidea
  - Asteroidea
  - Ophiuroidea
  - Holothuroidea
    - *Leptosynapta inhaerensis*
    - *Stichopus regalis*
  - Crinoidea
    - *Antedon cf.bifida*
    - *Leptometra phalangium*
- CHAETOGNATA
  - Chaetognata UN
- TUNICATA
  - Tunicata UN
- FISH
  - Condroichthyes UN
    - *Etmopterus* sp
  - Osteichthyes UN
  - Myctophidae
    - *Lampanyctus crocodilus*
  - Macrouridae

sexes or size classes of the same species, it was decided to consider the value 0.8 as Cartes and Sardà (1989) did. Trophic diversity (H') in the diet was established using the Shannon-Weaver (Poole, 1974) index. For all calculations prey-groups where used, excluding foraminifera and non-identified material.

RESULTS

The cumulative trophic diversity curve (Fig.1), that was constructed to obtain the minimum number of stomachs to be analysed in order to ensure that a substantial percentage of the total prey items in the diet are represented, gave a value of 20 stomachs.

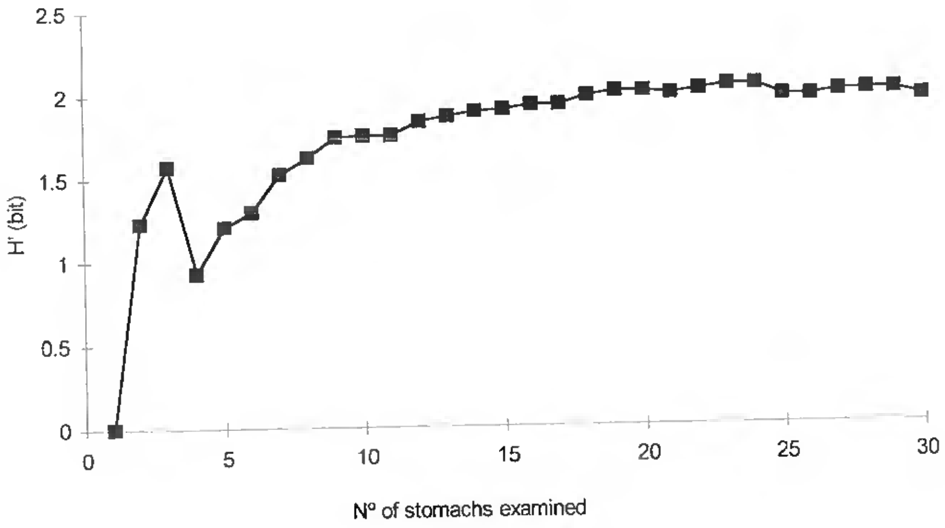

Fig.1. *Nephrops norvegicus*. Cumulative trophic diversity values

When analysing the diet of the Norway lobsters the most common items in the stomach were fragments of crustacean carapace, buccal parts, pleopods, as well as fish vertebra otholits and scales. Other distinct components were bivalve and gastropod shells, mandibles of polychaets and spicula and calcified parts of echinoderms. A total of 2658 food-items belonging to 99 prey categories were identified (Table 1). From this analysis 23 prey-groups were

identified, excluding Foraminifera, but including non-identified material. This non-identified material was composed mainly of amorphous soft portions that could not be assigned with certainty to any taxon (in some cases it could have belonged to gelatinous plankton or molluscs, and was always in an advanced state of digestion). Percentage frequency of occurrence (%F), percentage in number (%N) and percentage by points (%P) results were based on these 23 major groups (Table 2), including non-identified material. The result of the

Table 2 *Nephrops norvegicus.* Composition of the diet of males and females, by prey groups. % N = percentage number; %F = frequency of occurrence; %P= percentage by points.

	% N	%F	%P	% N	%F	%P	% N	%F	%P
	Males			Females			Total		
porifera	0.24	0.75	0.04	0.34	0.96	0.09	0.34	0.62	0.07
cnidaria	3.60	10.15	1.85	6.19	17.22	3.91	5.58	9.71	2.90
scaphopoda	0.12	0.38	0.03	-	-	-	0.08	0.15	0.02
prosobranchia	0.60	1.50	0.39	1.55	3.83	0.60	1.18	1.85	0.51
opistobranchia	18.94	12.78	4.37	18.73	13.88	5.28	22.59	9.71	5.03
bivalvia	2.16	6.39	1.01	3.09	6.70	1.55	3.05	4.78	1.31
cephalopoda	1.20	3.76	0.88	0.52	1.44	0.39	1.10	2.00	0.70
polychaeta	4.20	13.16	3.64	3.44	10.05	4.54	4.65	8.63	4.25
ostracoda	0.24	0.75	0.03	0.52	1.44	0.12	0.42	0.77	0.07
mysidacea	0.36	1.13	0.16	0.69	1.91	0.39	0.59	1.08	0.27
cumacea	-	-	-	0.17	0.48	0.06	0.08	0.15	0.03
tanaidacea	0.12	0.38	0.23	0.17	0.48	0.23	0.17	0.31	0.24
isopoda	0.60	1.88	0.92	1.37	3.35	2.59	1.10	1.85	1.74
amphipoda	3.24	8.27	1.98	4.98	9.09	2.68	4.74	6.32	2.41
euphausiacea	21.34	31.20	19.17	19.07	33.97	22.58	24.45	23.73	21.79
natantia	7.43	22.18	11.65	8.59	23.92	14.34	9.48	16.80	13.53
reptantia	11.63	36.09	16.85	7.90	21.53	9.32	12.10	21.73	14.32
sipunculida	0.60	0.75	0.12	-	-	-	0.42	0.31	0.07
equinodermata	2.52	7.52	2.06	1.72	4.78	0.98	2.62	4.62	1.68
chaetognata	0.12	0.38	0.06	-	-	-	0.08	0.15	0.03
tunicata	0.12	0.38	0.47	-	-	-	0.08	0.15	0.28
fish	14.75	45.11	24.27	14.43	40.19	20.45	17.51	31.43	23.85
NI Material	6.47	20.68	10.54	6.53	18.18	9.90	7.78	14.33	10.83

Kendall's coefficient of concordance between the three methodologies used over the total diet analysis, gives the high value of 0.97 and the test statistics applied rejects the null hypothesis (H_0: there is no association among the three variables) (p-value 0.019).

Table 3 *Nephrops norvegicus*. Percentage of empty stomachs of males and females over the months, and per length classe (LC1 < 30mm carapace length; LC2 [30 mm; 50mm [carapace length; ≥ 50 mm carapace length).

		% Empty stomachs		
	Total number	Males	Total number	Females
January	112	25.00	80	32.50
February	76	26.32	54	29.63
March	56	17.86	48	29.17
April	48	16.67	88	18.18
May	90	57.78	66	48.48
June	64	31.25	60	23.33
July	70	14.29	60	10.00
August	52	15.38	62	41.94
September	52	3.85	50	20.00
October	74	16.22	26	0.00
November	66	9.09	78	25.64
December	78	23.08	64	68.75
Annual	838	23.15	736	30.43
LC 1	84	21.43	164	24.39
LC 2	620	23.23	558	31.54
LC 3	134	23.88	14	57.14

Stomach fullness

The % of empty stomachs (0% to < 20%) and mean fullness was calculated separately (Table 3). Fig 2 represents mean fullnes (±SE) for males and females per month and per length class. The Kolmorov-Smirnov test, applied to the % of empty stomachs between males and females over the months, fail to reject the null hypothesis (p-value 0.2558). However the differences between % of empty stomachs per length classes among sexes are significant,

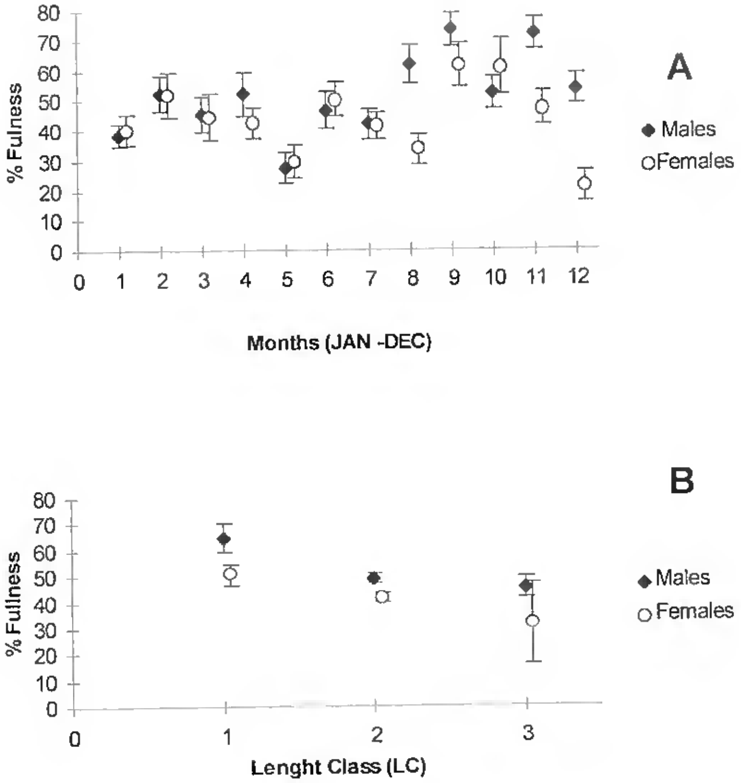

Fig. 2 -*Nephrops norvegicus* -Mean average fullness (±SE), for males and females (A) per month; (B) per lenght class

thought rejecting the null hypotesis (p-value 0.05). It was also found that egg bearing influences the feeding activity negatively (p-value 10.887 for H_0: no differences between non ovigerous and ovigerous females) since berried females have a a higher number of empty stomachs than expected. The chi-square test to check for the influence of maturity stage on feeding was made for non-berried females and berried females separetely, and showed to be significant (p-value 16.089) for non-berried females group but not for berried ones. In this case the limiting factor was already define by the fact that they are berried.

Feeding and sex

The overlap index between males and females, based on %N was 90.9 (Table 4), showing that there are no quantitative differences among prey-

groups in the diet of the 2 sexes. This was also shown by means of a chi-square test that yielded no significant difference (p-value 4.730).

Table 4 *Nephrops norvegicus*. Chi-square, and percentage similarity between stomach contents parameters (+ : significant difference; -: non significant difference)

Comparison	$\chi 2$ (p=0.05)	Percentage similarity
Male/Females	-	90.9
LC1 / LC2	-	70.5
LC2 / LC3	-	76.4
LC1 / LC3	+	53.7

Predominant prey-groups were euphausids, (mainly *Meganyctiphanes norvegica*), decapods (Caridea, Penaeiodea, Brachiura), and fish (mainly Macruridae). Another important group in quantitative terms was Opistobranchia (chiefly Cavolinidae), which however in terms of percentage of occurrence (%F) or points (%P) accounted for the same order of magnitude as polychaets, amphipods or cnidaria (mainly siphonofora).

Table 5 *Nephrops norvegicus*. Percentage of stomachs with identifiable number of prey groups

Nº of prey groups	% of stomachs	
	Females	Males
1	42.42	39.76
2	36.36	31.73
3	12.12	15.66
4	5.56	8.43
5	2.53	2.41
6	0.00	1.20
7	0.51	0.40
8	0.51	0.40

The percentage distribution of stomachs with different number of prey groups for males and females is presented in Table 5. The number of prey items in the stomachs varied from 1 to 26 (F. max 22; M. max 26)

Feeding and size classes

Table 6 *Nephrops norvegicus.* Composition of the diet by lenght classes (LC). % N = percentage number; %F = frequency of occurrence; %P= percentage by points.

	% N	%F	%P	% N	%F	%P	% N	%F	%P
	LC1			LC2			LC3		
porifera	-	-	-	0.40	4.55	0.09	-	-	-
cnidaria	2.74	6.82	1.35	5.34	60.23	3.45	3.57	8.00	0.70
scaphopoda	-	-	-	0.10	1.14	0.02	-	-	-
prosobranchia	0.68	2.27	0.48	1.19	11.36	0.55	-	-	-
opistobranchia	37.67	18.18	10.41	14.62	47.73	3.63	8.04	10.00	0.97
bivalvia	0.68	2.27	0.56	3.16	30.68	1.56	1.79	4.00	0.42
cephalopoda	1.37	4.55	1.45	0.89	10.23	0.53	-	-	-
polychaeta	3.42	11.36	5.11	3.66	43.18	3.70	7.14	16.00	4.05
ostracoda	0.68	2.27	0.20	0.30	3.41	0.04	-	-	-
mysidacea	-	-	-	0.69	7.95	0.37	-	-	-
cumacea	-	-	-	0.10	1.14	0.04	-	-	-
tanaidacea	-	-	-	0.20	2.27	0.33	-	-	-
isopoda	-	-	-	1.09	11.36	1.90	1.79	4.00	3.32
amphipoda	3.77	9.09	2.47	4.25	35.23	2.48	1.79	4.00	0.50
euphausiacea	25.34	56.82	41.66	19.76	106.82	16.18	13.39	20.00	8.12
natantia	7.53	25.00	15.78	7.71	86.36	12.42	10.71	22.00	9.43
reptantia	3.77	12.50	3.93	10.47	118.18	13.74	23.21	52.00	32.68
sipunculida	-	-	-	0.49	2.27	0.10	-	-	-
equinodermata	0.34	1.14	0.16	2.77	30.68	2.19	1.79	4.00	0.30
chaetognata	-	-	-	0.10	1.14	0.05	-	-	-
tunicata	-	-	-	0.10	1.14	0.38	-	-	-
fish	7.19	23.86	8.11	16.40	186.36	25.70	17.86	38.00	31.25
NI Material	4.79	15.91	8.34	6.72	78.41	11.12	8.93	20.00	8.24

As results showed no differences between the diets of males and females, the feeding size class analysis was done on all the specimens

observed. Three size classes were considered (LC1, LC2 and LC3) (Table 6). The predominant prey-groups are the same as previously described. However same differences can be detected, especially between LC1 and LC3, since in the first length class we can find relatively more representatives of small specimens (Euphausids and Opistobranchia) and in the third class, more representatives of bigger size (Reptantia and fish).

The overlap indexes calculated between these length classes are presented in Table 4. According to the classification adopted the overlap is low, indicating that there are differences in the diet. However the results of the chi-square tests only yields significant differences (p-value 51.380) in the diets of LC1 / LC3 length classes.

Diversity

The diversity values calculated for the various associations are presented in Table 7. Considering that the diversity was calculated using prey-groups, it can be considered medium low, showing same differences between them. This variability is also expressed by the differences between the ratio of the mean number of prey items and the mean number of different prey groups per stomach by size class, which exceeds 36%.

Table 7 *Nephrops norvegicus*. Diversity index values of stomach content by sex and length class.

Factor		H'
Sex	Males	2.1646
	Females	2.2740
Size	LC1	1.7801
	LC2	2.3193
	LC3	2.0508

Fig 3 represents the ratio between the mean number of prey items and the meam number of different prey groups per stomach by size class.

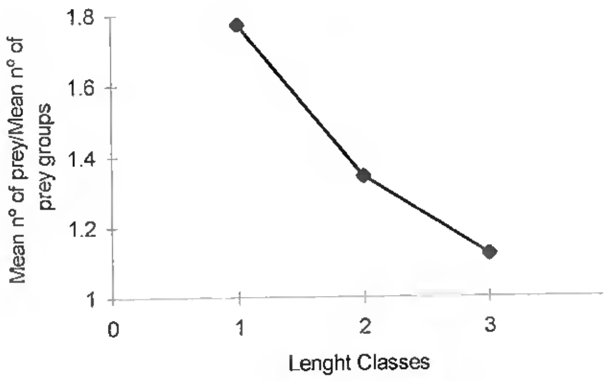

Fig. 3 *Nephrops norvegicus.* Relationship between mean number of prey items and mean number of prey groups per stomach by length class

DISCUSSION

Deep water decapod crustaceans, including *Nephrops norvegicus*, generally exhibit, highly diversified diets in many different geographic areas (Cristo and Cartes, 1998): this is true for species that occupy a similar depth distribution range, for example *Plesionika* spp. (Figueiredo, 1989; Cartes, 1993a) or other commercially important species such as *Aristeus antennatus* or *Aristomorpha foliacea* that only have small overlapping areas with *N. norvegicus* (Lagardère, 1972; Relini Orsi and Würtz, 1977; Rainer, 1992; Cartes and Sardà, 1989; Cartes and Sardà, 1992; Cartes, 1995), or even for polychelid species (Cartes and Abelló, 1992) or geryonids (Relini Orsi and Mori, 1977;Cartes, 1991) which have deeper distribution ranges.

Results indicate that the diet of *Nephrops norvegicus* consists of benthic and pelagic organisms, that can be divided into 4 main categories: (1) organisms that live buried in the substratum, such as glycerids (Fauchauld and Jumars, 1979), or bivalves; (2) organisms that live on (Aphroditids and *Nephthys* (Fauchauld and Jumars, 1979), or just beneath the surface of the substratum (endobenthic amphipods, *Harpinia* sp, isopods, crinoids); (3) suprabenthic or nektobenthic (*Plesionika, Cirolana borealis*) organisms that

exhibit natatory ability close to the sediment-water interface, and about which no diel vertical migration are documented; and (4) meso or bathypelagic organisms that as a result of vertical migrations may dwell close to the bottom (them being benthopelagic) tipically during daytime (i.e. *Pasiphaea spp.,Meganyctiphanes norvegica...*).

An important aspect that can be drawn from the present results is that the three diet evaluation methods used give similar information with respect to the important prey groups. This conclusion was also reached in the study of the diet of species of the Sepioidea family (Castro and Guerra, 1990). So, at leats for species that usualy prey upon a narrow size range of preys and present a low nº of prey per stomach, the validity of these methods is not so controversal as was suggested by Hansson (1980) or Hyslop (1980).

The Norway lobster can therefore be considered as an euryphagous and scavenger species (Lagardère, 1977; Cristo and Cartes, 1998) in view of the fact that the presence in the stomach of parts of large specimens, such as elasmobranch skin, were often found.

When we compare the diet of *Nephrops norvegicus*, with the diet of the large penaeoideans, *Aristeus antennatus* (Cartes and Sardà, 1989) and *Aristomorpha foliacea* (Cartes, 1995) is easy to verify that it partly resembles both: pelagic resources, as well as *Aristomorpha foliacea,* and benthic resources, as well as *Aristeus antennatus,* are exploited. Such that *N. norvegicus* can be considered a generalist in trophic terms.

This is important, as these three large decapods occupy similar habitats (Figueiredo, 1989; Cartes and Sardà, 1992), and the question of how they adjust to avoid interspecific competition can be posed. For the two penaeoideans the exploitation of different resources allows coexistence (Lagardère, 1972; Cartes and Sardà, 1989; Cartes, 1995); for *N. norvegicus*, a generalist strategy, to eat the available prey (dead or alive), permits the survival in an community occupied by diverse decapod crustaceans, thus exhibiting low levels of competition, which is a general characteristic of marine invertebrate communities in deep-water habitats (Macpherson, 1981; Blaber *et*

al, 1987). This same trend (low levels of possible competition) tend to increase at greater depths (Cartes, 1998).

N. norvegicus does not exhibit sexual dimorphism or size segregation. Perhaps as a consequence of this, there is almost no difference between the diets of males and females (909 % similarity), a result that is consistent with the findings of Mytilineou *et al*, (1992) for the North Aegean Sea. However the diet seems to be size dependent: there are differences in the diet composition between size classes, which seem to be more significative when we consider small *versus* large specimens. This is a common fact, since populations tend to adopt a structure that minimises intraspecific competition between size classes (Keast, 1978). The differences found are mainly related to the ability to capture and process larger prey, which small lobsters tend to avoid. There seems therefore to be a gradation between the diets of the various sizes, evidenced by variation in the percent share of the different taxonomic prey groups (opistobranchids, amphipods, euphausids, decapods). This pattern was already found for *A. antennatus*, which did not exibit differences between males and females of the same size (Cartes and Sardà, 1989).

The diversity index values yielded non significant differences between sexes or size class. These values are within the range of those obtained, with a similar methodology, for several locations in the Mediterranean (Cristo and Cartes, 1998). They are also within the range of values obtained for other decapods: H' = 1.99 for *Plesionika martia* (Cartes, 1993a) and H' = 5.38 for *Parapenaeus longirostris* (Cartes, 1995). The relatively low diversity index values in the diet of *N. norvegicus* are however consistent with the also relatively low mean number of prey items per stomach (LC1 = 3.16; LC2 = 2.8; LC3 = 2.04) when compared with the 13.4 medium prey items per stomach presented by *P. longirostris* (Cartes, 1995). The low mean number of prey items per stomach, which is related to dietary diversity, may be the result of discontinuous feeding activity, with well marked peaks (Farmer, 1974; 1975; Atkinson and Naylor, 1976; Cristo and Castro, submitted), and low feeding rate (Sardà and Valladares, 1989; Cristo, 2000).

The Norway lobster foraging strategies that were discussed in the 70ths by several authors for the North sea (Dunthorn, 1967; Farmer 1974; 1975), deal with specimens that live in relatively shallow water environments compared to the 600 m depth that we are dealing with in the south of Portugal; in that situation, those strategies, are therefore much influenced by the light regime. In deepwater environments, the light might act more as a secondary factor that influences other organisms upon which lobsters are dependent for food. The vertical movements that are performed by euphausids, *Sergestes* or *Pasiphaea* species, main prey items for Norway lobsters, may indirectily determine rhythm in its feeding behaviour. An activity peak of feeding intensity towards noon was demonstrated at these depths (Cristo and Castro, submitted).

In deep environments, sight might be less important than the sense of touch . That's why the author feels that foraging strategies are much of the type "sit and wait" and that the out-of-burrow escapades might also be concerned with definition of territories and mating purposes. This can be supported by: (a) the wide range of prey, that vary from organisms that are benthic, bathypelagic and planctonic, showing that they eat whatever "fall" on them; (b) in the females there is a strong influence of the maturity stage over the feeding activity; (c) feeding activity for males and females show the same patern, sugesting that feeding activity in males also follows a sexual pattern; (d) berried females decrease their feeding activity.

The first assumption can explained by the natural behaviour of this species emphasised by the fact that there are in this fishing area large quantities of food originating from discards from the by-catches of crustacean fishing activity (Borges *et al*, 1997; 2000) fact already reported for other decapod species (Wassenberg, 1987). The second assumption is not in disagreement with Farmer (1974) since the confinement of berried females to their burrows and subsequent fasting periods (Dunthorn, 1967; Farmer, 1975), besides the fact that they are avoiding predators, can also be explained by the fact that there is no mating during this period.

This behaviour was also found in another lobster of the family Nephropidae, *Homarus americanus*, (Karnofsky *et al*, 1989; Cowan and Atema, 1990), suggesting that most of the movements between shelters are in fact more related to a sexual pattern than to a foraging activity. However all these assumptions should be subjected to further studies, which are however very difficult to achieve in field conditions, but could perhaps be accomplished in large aquaria (Cowan and Atema, 1990).

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GUT EVACUATION RATES IN *Nephrops norvegicus* (L.): LABORATORY AND FIELD ESTIMATES

ABSTRACT

Estimates of gut evacuation rates of *Nephrops norvegicus* were obtained during laboratory and field experiments. Individuals were collected off the south coast of Portugal in December 1997 and July 1998. Gut evacuation rates ($R.h^{-1}$) were calculated from the slope of the regression of the natural logarithm of dry stomach content weigh versus time, using data obtained by the "serial slaughter method". The values obtained during laboratory ($R=0.172\ h^{-1}$) and field experiments ($R=0.177\ h^{-1}$) are compared with gut evacuation rates reported for other marine organisms.

Key words: Gut evacuation rates. *Nephrops norvegicus*. Feeding ecology

INTRODUCTION

The determination of the evacuation rate of a certain species is important when feeding studies are addressed (Joll, 1982) and it is also a necessary parameter to evaluate daily rations grounds (Maynou and Cartes, 1997; 1998).

Gut evacuation rates have been mainly determined in fish, either during field or laboratory experiments (Persson, 1979; Jobling, 1980a, 1980b; Brodeur, 1984; Garcia and Adelman, 1985; Brodeur and Pearcy, 1987; Amundsen and Klemetsen, 1988; Héroux and Magnan, 1996). However, the methodologies used for fish have rarely been applied to invertebrates such as decapod crustaceans. In fact, only in a few studies, decapod crustacean gastric evacuation rates of different types of food have been estimated and all were laboratory experiments (Hill, 1976; Joll, 1982; Sardá and Valladares,

1990). Several studies have also been carried out on non-decapod crustaceans to determine *in situ* and *in vitro* evacuation rates (Murtaugh, 1984; Kiorbe and Tiselius, 1987; Clarke *et al*, 1988; Dam and Peterson,1988; Perissinotto and Pakhomov, 1996). However, no studies were conducted to date to determine *in situ* gut evacuation rates of deep water decapod crustaceans, mainly due to logistical constrains.

The aim of the present study was to estimate gut evacuation rates of the decapod *Nephrops norvegicus,* one of the dominant species in bathyal crustacean decapod assemblages in the eastern Atlantic (Figueiredo, 1988;1989), based on field and laboratory observations, and to compare the results obtained by both techniques.

MATERIALS AND METHODS

Field study

Norway lobsters, *N. norvegicus*, were collected off the south coast of Portugal, from a single trawl conducted from a commercial boat, during July 1998 on fishing grounds at a depth of 600 m, in the vicinity of 36° 51' N and 7° 43' E. This was a short two-hour trawl, in order to guarantee the maximum survival rate of the lobsters.

Immediately after capture, a first batch of 10 individuals, randomly selected, consisting of both males and females (sex ratio, length range and mean given in Table 1), were killed by immersion in 10% buffered formalin. These were considered time 0 (T_0) individuals.

The remaining individuals were divided in 5 similar groups of 10 (Table 1) and placed in 5 insulated 60 l boxes with lid and filled with seawater, to minimize temperature changes. The boxes were kept on deck. The seawater temperature was lowered, and maintained at 14° C for the duration of the experiment. The temperature in the experiment represented an average temperature at the depth of capture (Ambar, 1983).

Table 1. *Nephrops norvegicus*. Field study experiment: characteristics of lobster groups; T_i - group slaughtered at time I; Sex ratio - Male:Female; CL - Carapace length.

Groups	Sex ratio	CL (mm) range	Mean CL (mm)	standard error
T_0	4:6	32.81 - 48.93	37.15	1.49
T_1	6:4	31.86 - 46.91	39.72	1.94
T_2	4:6	29.81 - 50.08	37.69	1.63
$T_{3.5}$	4:6	32.15 - 46.64	39.95	1.53
T_5	5:5	31.28 - 49.36	39.06	2.19
T_7	6:4	28.46 - 46.5	38.18	1.17

This relatively low temperature was achieved by means of ice packs, to avoid any salinity change. The water was aerated by means of aquarium pumps powered by AA batteries.

At time intervals of 1, 2, 3.5, 5 and 7 hours one group of 10 individuals were sacrificed, by immersion in 10% buffered formalin ("serial slaughter method"; Windell, 1967) (Thorpe, 1977; Héroux and Magnan, 1996).

The sacrificed lobsters were transported to the laboratory and 48 hours later were transfered into 70° ethyl-alcohol. The biological sampling analysis included carapace length measurements (to the nearest 0.01 mm), sex determination and stomach removal. The latter were preserved in 70° alcohol.

Stomach content treatment

Each of the 60 stomachs collected, was cut open under a stereomicroscope. The content was then dispersed in distilled water and filtered through a pre dried and weighed Whatman-GF/C glass microfibre filter, using a vacuum pump system. The filters with the stomach contents were then dried for 48 hours at 60° C. The stomach content weights were calculated by subtraction of the filter dry weights (to the nearest 0.0001 g).

Laboratory experiments

The Norway lobsters used in this experiment were also caught with a trawler off the south coast of Portugal, during December 1997 at depths of 600 m, in the vicinity of 36° 50' N and 7° 43' E.

All the individuals were maintained in a closed sea water system (Encarnação *et al*, 2000), at a temperature of 14° C, a salinity of 37‰, a pH=8, and stabilised levels of nitrites and ammonia (<0.2 mg/l). The acclimatisation period took several weeks during which lobsters were fed shrimp, fish and pelleted food.

In January 1998, the lobsters were measured (carapace length to the nearest 0.01mm), weighed (to 0.01g) and sexed. The specimens were assigned to one of 7 groups of 10 individuals, making sure that all groups had small, median and large individuals in the same proportion (Table 2). Each individual was kept in its own individual plastic compartment, with water flowing and circulating over all the compartments.

Table 2. *Nephrops norvegicus.* Laboratory experiment: characteristics of lobster groups. T_i - group slaughtered at time i; Sex ratio - Male:Female; CL - Carapace length.

Groups	Sex ratio	CL (mm) range	Mean CL (mm)	standard error
T_0	9:1	26.2 - 42.92	35.16	1.76
$T_{0.5}$	6:4	27.09 - 42.41	35.97	1.6
T_1	7:3	27.88 - 43.96	36.47	1.61
T_2	9:1	27.92 - 43.14	36.3	1.52
$T_{3.5}$	7:3	28.3 - 44.1	37.07	1.54
T_5	9:1	28.5 - 44.16	37.84	1.54
T_7	5:4	29.03 - 47.67	38.55	1.86

Before the experiment was carried out, the lobsters were starved for 8 days. The specific diet chosen was a small shrimp of the family Crangonidae *Palaemonetes varians*. The choice of this material, was based on the fact that crustaceans are one of the main sources of food for *Nephrops norvegicus* (Cristo, 1998; Cristo and Cartes, 1998) and one of the preferred preys in

laboratory experiments (Cristo and Encarnação, 2000). In addition, this species is very easy to collect, and therefore the experiment could be based on freshly caught food. Approximately 2 g of fresh whole shrimp was given to each lobster. The relationship between shrimp dry weight (DW g) on shrimp wet weight (WW g) was determined by linear regression:

$$DW\ (g) = 0.25475\ WW\ (g) - 0.00791\ (n = 32,\ r^2 = 0.959)$$

As most of the lobsters literally "attack" food, 15 minutes after the shrimp has been supplied all the uneaten shrimp was removed from each compartment and stored separately for posterior drying (at 60° C for 48 hours) and weighing (to the nearest 0.0001g)

At this time, the first group of 10 individuals was sacrificed (in 10% buffered formalin) and this was considered time 0 (T_0) group. The "serial slaughter method" was used at time intervals of 0.5, 1, 2, 3, 5 and 7 hours (Hill, 1976; Joll, 1982; Amundsen and Klemetsen, 1988; Sardá and Valladares, 1990).

Stomach content treatment

The method to accurately determine the stomach content dry-weight was the same as previously described for the field study.

The amount of dry food ingested was determined by the difference between the calculated dry food supplied and the dry food removed from the boxes. This value is usually superior to the amount of food that really reaches the stomach (Dagg, 1974; Hill, 1976), due to the loss of body fluids and small particles produced during the process of mastication, which are impossible to recover from the boxes. Therefore the percentage of loss was determined by the analysis of the stomach content in the T_0 individuals. It was estimated that only 52% of the food virtually ingested actually reached the stomach. This correction factor (CF) was applied to all individual ingested food values.

In both trials, the analysis was carried out using the mean values of stomach contents in each batch (n=10). Standard errors were estimated for the field study.

The exponential model was used to describe the relation between food evacuation and time and for the determination of the instantaneous evacuation rate (R) . This model is more appropriate for describing the evacuation of small, relatively easily digested particles from the stomach (Jobling, 1986), which is the case for *Nephrops norvegicus*. This approach has been widely used both in fish (Persson, 1986, Brodeur and Pearcy, 1987; Andrade *et al*, 1996) and crustaceans (Hill, 1976; Sardá and Valladares, 1990).

Following Elliott (1972):

$$W_t = W_0 \, e^{-Rt} \qquad (1)$$

where W_0 is the stomach content weight at the beginning of the time interval (T_0), W_t is the stomach content weight at time t, and R is the instantaneous evacuation rate.

W_t can also be expressed as percentage of the initial food ingested, where

$$W_t = \frac{\text{W of stomach content}}{W_0} \times 100 \qquad (2)$$

or for the laboratory study

$$W_t = \frac{\text{W of stomach content}}{(\text{W of food supplied} - \text{W of food uneaten}) \times \text{Correction Factor}} \times 100 \qquad (3)$$

where the correction factor CF = 0.52.

RESULTS

Field study

In field studies, since we have no possibility to determine the amount of food in the stomach of the individuals without sacrificing them, we have to assume that the mean stomach content of all the individuals used in the experiment is comparable to the sample taken at time T_0. The serial analysis of the mean dry weight stomach content showed a continuous decrease over the duration of the experiment (Fig. 1). After 7 hours only approximately 30% of the initial content remained in the stomach (Fig. 2).

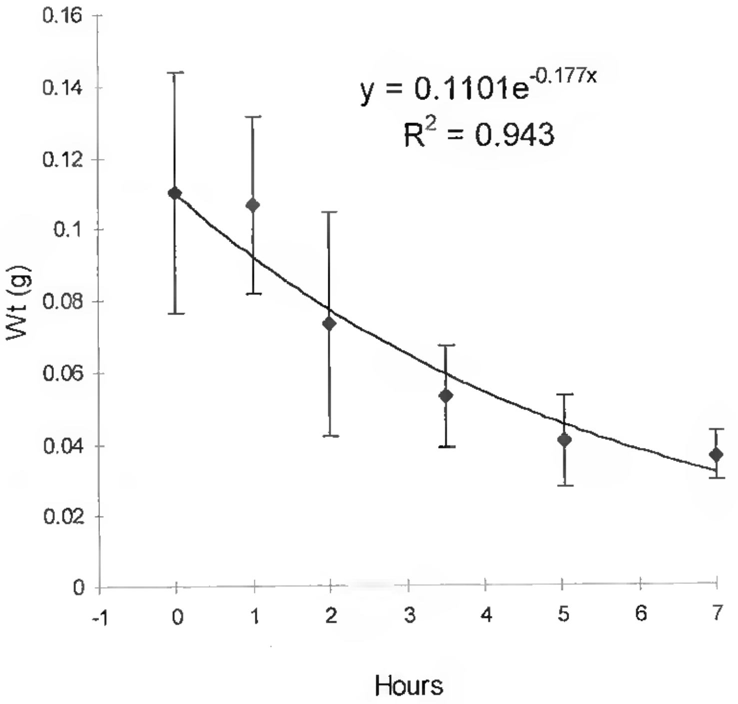

Fig. 1 - Field study. Exponential curve of decrease in the mean stomach contents (g) and standard errors over time

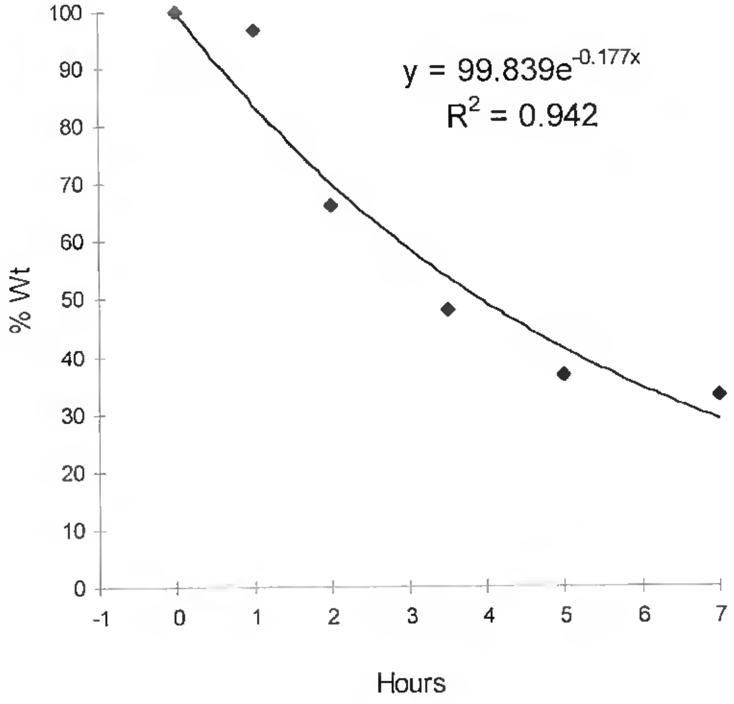

Fig. 2 - Field study. Exponential curve of the percentage of the mean stomach contents as a function of the initial content over time

Fig. 1 represents the approach of equation (1), Fig. 2 the approach of equation (2).

The estimated instantaneous evacuation rate obtained was R = 0.177 h^{-1}

Laboratory study

The results from laboratory experiments are presented in Fig. 3 which represents the approach of equation (1), with dry weights fitted to mean dry weigh at T_0, and Fig. 4 represents the approach of equation (3), since in this case, each group of 10 individuals had different initial mean dry weights. The amount actually consumed was accurately determined for each group slaughtered.

The estimated instantaneous evacuation rate obtained was R = 0.172 h^{-1}

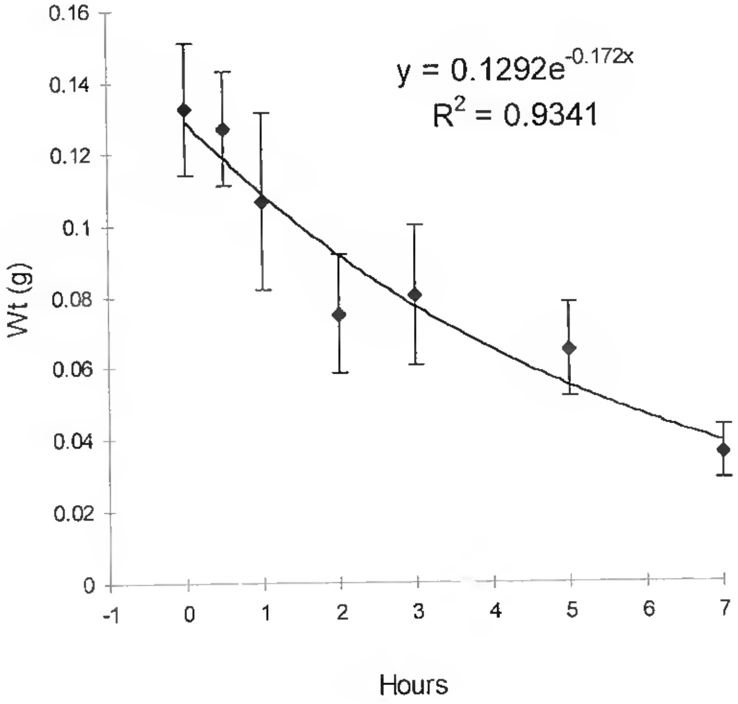

Fig. 3 - Laboratory experiment. Exponential curve of decrease in the mean stomach contents (g) and standard errors over time

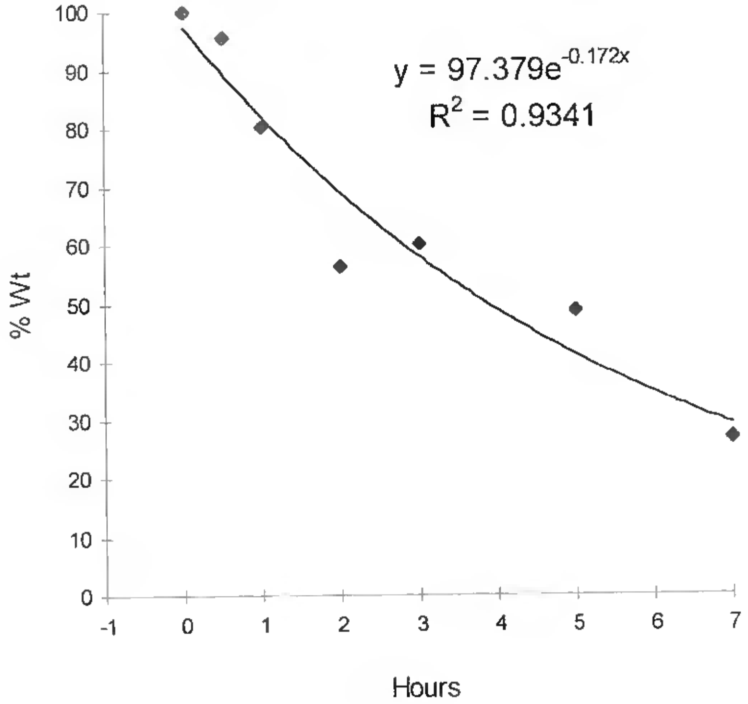

Fig. 4 - Laboratory experiment. Exponential curve of the percentage of the mean stomach contents as a function of the initial content over time

DISCUSSION

According to this model, the instantaneous evacuation rate R corresponds to the slope of the relation between ln W_t at time t. R values have often been estimated for fish through laboratory experiments (Brodeur and Pearcy, 1987; Amundsen and Klemetsen, 1988; Parrish and Margraf, 1990; Andrade et al, 1996). Thought this laboratory methodology has been widely applied to marine invertebrates such as copepods, amphipods or euphausids (Kiörbe and Tiselius, 1987; Clarke *et al*, 1988; Dam and Peterson,1988; Perissinotto and Pakhomov, 1996), to the best of my knowledge, only Hill (1976), Joll (1982) and Sardá and Valladares (1990) have applied this methodology to decapod crustaceans.

This method assumes that laboratory conditions, starvation before feeding, and lack of prey diversity, do not affect evacuation rate (Héroux and Magnam, 1996). According to the same authors, one advantage of this method is that individuals are presumed to be unstressed after acclimatisation and

during the experience; it is also possible to control the quantity of food ingested by each individual.

Determination of R, using field experiments, has also been carried out for fish (Garcia and Adelman, 1985; Boisclair and Leggett, 1988; Parrish and Margraf, 1990; Héroux and Magnan, 1996). However, in crustaceans, *in situ* experiments have been carried out only with non-decapods, like copepods (Kiørboe and Tiselius, 1987; Dam and Peterson,1988), amphipods (Pakhomov and Perissinotto, 1996) or euphausids (Clarke *et al*, 1988; Perissinotto and Pakhomov, 1996). An alternative method to estimate R is based on the R_{max} procedure (Héroux and Magnan, 1996; Maynou and Cartes, 1998).

In field studies it is assumed that the stress due to capture and holding does not affect evacuation rate. This method has the advantage of integrating all field conditions, natural prey diversity, and evacuation rate without any forced starvation period (Héroux and Magnam, 1996).

According to Elliott (1972) and Irigoien (1998) the initial gut content should not significantly affect the evacuation rate, with temperature being the limiting factor. Other authors (Jobling and Davies, 1979; Dam and Peterson, 1988) also concluded that temperature was the most important factor affecting evacuation rate, and since this parameter was maintained constant throughout both the experiments, the instantaneous evacuation rate should be similar.

The R values estimated from laboratory experiments $R = 0.172\ h^{-1}$ and field experiments $R = 0.177\ h^{-1}$ are almost identical, suggesting that these are realistic values for the temperature considered (14° C) (Elliott, 1972).

Table 3 summarises gut evacuation rates calculated in previous published data for several different crustaceans. The results we obtained for both experiments are very similar, and are within the range of the values in the literature, even in the case where different methodologies were used (i. e. Rmax of Maynou and Cartes, 1998).

From data collected in previously published fish studies Worobec (1984) and Pakhomov *et al* (1996) established equations relating temperature T with gut evacuation rates R. For T=14° C, the temperature at which we conducted

Table 3. *Nephrops norvegicus*. Comparison of gut evacuation rates (GER) (h^{-1}). Temperature T(ºC). Sources: (1) recalculated from Sardá and Valladares, 1990, (2) Hill, 1976, (3) recalculated from Joll, 1982, (4) Maynou and Cartes 1998, (5) Pakhomov and Perissinotto 1996, (6) Perissinotto and Pakhomov, 1996.

	F	T	Source
Nephrops norvegicus (field estimates)	0.177	14	This study
Nephrops norvegicus (laboratory estimates)	0.172	14	This study
Nephrops norvegicus	0.157	14	(1)
Scylla serrata	0.214	18-22	(2)
Panulirus cygnus	0.416-0.520	25	(3)
Geryon longipes (R_{max})	0.183	13	(4)
Themisto gaudichaudi	0.133	not specified	(5)
Euphausia superba	0.101-0.424	not specified	(6)

our experiments, both Worobec's linear model (1984) and the power relation of Pakhomov *et al* (1996) gives R = 0.20 h^{-1}.

Considering all these, it is not unreasonable to assume that gut evacuation rates obtained in this study are close to the real values.

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LABORATORY ESTIMATES OF THE DAILY RATION OF THE NORWAY LOBSTER *Nephrops norvegicus*(L.) (DECAPODA) FROM THE SOUTHERN COAST OF PORTUGAL

ABSTRACT

Daily ration and preference for different types of food were studied in *Nephrops norvegicus* (L.) by means of simple laboratory experiments. Lobsters were collected off the south coast of Portugal at depths of 600 m in 1997 and were held in captivity individually for a period of several weeks at 14° C of water temperature in a closed circuit of seawater with a salinity of 37%o, for adaptation. Two groups of 10 lobsters were fed three different types of food alternate: a) Fish - *Engraulis encrassicolus*; b)Polychaeta - *Diopatra neapolitana* or *Marphisa sanguinea; c) Crustacea - Palaemonetes varians.* Daily ration was estimated at 0.0077g dried weight (DW) per g body weight per day, for the group fed every 24h, and 0.0087g DW per g body weight per day for the second group, fed every 48 h. These can therefore be considered as maximum values for food intake per day. Considering the amount of food ingested daily as a measure of preference of different types of food, we can also conclude that Norway lobsters prefer Crustaceans to Fish and these to Polychaeta.

Keywords: Feeding ecology, *Nephrops norvegicus*, daily ration.

INTRODUCTION

In any feeding ecology study several complementary aspects must be considered. Although the description of the preys of a certain species, based on the analysis of stomach contents, is the basis for any feeding study, these qualitative studies should be complemented with quantitative studies, such as

determination of daily ration and of gastric evacuation rate. The latter rates, can be determined by means of field experiments or laboratory experiments.

Over the past decades, numerous studies have focused on daily rations estimates in fish, either through field experiments (Brodeur and Pearcy 1987, Amundsen and Klemetsen 1988, Tudela and Palomera 1995, Pakhomov et al. 1996) or laboratory experiments (Walh and Stein, 1991). In crustaceans, however, comparatively few experiments on this subject were carried out in the field (Pakhomov and Perissinotto 1996, Perissinotto and Pakhomov 1996, Maynou and Cartes 1997) or in laboratory (Sardá and Valladares 1990). All the results derived from these studies have direct application in the field of trophic ecology, for example the determination of predation pressure on prey species, sustainable yields of different habitats, impact of environmental modifications, or even for testing bioenergetic models in different species (Héroux and Magnan 1996).

The present work arises as a complement of a feeding study on *Nephrops norvegicus* off the south coast of Portugal (Cristo, submitted), and is part of a broader study that has as objective the estimation of gastric evacuation rates and daily ration in the laboratory and in the field.

MATERIAL AND METHODS

The methodology assayed differs from the work of Sardá and Valladares (1990), since the specimens were kept individually, making possible the accurate knowledge of the food ingested. Also in our case food was given in excess, to make sure the full satiation of the individuals.

Experimental conditions

The specimens of *Nephrops norvegicus*, used in the present experiment were collected as a single sample in the winter of 1997 by means of a trawler at depths of approximately 600 m off the South coast of Portugal. The lobsters were transported without water in humid conditions in insulated plastic

containers, and acclimatised in a closed-sea water circuit. They were held in captivity individually for a period of several weeks for adaptation. During this period they were fed with food pellets. The physico-chemical conditions of the water through out the experiment were: 14° C water temperature, 37%o salinity, 8 pH and stabilised levels of nitrites and ammonia (<0.2 mg/l) (Encarnação et al. 1998). The light regime corresponded to total darkness, to simulate the light regime observed at the depth at which the lobsters were caught. All the specimens used fell within the carapace length classes of 30 and 40 mm, in order to eliminate possible variations due to size. All individuals were at intermoult stage C (Sardà 1983). Only lobsters in good physical conditions were used in the experiments.

Description of the experiments

An 8 days period in which the individuals were deprived of food, preceded the experiment, in order to guarantee the total emptiness of the digestive tract. Two sets of ten individuals were used. Each group was composed of males and females (2 berried/3 not berried), in a proportion of 1 to 1. Each individual was held in it's own plastic box, so that the food supplied could only be eaten by itself, and the remainder could not be lost. All the plastic boxes were immersed in flowing seawater in a 200 l tank. (Encarnação et al. 1998). The three types of food supplied were: a) Fish - *Engraulis encrassicolus*; b) Polychaeta - *Diopatra neapolitana* or *Marphisa sanguinea; c)* Crustacea - *Palaemonetes varians.*The first group was fed every day, and the second group every second day. Only one type of food per day was given.

Experiment 1

For the first group of lobsters the fresh food supplied was weighed individually. The food was given in excess, (approximately 2g) so that the lobster could eat at libidum. The first days meal was composed of fish, the second of Polychaeta, the third of Crustacea, the fourth fish and so on until the fourteenth day, which was the last day of the experiment. Every day, before supplying new food, the uneaten remains were individually collected and dried at 60° C until there was no further lost of weight, usually 48 hours, in order to obtain dry weight.

Experiment 2

For the second group of lobsters the supplying of food was done the same way as before (experiment 1), but the lobsters were only fed every second day, although the remains were removed the day after feeding. The remains were also dry weighed. This experiment also had a duration of 14 days.

Data processing

Since the presentation of data in fresh weights could lead to significant errors, due to the fact that the tissues not eaten absorb water; the data are presented in dry weight. Regressions of fresh weight against dry weight were established, for the three types of food supplied

RESULTS

The results of the regressions of wet weight (WW) against dry weight (DW), are:

- Fish - *Engraulis encrassicolus*: DW=0.0015+0.2871WW, r=0.9919, n=30;
- Polychaeta - *Diopatra neapolitana*: DW=-0.0043+0.227WW, r=0.9835, n=30 or *Marphisa sanguinea*: DW=0.0329+0.1752WW. r=0.8919, n=30;
- Crustacea - *Palaemonetes varians*: DW=0.0013+0.2679WW, r=0.9897, n=30.

Experiment 1

During the total duration of the experiment the average amount of fresh food supplied was 2.15g, which is equivalent to an average of 0.55g in dry weigh. The average amount of food actually eaten was 0.25g. Table 1 shows the actual food ingested in dry-weight (g) per g of lobster body weight, for the three categories of food.

Experiment 2

In this second experiment where the lobsters were deprived of food in alternate days, the results do not differ greatly from the results in experiment 1. Table 2 presents the results of the amount of food ingested in dry-weight (g) per g of lobster body weight, for the three categories of food, every second day.

Table 1. Average values of dry-weigth ingested (DW Ing.) in g, per g of lobster body weight (BW), from experiment 1.

Date	Type of food	DW Ing. (g)/g of BW
22-10-1997	Fish	0.0132
25-10-1997		0.0058
28-10-1997		0.0069
31-10-1997		0.0069
03-11-1997		0.0056
Average	Fish	0.0077
24-10-1997	Crustacea	0.0114
27-10-1997		0.0112
30-10-1997		0.0147
02-11-1997		0.0124
Average	Crustacea	0.0115
23-10-1997	Polychaeta	0.0077
26-10-1997		0.0045
29-10-1997		0.0019
01-11-1997		0.0017
04-11-1997		0.0044
Average	Polychaeta	0.0040
Total Average		0.0077

The total amount of food ingested in each experiment was compared using a Mann-Whitney test (Conover 1980). The differences where not significant ($p>0.05$).

To compare the amount of food ingested by species, the Kruskal-Wallis test was used (Freund 1979). Three classes of food were compared, fish, Crustacea and Polychaeta. The test was significant ($p<0.05$). The consumption of Crustacea was higher than fish and fish higher than Polychaeta.

Table 2. Average values of dry-weight ingested (DW Ing.) in g, per g of lobster body weight (BW), from experiment 2.

Date	Type of food	DW Ing. (g)/g of BW
22-10-1997	Fish	0.0107
28-10-1997		0.0105
03-11-1997		0.0061
Average	Fish	0.0091
24-10-1997	Crustacea	0.0107
30-10-1997		0.0138
Average	Crustacea	0.0123
26-10-1997	Polychaeta	0.0053
01-11-1997		0.0037
Average	Polychaeta	0.0045
Total Average		0.0086

DISCUSSION AND CONCLUSIONS

There are very few studies concerning daily ration or maximum daily ration either in the field or in the laboratory, for decapod crustaceans (Sardá and Valladares 1990, Maynou and Cartes 1997).

From the results obtained with experiment 1 and 2, which revealed that the amount of food ingested is independent of the quantity available, we can assumer that the daily ration for this species is also the maximum daily ration that an individual can ingest any time (considering the source of food is not limited). In contrast to fish, lobster stomachs do not expand to any great extent. Therefore lobsters are more easily satiated. It should be noted that this

maximum amount of food ingested did not seem to be affected by the period of starvation to which they were submitted every other day.

The greater preference for crustaceans, followed by fish and polychaeta, are consistent with the results from field studies (Gual-Fau and Gallardo-Cabello 1988, Sardá and Valladares 1990, Mytilineou et al. 1992, Cristo and Cartes 1998)

The results obtained in this particular study are within the range of other published daily rations estimates (Table 3). Our results are quite similar to those obtained by Sardá and Valladares (1990) for the this species, and are of the same order of magnitude of the values calculated for *Aristeus antennatus* (Maynou and Cartes 1997) both for field observations and for the daily ration estimates. These two species are decapods of the upper slope, with *N. norvegicus* being a less mobile and burrow related species and *A. antennatus* a more active benthic crustacean one. Maynou and Cartes (1997) consider *A. antennatus* an atypical species among deep-water decapods having probably one of the highest daily rations within the benthic bathyal decapod communities, since it is always characterised by high stomach fullness (Cartes 1994). Maynou and Cartes (1997) also consider the values of daily ration obtained for *N. norvegicus* by Sardá and Valladares (1990) as overestimated. However, these results were not unexpected since in contrast to what has been reported in the literature for *N. norvegicus* in other areas (Lagardère 1977, Mytilineou et al. 1992), in our study area very low proportions of empty stomachs were found (Cristo and Cartes, 1998). On the other hand in our experiments, despite the continuous presence of food, individuals did not eat more and there were always leftovers of all three types of food to remove. So in this particular case, although the experiments took place under conditions that were very different from those in nature, we believe that the daily ration was mainly dependent on the volume of the stomach, and could be considered as the maximum food intake of *Nephrops norvegicus*.

Our results are comparable, to the daily ration estimates of the brook charr in an oligotrophic lake (T= 17.8 to 19° C) in Canada (Héroux and Magnan 1996) or to those obtained by Tudela and Palomera (1995) for the European

anchovy (T>20° C). However they are one or two orders of magnitude lower than those obtained for an Antarctic amphipod (T<10° C). In spite of the different temperatures at which these estimates were obtained, we might expect that the Norway lobster being an opportunistic/scavenger species, and characterised by a burrowing live style, might have a lower daily ration in relative terms to body weight than species, lower in the food chain, but higher daily rations than predators higher in the food chain (Maynou and Cartes 1997).

Table 3. Comparison of daily-ration in %BW Wet = (g Wet Weight /g Body Weight Wet) x 100 and % BW Dry = (g Dry Weight /g Body Weight Wet) x 100 of *Nephrops norvegicus* with daily-rations obtained for other species. Sources: (1) Sardá and Valladares 1990, (2) Maynou and Cartes 1997, (3) recalculated from Pakhomov andPerissinotto 1996. (4) Héroux and Magnan 1996, (5) Tudela and Palomera 1995).

	% BW Wet	% BW Dry	Source
Nephrops norvegicus (minimum - maxinum values)	2.65 - 4.11	0.40 - 1.23	This study
N. norvegicus (average values)		0.77 - 0.86	This study
N. norvegicus (maximum food consumption)	2.5	0.86	(1)
Aristeus antennatus (actual ration)	2.588		(2)
A. antennatus (range of daily ration models)	1.666 - 2.315	0.130 - 0.223	(2)
Themisto gaudichaudi (field estimates)		4.5	(3)
T. gaudichaudi (laboratory experiments)		5.2 - 13.4	(3)
Salvelinus fontinalis (field estimates)		0.62	(4)
Engraulis encrasicolus (field estimates)	3.70 - 3.92		(5)

In conclusion the experiments revealed that an average lobster of 40g, can eat approximately 0.3g of dry food,(0.304g for experiment 1 and 0.344g for experiment 2) which corresponds to approximately 1g of fresh food a day. This daily ration seems not to be greatly affected by food deprivation in alternate days. We consider that these kinds of studies are important but have to be accompanied by field evaluations such as those which we are presently undergoing.

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FIELD ESTIMATION OF DAILY RATION OF NORWAY LOBSTER - *Nephrops norvegicus* (L.)- IN THE SOUTH OF PORTUGAL

ABSTRACT

Daily ration estimates from field samplings over a 24 hour cycle were obtained. Four tows were conducted in the middle continental slope, off the south coast of Portugal. The results from three daily ration models are compared, showing no significant differences among them. The estimates of food consumption obtained varied from 1.098g - 1.170g dry food per 100g body wet weight in males and 1.642g - 1.755g dry food per 100g body wet weight in females. Daily ration between sexes were significantly different.

Key words: Daily ration. *Nephrops norvegicus*. Feeding ecology.

INTRODUCTION

The Norway lobster (*Nephrops norvegicus* (L.), is one of the dominant crustacean species in the bathyal assemblages in the North-Atlantic (Farmer 1975); the eastern Atlantic (Figueiredo, 1988; 1989); the western Mediterranean (Abelló *et al*, 1988; Cartes et al, 1994); the eastern Mediterranean (Froglia and Gramito, 1995). This is a species that has been widely studied in it's different aspects of biology and fisheries (Figueiredo and Thomas, 1967; Farmer, 1975; Chapmam, 1980; Sardà, 1995), but as Sardà (1995) pointed out feeding studies were poorly covered.

For this reason the feeding ecology of *Nephrops norvegicus* from the south coast of Portugal has been subject of several recent studies, (Cristo, 1998; Cristo and Cartes, 1998; Cristo and Encarnação, 2000; Cristo, submitted).

However, daily ration estimates based on field experiments, are still lacking for Norway lobster. This field widely studied and developed for fish (Worobec, 1984; Macpherson, 1985; Héroux and Magnan, 1996; Pakhomov *et al*, 1996) was also successfully applied recently to decapod crustaceans from bathyal grounds (Maynou and Cartes, 1997; 1998).

These are important studies because the estimation of daily rations in deep-water organisms can be a source of indirect information on the carrying capacity of deep environments to sustain given levels of abundance, biomass and diversity (Maynou and Cartes, 1997)

Decapod crustaceans are important in this context because they play an important role in the structure of the food webs, establishing the link between macrofauna and megafauna top predators (Cartes and Sardà, 1992; Cartes, 1998).

The present daily ration study is of particular interest for the previously discussed ecological reasons and because it is based on a field study of *Nephrops norvegicus*.

Several authors developed daily ration models based on field experiments (Eggers, 1977; 1979; Elliott and Persson, 1978) that have been applied to fish and decapod crustaceans.

Results from feeding studies reveal that *N. norvegicus* feeds on a wide variety of prey (Thomas and Davidson, 1962; Lagardère, 1977; Cristo, 1998), presents median stomach fullness indices (Mytilineou *et al*, 1992; Cristo and Cartes, 1998) and has lower evacuation rates compared to other decapods (Cristo, submitted). The objective of our study was to produce estimates of food consumption by *Nephrops norvegicus* in the wild, based on daily ration models, as a quantitative complement of the feeding ecology studies of this important species.

MATERIAL AND METHODS

Data sampling and data treatment

This field experiment was conducted on a commercial trawler, in the Spring (26-27 April) of 1999 at depths of 600 m in the vicinity of 36° 45’ N, 7° 50’ E. Four trawls were completed during a 24 h period: dawn, noon, sunset and night. Table 1 presents the data relative to the samples and sampling sites. Because of the low densities of Norway lobster at these depths and the duration of the fishing operations, tows of 4 to 5 hours were required in order to guarantee adequate sample sizes.

Table 1. Trawl samples of *Nephrops norvegicus* collected for daily ration determination in the south off Portugal. N: number of individuals analysed

Haul	Dept (m)	Star time (h GMT)	End time (h GMT)	N	Size Range (mm CL)	Sex ratio (% females)	Mean weight (g)
1	578-615	5:30	9:30	52	31.5-53.9	40.4	49.62
2	578-639	10:45	15:15	51	32.8-56.6	50.9	51.37
3	547-617	17:15	21:15	52	30.2-51.2	59.6	40.99
4	594-637	22:45	4:15	49	30.8-52.5	53.1	45.52

The water masses in the surrounding area show characteristics of Eastern North Atlantic Water (ENAW) (Relvas de Almeida, 1999). However, the water in the sampling area, a canyon that runs east-west, shows well marked characteristics of Mediterranean Water (MW) that is known to flow out of this basin through these submarine canyons (Madelain, 1970). This water masses corresponds to the shallow core of MW, with temperatures that are constant and relatively high throughout the year: 13° C ± 0.5° C (Ambar, 1983).

From each haul, a sample of *ca*.50 individuals was randomly collected, and preserved on board in 4% buffered formalin. In the laboratory the samples were transferred to 70% ethanol, after 48 hours. Sex, standard cephalothorax length (mm CL) and wet weight, with no claws (WNC), were recorded. This last parameter, is important because not all specimens had the two claws, and so it is preferable to register the weight with no claws, and after transform those values to wet weight with claws (WC), through a linear regression: $WC = a + b\ WNC$. Size varied between 30.2 mm and 48.1 mm CL for females and 31.4 mm and 56.6 mm CL for males.

Stomachs were removed, and the contents carefully washed and dispersed in distilled water and then filtered through a pre-dried and weighed

Whatman-GF/C glass microfibre filter, in a vacuum water jet pump system, to guarantee no loss of content. The filters with the stomach contents were then dried for 48 hours at 60° C. The stomach content dry weights (DW), were calculated by subtraction of the filter dry weights.

The gut fullness index is expressed as g dry food weight per 100g fresh lobster weight. The stomach fullness index (F) was computed for each individual as (Maynou and Cartes, 1998):

$F = (\text{g stomach content DW}).\ (100\text{g lobster WC})^{-1}$

A 2-way ANOVA with interaction was used to test the effect of sex and time of the day on the F index.

Daily ration models

The models and methods usually used for the determination of daily ration in fish, have been reviewed by several authors (Boisclair and Leggett, 1988; Boisclair and Marchand, 1993; Bromley, 1994; Héroux and Magnan, 1996). Maynou and Cartes, (1997; 1998) assessed their applicability of fish models to decapod crustaceans.

Daily ration models are based on the assumption that gastric evacuation is an exponential decay function (Eggers, 1977; Elliot and Persson, 1978) which includes a constant for gastric evacuation rate (R).

This value of R can be obtained from the results of field experiments under certain conditions (Héroux and Magnan, 1996; Cristo, submitted), or by laboratory experiments (Sardà and Valladares, 1990, Héroux and Magnan, 1996; Cristo, submitted).

The value of R used in this study is $R=0.177\ h^{-1}$. This was derived, for the same species, from the results of a field study conducted in the same area (Cristo submitted). As temperature and prey composition are the main factors affecting R (Elliot, 1972; Elliot and Persson, 1978; Bromley, 1994), and assuming these conditions are maintained, this value is appropriate.

The 3 most widely used models to calculate daily ration in fish are those of Eggers (1977, 1979) and Elliot and Persson (1978). These models were

successfully applied to decapod crustaceans by Maynou and Cartes (1997,1998), and can be expressed as:

Eggers (1977):

$$C_{(24E)} = F_{24}\, R\, 24 \qquad (1)$$

where F_{24} is the mean stomach fullness index over 24 h, as F_{wet}. This model assumes that the feeding periodicity is such that the fullness index at the beginning and at the end of a 24 h period are equal (Eggers, 1979, Boisclair and Leggett, 1988).

Eggers (1979): when this assumption cannot be met, Eggers (1979; see also Boisclair and Marchand , 1993) proposed the corrected model:

$$C_{(24EC)} = C_{(24E)} + (F_{t=24} - F_{t=0}) \qquad (2)$$

where $F_{t=24}$ and $F_{t=0}$ are the values of stomach fullness index as F_{wet} at the end and the beginning of the 24 h sampling period.

Elliot and Persson (1978): The food consumed during the time interval t_i is:

$$Ct_i = \frac{(Ft_i - Ft_0\, e^{-Rt_i})Rt_i}{1 - e^{-Rt_i}} \qquad (3)$$

and the daily ration is the summation, over 24 h, of the K time intervals considered:

$$C_{(24EandP)} = \sum_{i=1}^{K} Ct_i \qquad (4)$$

This model assumes, as do the others, that food evacuation is exponential and that the rate of food consumption within each sampling interval is constant. It does, however, have an important limitation: that time intervals should not be greater then 3 hours. With longer time intervals, we should bear in mind that estimates of daily ration tend to decrease.

In the calculation of daily ration, we used the fullness index F instead of the stomach content dry weight, after verifying that the relationship between wet body weight and dry stomach content weight is isometric for both sexes (see discussion in Héroux and Magnan, 1996).

Following Worobec (1984) the standard error of the Elliott and Persson model was computed. The same δ - method approximation was employed to compute the standard errors of the other two Eggers models. In all cases the standard errors can be considered as overestimated, since covariance was not included in the calculations - negative terms in all calculations according Worobec (1984)

RESULTS

The results of the 2-way ANOVA on stomach fullness indexes, with factors time of the day, sex and their interaction are presented in Table 2. For both sexes time of the day (TOW) and sex were significant. The interaction was not, meaning that males and females exhibit the same trends in stomach fullness along the day but with average values lower for males.

Table 2. Results of 2-way ANOVA. The response variable is the stomach fullness index (F) and the factors are time of the day, expressed by the variable TOW and sex. The interaction factor was also considered.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	7	2.41	0.34	7.72	0.0001
TOW	3	1.62	0.54	12.09	0.0001
SEX	1	0.74	0.74	16.68	0.0001
TOW*SEX	3	0.05	0.02	0.37	0.7768
Error	196	8.73	0.04		
Corrected Total	203	11.13			

Table 3. Mean stomach fullness (F) in g stomach content dry weight per 100 g lobster wet weight. Standard error in parentheses.

Haul	F for females	F for males
1	0.260 (±0.029)	0.167 (±0.027)
2	0.497 (±0.046)	0.366 (±0.056)
3	0.456 (±0.049)	0.288 (±0.039)
4	0.333 (±0.037)	0.239 (±0.032)
All hauls	0.396 (±0.023)	0.258 (±0.021)

As there are significant differences regarding fullness index between females and males, all the calculations were done separately by sex. Table 3 summarises the fullness index calculated per haul and for all hauls. Average values are also presented in Fig. 1.

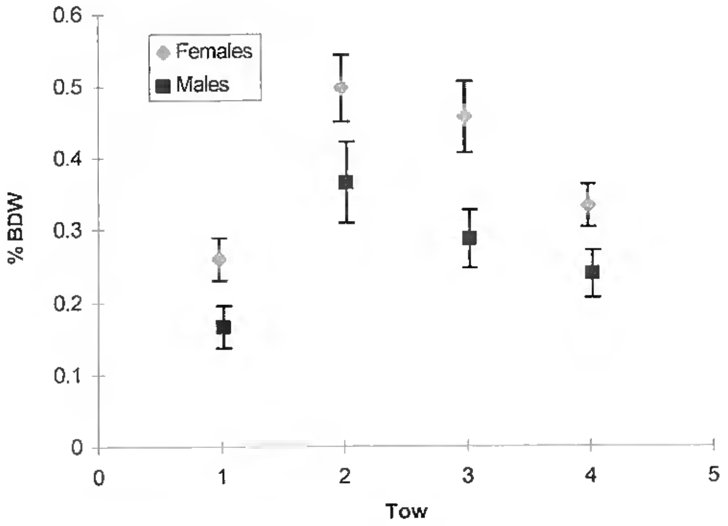

Fig. 1. Average fullness index values and standard errors for females and males per tow.

Fig.1 clearly shows that despite the absence of a period of no food consumption, there is an increase in the feeding activity corresponding to noon (2° haul), and that this activity decreases afterwards.

Table 4. Comparison of daily ration estimates in *Nephrops norvegicus* by 3 different models: $C_{(24E)}$ (Eggers, 1977); $C_{(24EC)}$ (Eggers, 1979) and $C_{(24EandP)}$ (Elliott and Persson, 1978); R=0.177 h^{-1} (Cristo, submitted). Values of C in g stomach content dry weight per 100 g lobster wet weight. Standard error in parentheses. Bold indicates the values of daily ration retained based on theoretical considerations of the models

Model	Daily ration for females	Daily ration for males
$C_{(24E)}$	**1.682 (±1.032)**	**1.098 (±0.899)**
$C_{(24Ec)}$	**1.755 (±1.058)**	**1.170 (±0.942)**
$C_{(24EandP)}$	1.642 (±0.743)	1.125 (±0.687)

The daily ration estimates by the 3 models presented, are given in Table 4. The Eggers's (1979) model estimates are the highest, and between the other

two models, Eggers's (1977) gives slightly higher values than Elliot and Persson's (1978) model. However the values are very similar among sexes, with females showing higher daily ration values than males.

DISCUSSION

Daily ration models, originally developed for fish are also applicable to decapod crustaceans (Maynou and Cartes, 1997; 1998). The estimates of daily ration resulting from the 3 models considered give similar values, despite the fact that they are based on different assumptions (Eggers, 1977; 1979; Elliott and Persson, 1978).

The limitations were mainly related with the operation procedures of the boat (see "Material and Methods"), It was, however, possible to make at least 4 tows, at critical hours of the day (Farmer 1974). Other authors have obtained reliable results with the same methodology using 5 tows per 24 hours(Maynou and Cartes, 1997, 1998).

However, given the previously discussed limitations and considerations, the values obtained by the two first models (Eggers, 1977; 1979) may be considered more appropriate.

The R value used in the 3 daily ration models, $R=0.177\ h^{-1}$ (Cristo, submitted), is very similar to the value used for daily ration estimates of *Aristeus antennatus* ($R=0.179\ h^{-1}$) (Maynou and Cartes, 1997) and is well within the range of the values used for other nine species of deep-water decapods (Maynou and Cartes, 1998) (R values between $0.150\ h^{-1}$ and $0.312\ h^{-1}$). The values used by these authors were recalculated from previously published data obtained from laboratory experiments (Sardà & Valladares, 1990) or based on the value of Rmax (Héroux & Magnan, 1996) (Rmax for *Gerion longipes*: 0.183).

However, the important consideration seems to be the fact, as pointed out by Bromley (1994), that whatever method is used, R values are similar because the temperature is the limiting factor.

It proved to be important to test sex influence on the index of stomach fullness, since different fractions of the population may have different daily

rations. In the case of *Nephrops norvegicus*, females at this time of the year (April), had a higher daily ration than males. An explanation for this may be the fact that this is a period of active growth in females (Gramitto, 1998), confirmed by the occurrence of gastroliths, precluding molting, which in turn increases the metabolic demands. Maynou and Cartes (1998) observed the same occurrence in *Munida tenuimana*, and they also justified this fact for the higher metabolic requirements active growth.

The occurrence of an increase in the feeding activity towards noon is well demonstrated both by the existence of a unimodal exogenous rhythm (Farmer, 1975) or by an endogenous rhythm (Atkinson and Naylor,1976).

Table 5. Comparison of daily-ration in F = (g stomach content Dry Weight /g Body Weight Wet) x 100 of *Nephrops norvegicus* with daily-rations obtained for other species. Sources: (1) Cristo and Encarnação 2000, (2) Sardà and Valladares 1990, (3) Maynou and Cartes 1997, (4) Maynou and Cartes 1998, (5) recalculated from Pakhomov and Perissinotto 1996.

	F	Source
Nephrops norvegicus females	1.642 - 1.755	This study
Nephrops norvegicus males	1.098 - 1.125	This study
Nephrops norvegicus (Min.- Max. values)	0.40 - 1.23	(1)
N. norvegicus (average values)	0.77 - 0.86	(1)
N. norvegicus (maximum food consumption)	0.86	(2)
A. antennatus (range of daily ration models)	0.130 - 0.223	(3)
Munida tenuimana females	0.610 ± 0.159	(4)
Munida tenuimana males	0.407 ± 0.143	(4)
Geryon longipes	0.065 ± 0.017	(4)
Polycheles typhlops	0.096 ± 0.043	(4)
Themisto gaudichaudi (field estimates)	4.5	(5)

Comparing our daily ration results, with previously published data, at similar temperature ranges — 13° C ± 0.5° (Maynou and Cartes, 1998) — (Table 5), we notice that: (1) field estimates of daily ration for *N. norvegicus* are higher than estimates obtained from laboratory experiments (Cristo and Encarnação, 2000); (2) our daily ration estimates are in generally higher than the estimated values found for other decapod crustaceans with a similar ecological niche (benthic, reptant decapods) (Maynou and Cartes, 1998).

The first difference may derive from the fact that, studies based on field sampling allow estimates of daily rations based on the natural diets, which are, in this case, very difficult to replicate in laboratory, due to the great natural

diversity in the diet of *Nephrops norvegicus* (Cristo and Cartes, 1998), and of course the conditions in which animals are in confined conditions with limited mobility, and under stress, certainly reduce food consumption.

Relative to the second point we have to bear in mind that these are values computed from only one survey, that need subsequent studies, since daily rations may vary greatly with season. However, the same methodology was followed by Maynou and Cartes, (1997; 1998) with consistent results, although somewhat contradictory to our findings.

According to these authors reptantian benthic species usually show low daily rations and high trophic diversity. According to our results *N. norvegicus,* though it is considered a reptant species presents a relatively low trophic diversity (H' = 2.02) (Cristo and Cartes, 1998), and a relatively high daily ration. Maynou and Cartes (1998) proposed a daily ration model at 13ºC, the same temperature at which our lobster were capture ($T=13^{\circ}C \pm 0.5$), that can be expressed as $DR=0.814 + 0.217CL/CW - 0.252H'$, in which DR is the daily ration, CL/CW the carapace length/carapace width ratio in mm and H' the Shannon-Weaver trophic diversity. According to this model the *N. norvegicus* daily ration is of DR=0.928 a value that is within the values calculated by the three methods (Table 4). Perhaps we can consider Norway lobster as an extreme species that compensates it's low trophic diversity and higher activity with a bigger consumption rate.

Further studies have to be developed on a wider spatio-temporal scale to have a better picture of the food consumption by deep sea crustaceans and to investigate metabolic rates among benthic crustaceans, as was done for fish (Koslow, 1996).

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FINAL CONCLUSIONS

After the extensive analysis of the diet of Nephrops norvegicus (L.), we can conclude that this species has a broad prey range, eating most things available in its surroundings.

The present work, that includes an extensive study of feeding habits of the Norway lobster in a wide geographic region of the Mediterranean basin and adjacent Atlantic, demonstrated that their diet is diversified, reflecting the diversity of the habitat in which they live. Norway lobsters are euriphageous and scavengers, and they may play an important role in the control of the effect of discards from crustacean fisheries. In their diet we can find endobenthic (*Glycera* sp), epibenthic (Echinoidea, Ophiuroidea, Holoturoidea, Brachiura), benthopelagic (*Pasiphaea sivado*), and planktonic organisms (Siphonophora). However, there are some preferred prey that dominate the diet in all the locations studied and regardless of season. They are: Crustaceans (peracarids, euphausids and decapods) and fish. All the additional prey groups, covering almost all the phyla in the animal kingdom, and even ocasionaly the plant matter reflect the variations of prey availability, which are partly dependent on seasonal, geographic and/or bathymetric factors.

In general, however, season and location in the Mediterranean area, are factors that do not influence the diet of the Norway lobster.

In females feeding is negatively influenced by egg bearing, and there are also significant differences in the feeding intensity between females in different maturity stages: females in state 3 and 4, show a higher percentage of empty stomachs. In males the feeding activity also decreases during the mating season.

Another important conclusion from this study is that there are, apparently no differences between male and female diet, translated by a very high overlap among male and female diets. However, we noticed same differences in the diet between size classes. These differences were not in the targeted preys, but rather the proportions in which the prey-groups appeared in the diet. There

seems to be a gradation between the diets of the various lobster sizes, with smaller lobsters eating smaller preys and larger lobsters preferring larger specimens.

Another aspect that can be drawn from this study is that the observed low female/male ratio in the fisheries can't be explained by the feeding behaviour alone, since no significant differences were detected in the feeding intensity between non ovigerous females and males. Other behaviour patterns need to be studied to fully comprehend the interactions male/female at the population level.

Gut evacuation rates in decapods can be determined through both laboratory and field experiments, and comparable results, are obtained, so long as the main limiting factor, temperature, can be controlled.

The evacuation rate of the Norway lobster is relatively high, with a turnover time of approximately 6 hours. However their metabolic rate must be low, since this species only has one daily period of higher feeding intensity, and can withstand long periods of starvation with no apparent physiological damage.

The daily ration with which they survive is proportionally higher for females than for males. However this observation has to be confirmed, since only one survey was conducted. This survey covered exactly the period of female gametogenesis, which is very demanding in terms of energetic requirements. So, other year periods should be covered, especially the egg bearing period and female post-moult period.

The apparently high daily ration, compared to other decapods, also needs to be confirmed with further surveys, using a more adequate methodology. Unfortunately, this could only be achieved with the back up of a research vessel, which is not available to our academic institution.

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2000

Trophic ecology of the Norway lobster *Nephrops norvegicus* (L.) (Crustacea: Nephropidae) in the Mediterranean and adjacent Atlantic: diets, evacuation rates and daily rations