

## Field estimation of daily ration of Norway lobster (*Nephrops norvegicus*) in the south of Portugal

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**Abstract** Daily ration estimates of Norway lobster (*Nephrops norvegicus*) from field samplings over a 24-h cycle were obtained. Four tows were conducted in the middle continental slope, off the south coast of Portugal. The results from Eggers (1977, 1979) and Elliot & Persson (1978) daily ration models were compared, by the Worobec  $\delta$ -method (1984), showing no significant differences among them. The estimates of food consumption obtained varied from 1.098 to 1.170 g dry food per 100 g body wet weight in males and 1.642 to 1.755 g dry food per 100 g body wet weight in females. Our results were compared with daily rations reported for other crustaceans. Daily ration values were compared and tested by a two-way ANOVA, with interaction, showing significant differences between sexes. This has been registered for other decapods and may be explained by a period of active growth in females, on the onset of vitellogenesis, increasing their nutritional/feeding needs.

**Keywords** daily ration; *Nephrops norvegicus*; feeding ecology

## INTRODUCTION

The Norway lobster (*Nephrops norvegicus* (L.)), is one of the dominant crustacean species in the continental shelf assemblages in the North Atlantic (Farmer 1975), at bathyal depths in the eastern Atlantic coast (Figueiredo 1988, 1989), the western Mediterranean (Abelló et al. 1988; Cartes et al. 1994), and the eastern Mediterranean (Frogliia & Gramito 1995). This is a species that has been widely studied in its different aspects of biology and fisheries (Figueiredo & Thomas 1967; Farmer 1975; Chapman 1980; Sardà 1995) but, as Sardà (1995) pointed out, feeding studies were poorly covered. For this reason the feeding ecology of *N. norvegicus* from the south coast of Portugal has been the subject of several recent studies (Cristo 1998, 2001; Cristo & Cartes 1998; Cristo & Encarnação 2000).

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

Decapod crustaceans are significant in this context because they play an important role in the structure of the food webs, making the link between macrofauna and megafauna top predators (Cartes & 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 *N. norvegicus*.

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

Results from feeding studies reveal that *N. norvegicus* feeds on a wide diversity of prey (Thomas & Davidson 1962; Lagardère 1977; Cristo 1998), presents median stomach fullness indices (Mytilineou et al. 1992; Cristo & Cartes 1998), and has lower evacuation rates compared with other decapods (Cristo 2001). The objective of our study was to estimate food consumption by *N. norvegicus* from the south of Portugal, based on daily ration models, as a quantitative complement to the feeding ecology studies of this important species.

## MATERIALS AND METHODS

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). These water masses correspond to the shallow core of MW, with temperatures that are constant and relatively high throughout the year:  $13^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$  (Ambar 1983).

### Data sampling and data treatment

This field experiment was conducted on a commercial trawler, in spring (26–27 April) 1999 at depths of 600 m in the vicinity of  $36^{\circ}45'\text{N}$ ,  $7^{\circ}50'\text{E}$ . 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 4–5 h were required to guarantee adequate sample sizes.

From each haul, a sample of c. 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 h. 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 two claws, so it is preferable to register the weight with no claws and then transform those values to wet weight with claws (WC), through linear regressions—

Female:  $\text{WC} = 1.1744 \text{ WNC} + 0.8898$  ( $r^2 = 0.9984$   $n = 30$ ); and

Male:  $\text{WC} = 1.4492 \text{ WNC} - 3.3001$  ( $r^2 = 0.9912$   $n = 44$ ).

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 h at  $60^{\circ}\text{C}$ . The stomach content dry weights (DW) were calculated by subtraction of the filter DW.

The gut fullness index is expressed as g dry food weight per 100 g lobster wet weight (%DW/WC). The stomach fullness index (F) was computed for each individual as (Maynou & Cartes 1998):

$$F_{\text{wet}} = (\text{g stomach content DW}) \times (100 \text{ g lobster WC})^{-1}$$

A two-way ANOVA with interaction was used to test the effect of sex and time of day on the stomach fullness ( $F_{\text{wet}}$ ).

### Daily ration models

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

Daily ration models are based on the assumption that gastric evacuation is an exponential decay

**Table 1** Trawl samples of *Nephrops norvegicus* collected for daily ration determination in the south off Portugal. (N, number of individuals analysed; CL, carapace length.)

Tow	Depth (m)	Start time (h GMT)	End time (h GMT)	N	Sex ratio (% females)	Size range (mm CL)		Mean weight (g)	
						Females	Males	Females	Males
1	578–615	5:30	9:30	52	40.4	31.5–48.1	31.9–53.9	36.52	58.43
2	578–639	10:45	15:15	51	50.9	32.8–46.3	35.5–56.6	35.00	68.37
3	547–617	17:15	21:15	52	59.6	30.2–47.2	31.4–51.2	33.04	52.71
4	594–637	22:45	4:15	49	53.1	30.8–47.0	32.3–52.5	35.60	56.14

function (Eggers 1977; Elliot & Persson 1978) which includes a constant for gastric evacuation rate ( $R$ ).

The  $R$  value can be obtained from the results of field experiments under certain conditions (Héroux & Magnan 1996; Cristo 2001) or by laboratory experiments (Sardà & Valladares 1990, Héroux & Magnan 1996; Cristo 2001).

The  $R$  value used in this study is  $R = 0.177 \text{ h}^{-1}$ . This was derived, for the same species, from the results of a field study conducted in the same area (Cristo 2001). As temperature and prey composition are the main factors affecting  $R$  (Elliot 1972; Elliot & Persson 1978; Bromley 1994), and assuming these conditions are maintained, this value is appropriate.

The three most widely used models to calculate daily ration in fish are those of Eggers (1977, 1979) and Elliot & Persson (1978). These models were successfully applied to decapod crustaceans by Maynou & Cartes (1997; 1998), and can be expressed as:

$$\text{Eggers (1977): } C_{(24E)} = F_{24} R \quad (1)$$

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

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

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

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

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

$$C_{t_i} = \frac{(F_{t_i} - F_{t_0} e^{-Rt_i}) R t_i}{1 - e^{-Rt_i}} \quad (3)$$

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

$$C_{(24E\&P)} = \sum_{t=1}^K C_{t_i} \quad (4)$$

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 than 3 h. With longer time intervals estimates of daily ration tend to decrease.

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

Following Worobec (1984) the standard error of the Elliott & Persson model was computed, using the  $\delta$ -method approximation. The same method was used to compute the standard errors of the other two Eggers models. In all examples the standard errors can be considered as overestimated, since covariance was not included in the calculations.

## RESULTS

The results of the two-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) was significant as were differences between sexes. The interaction was not, meaning that males and females exhibit the same trends in stomach fullness during the day but with average values lower for males (Fig. 1).

As there are significant differences regarding fullness index between females and males, all the

**Table 2** Results of two-way ANOVA. Response variable is the stomach fullness index ( $F_{\text{wet}}$ ) and the factors are time of the day (TOW) and sex. Interaction factor was also considered.

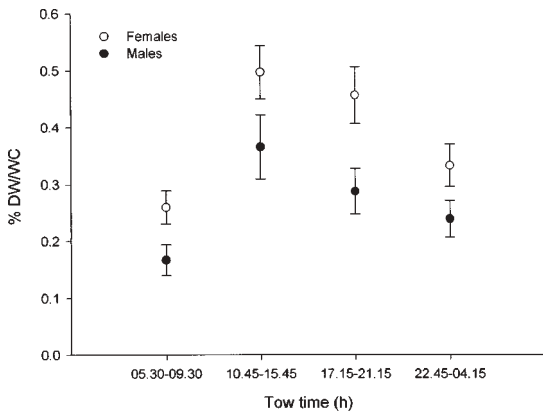
Source	d.f.	Sum of squares	Mean square	$F_{\text{wet}}$	$P > F$
Model	7	2.41	0.34	7.72	0.0001
TOW	3	1.62	0.54	12.09	0.0001
SEX	1	0.74	0.74	16.68	0.0001
TOW*SEX	3	0.05	0.02	0.37	0.7768
Error	196	8.73	0.04		
Corrected total	203	11.13			

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.

Figure 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.

The daily ration estimates calculated by the three 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 & Persson's (1978) model. However the values are very similar among sexes, with females showing higher daily ration values than males.



**Fig. 1** Average fullness index values and standard errors for females and males per tow (tow time in h GMT). (DW/WC, g stomach content dry weight per 100 g lobster wet weight.)

**Table 3** Mean stomach fullness ( $F_{wet}$ ) in g stomach content dry weight per 100 g *Nephrops norvegicus* wet weight. Standard error in parentheses.

Haul	$F_{wet}$ for females	$F_{wet}$ for males
1	0.260 ( $\pm 0.029$ )	0.167 ( $\pm 0.027$ )
2	0.497 ( $\pm 0.046$ )	0.366 ( $\pm 0.056$ )
3	0.456 ( $\pm 0.049$ )	0.288 ( $\pm 0.039$ )
4	0.333 ( $\pm 0.037$ )	0.239 ( $\pm 0.032$ )
All hauls	0.396 ( $\pm 0.023$ )	0.258 ( $\pm 0.021$ )

**Table 4** Daily ration estimates in *Nephrops norvegicus* by three different models:  $C_{(24E)}$  (Eggers 1977);  $C_{(24EC)}$  (Eggers 1979);  $C_{(24E\&P)}$  (Elliott & Persson 1978);  $R = 0.177 \text{ h}^{-1}$  (Cristo 2001). Values of C in g stomach content dry weight per 100 g lobster wet weight (% DW/WC). Standard error in parentheses. Bold indicates the values of daily ration based on theoretical considerations of the models.

Model	Daily ration	
	Females	Males
$C_{(24E)}$	<b>1.682 (<math>\pm 1.032</math>)</b>	<b>1.098 (<math>\pm 0.899</math>)</b>
$C_{(24EC)}$	<b>1.755 (<math>\pm 1.058</math>)</b>	<b>1.170 (<math>\pm 0.942</math>)</b>
$C_{(24E\&P)}$	1.642 ( $\pm 0.743$ )	1.125 ( $\pm 0.687$ )

**Table 5** Comparison of daily ration in %DW/WC (g stomach content dry weight per 100 g lobster wet weight) of *Nephrops norvegicus* with daily rations obtained for other species. (Sources: (1) Cristo & Encarnaçao 2000; (2) Sardá & Valladares 1990; (3) Maynou & Cartes 1997; (4) Maynou & Cartes 1998; (5) recalculated from Pakhomov & Perissinotto 1996.)

Species	Daily ration*	Experiment	Source
<i>Nephrops norvegicus</i> females	1.642–1.755	Field	This study
<i>N. norvegicus</i> males	1.098–1.170	Field	This study
<i>N. norvegicus</i> (min.–max. values)	0.40–1.23	Laboratory	(1)
<i>N. norvegicus</i> (range of average values)	0.77–0.86	Laboratory	(1)
<i>N. norvegicus</i> (max. food consumption)	0.86	Laboratory	(2)
<i>Aristeus antennatus</i>	0.130–0.223	Field	(3)
<i>Munida tenuimana</i> females	0.457–1.086	Field	(4)
<i>M. tenuimana</i> males	0.302–0.722	Field	(4)
<i>Geryon longipes</i>	0.054–0.061	Field	(4)
<i>Polycheles typhlops</i>	0.077–0.096	Field	(4)
<i>Themisto gaudichaudi</i> (average value)	4.5	Field	(5)

\*Range of daily ration models except were stated.

## DISCUSSION

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

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

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 three daily ration models,  $R = 0.177 \text{ h}^{-1}$  (Cristo 2001), is very similar to the value used for daily ration estimates of *Aristeus antennatus* ( $R = 0.179 \text{ h}^{-1}$ ) (Maynou & Cartes 1997) and is well within the range of the values used for nine other species of deep-water decapods (Maynou & Cartes 1998) (R values between 0.150 and  $0.312 \text{ h}^{-1}$ ). 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  $R_{\max}$  (Héroux & Magnan 1996) ( $R_{\max}$  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 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. *N. norvegicus* females at this time of the year (April) had a higher daily ration than males. The female reproductive season in this area starts in March and extends to October (Orsi Relini et al. 1998). During this period there is also an increasing percentage of gastroliths (Gramitto 1998), which precludes moulting, occurring once a year before mating. So, this is a high energy-demand period for females that may justify the increase in feeding activity. Maynou & Cartes (1998) observed the same occurrence in *Munida tenuimana*, and made the same justification for the higher metabolic requirements of active growth.

The occurrence of an increase in the feeding activity towards noon was also found by Aguzzi et

al. (2004). Coincidentally, those authors found a peak of emergence and a retrieve to their burrows during night time, also observed by Farmer (1975). This emergence cycle does not seem to be coupled to the peaks of endogenous rhythms of metabolism, demonstrated by Atkinson & Naylor (1976) and Aguzzi et al. (2004). Our interpretation is that the ingestion of prey is done outside the burrows and digestion inside, thus justifying the increase in oxygen consumption and cardiac rhythmicity. It is the metabolic process associated with digestion that appears to have an endogenous rhythm, whereas foraging activity is controlled by other factors of a more behavioural nature.

Comparing our daily ration results with previously published data at similar temperature ranges ( $13^{\circ}\text{C} \pm 0.5^{\circ}$ ) (Maynou & Cartes 1998) (Table 5), we noticed that: (1) field estimates of daily ration for *N. norvegicus* are higher than estimates obtained from laboratory experiments (Cristo & Encarnação 2000); and (2) our daily ration estimates are generally higher than the estimated values found for other decapod crustaceans with a similar ecological niche (benthic, reptant decapods, ex. *Aristeus antennatus*, *Munida tenuimana*, *Geryon longipes*, *Polycheles typhlops*) (Maynou & Cartes 1998).

The first difference may be because studies based on field sampling allow estimates of daily rations based on the natural diets which are, in this instance, very difficult to replicate in the laboratory, because of the natural diversity in the diet of *N. norvegicus* (Cristo & Cartes 1998). The animals are in confined conditions with limited mobility, and under stress which certainly may reduce food consumption.

Relative to the second point, these are values computed from only one survey, which need subsequent studies, since daily rations may vary greatly with season. However the same methodology was followed by Maynou & Cartes (1997, 1998) with consistent results, although somewhat contradictory to our findings. However those authors also compared daily rations from March and July, with consistent results. The question here is, "Does the geographic influence overcome the seasonal effect?" Only with daily ration studies covering all seasons can this question be answered.

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 & Cartes 1998), thus justifying the need of a relatively high daily ration. Maynou & Cartes (1998)

proposed a daily ration model at 13°C, the same temperature at which our lobsters were captured ( $T = 13^{\circ}\text{C} \pm 0.5$ ), that can be expressed as  $\text{DR} = 0.814 + 0.217\text{CL}/\text{CW} - 0.252\text{H}'$ , 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  $\text{DR} = 0.928$ , a value that is within the values calculated by the three methods (Table 4).

Further studies must be developed on a wider spatio-temporal scale to give 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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