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Gut evacuation rates in *Nephrops norvegicus* (L., 1758): laboratory and field estimates*

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SUMMARY: Estimates of gut evacuation rates of *Nephrops norvegicus* (Linnaeus, 1758) (Crustacea, Decapoda) 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 weight 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. The results obtained for both experiments are within the range of the values in the literature, even in the case in which different methodologies were used.

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, since the proportion of the various items in the diet may be affected by their different passage time through the gut (Joll, 1982; Sardà and Valladares, 1990). Evacuation rate is also a necessary parameter for estimating feeding rates (Bromley, 1987) and for evaluating daily rations in natural populations (Maynou and Cartes, 1997; 1998).

Gut evacuation rates have been mainly determined in fish, during either 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 have decapod crustacean gastric evacuation rates of different types of food been estimated and all these were obtained through 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; Kiørboe and Tiselius, 1987; Clarke *et al*, 1988; Dam and Peterson, 1988; Perissinotto and Pakhomov, 1996). However, to date, no studies have been conducted to determine *in situ* gut evacuation rates of deep water decapod crustaceans, mainly due to logistical constraints.

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 northeastern

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Atlantic and Mediterranean Sea (Udekem d'Acoz, 1999), based on field and laboratory observations, and to compare the results obtained by the two techniques.

MATERIAL AND METHODS

Field study

Norway lobsters, *N. norvegicus*, were collected off the south coast of Portugal, from a single trawl operation conducted from a commercial boat during July 1998 on fishing grounds at an average 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 randomly selected individuals, consisting of both males and females (Table 1), were killed by immersion in 10% buffered formalin. These were considered time 0 (T_0) individuals.

The remaining individuals were divided into 5 similar groups of 10 (Table 1) and placed in five insulated 60 l boxes with a lid and filled with sea water to minimise temperature changes. The boxes were kept on deck. The sea water temperature was lowered and maintained at 14ºC for the duration of the experiment, representing the average temperature at the depth of capture (Ambar, 1983). This relatively low temperature was achieved by means of ice packs to avoid any salinity change, and 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); 48 hours later, in the laboratory, they were transfered into 70º ethyl-alcohol. The biological sampling analysis included carapace length measurements (to the nearest 0.01 mm), sex determination and stomach removal (preserved in 70º alcohol).

Each of the 60 stomachs collected was cut open under a stereomicroscope. The content was then dispersed in distilled water and filtered through a predried 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 60ºC. The stomach content weights were calculated by subtraction of the filter dry weights (to the nearest 0.0001 g).

The trophic spectrum is dominated by decapod crustaceans, euphausids, peracarids and fish remains, and does not differ seasonally (Cristo, 1998).

Laboratory experiments

The Norway lobsters used in this experiment were also caught with bottom trawling off the south coast of Portugal during December 1997 at depths of about 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), with a temperature of 14ºC, salinity of 37‰, pH of 8, and constant levels of nitrites and ammonia (<0.2 mg/l). The acclimatisation period took several weeks, during which the lobsters were fed with 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 similar size ranges (Table 2). Each individual was kept in its own individual plastic compartment, with water flowing and circulating over all the compartments.

Before the experiment was carried out, the lobsters were starved for 8 days. The specific diet cho-

TABLE 1. – *Nephrops norvegicus*. Field study experiment: characteristics of Norway lobster groups; T_i, group slaughtered at time I; Sex ratio, male/female; CL, carapace length; s e, standard error.

Groups	Sex ratio	CL range (mm)	Mean CL (mm)	s e
T_0	4/6	32.81 - 48.93	37.15	1.49
T^1_2	6/4	31.86 - 46.91	39.72	1.94
$T^2_{3.5}$	4/6	29.81 - 50.08	37.69	1.63
T^5_7	4/6	32.15 - 46.64	39.95	1.53
	5/5	31.28 - 49.36	39.06	2.19
	6/4	28.46 - 46.50	38.18	1.17

TABLE 2. – *Nephrops norvegicus*. Laboratory experiment: characteristics of Norway lobster groups. T_i, group slaughtered at time i; sex ratio, male/female; CL, carapace length; s e, standard error.

Groups	Sex ratio	CL range (mm)	Mean CL (mm)	s e
T_0	9/1	26.20 - 42.92	35.16	1.76
$T^{0.5}_{0.5}$	6/4	27.09 - 42.41	35.97	1.60
T^1_2	7/3	27.88 - 43.96	36.47	1.61
$T^2_{3.5}$	9/1	27.92 - 43.14	36.30	1.52
T^5_7	7/3	28.30 - 44.10	37.07	1.54
	9/1	28.50 - 44.16	37.84	1.54
	5/4	29.03 - 47.67	38.55	1.86

sen was a small shrimp of the family Crangonidae *Palaemonetes varians*. This material was chosen considering that crustaceans are the main source 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, *P. varians* 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) and 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 feed avidly, 15 minutes after the shrimp had been supplied all the uneaten shrimp was removed from each compartment and stored separately prior to drying (at 60ºC for 48 hours) and weighing (to the nearest 0.0001 g). At this time, the first group of 10 individuals was sacrificed (in 10% buffered formalin) and this was considered the 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).

The method for accurately determining the stomach content dry-weight was the same as described for above 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, a value usually greater than 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. Therefore, the percentage of loss was determined by the analysis of the stomach content in the T_0 individuals. 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.

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 of *Nephrops norvegicus*. This approach has been widely use 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

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

or for the laboratory study

$$W_t = \frac{\text{W of stomach content}}{\text{(W of food supplied – W of food uneaten) Correction factor}} \text{ x } 100 \qquad (3)$$

RESULTS AND DISCUSSION

In field studies, since we have no possibility for determining 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 individuls 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 continous decrease over the duration of the experiment (Fig. 1). After 7 hours only aproximately 30% of the initial content remained in the stomach (Fig. 2).

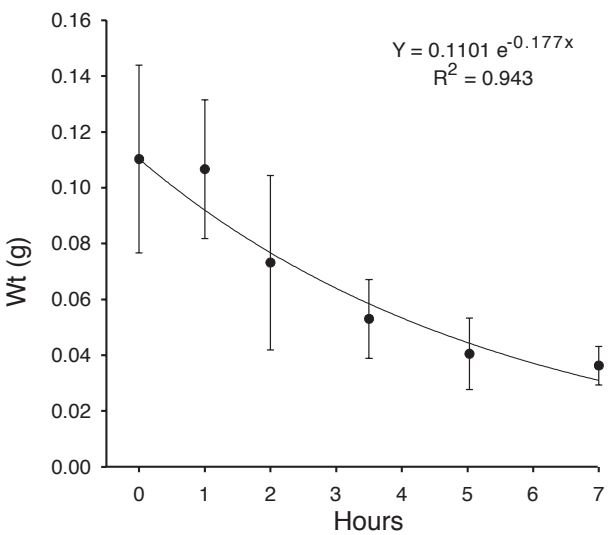

FIG. 1 – Field study. Exponential curve of decrease in the mean stomach contents (g) and standard errors over time in *Nephrops norvegicus*.

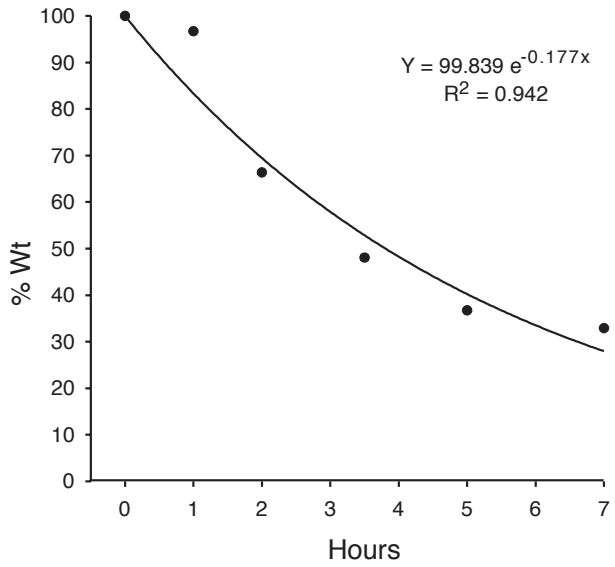

FIG. 2 – Field study. Exponential curve of the percentage of the mean stomach contents as a function of the initial content over time in *Nephrops norvegicus*.

The estimated instantaneous evacuation rate obtained was R = 0.177 h^{-1}, either using the approach of Equation 1 or Equation 2,
In the laboratory experiment, it was estimated that only 52% of the food ingested actually reached the stomach. The correction factor, CF = 0.52 was applied to all individual ingested food values in Equation 3.

The results from laboratory experiments are presented in Figures 3 and 4. The amount of food actually consumed was accurately determined for each group slaughtered.

The estimated instantaneous evacuation rate obtained was R = 0.172 h^{-1}, either using the approach of Equation 1 or Equation 3.

The instantaneous evacuation rate has often been estimated for fish through laboratory experiments (Brodeur and Pearcy, 1987; Amundsen and Klemetsen, 1988; Parrish and Margraf, 1990; Andrade *et al*, 1996). Though this laboratory methodology has been widely applied to marine invertebrates such as copepods, amphipods or euphausids (Kiørboe and Tiselius, 1987; Clarke *et al*, 1988; Dam and Peterson,1988; Perissinotto and Pakhomov, 1996), there have only been a few attemps to apply this methodology to decapod crustaceans (Hill, 1976; Joll, 1982; Sardá and Valladares, 1990).

This method assumes that laboratory conditions, starvation before feeding, and lack of prey diversity may have a limited effect on the evacuation rate (Héroux and Magnan, 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 limited to non-decapods such as copepods (Kiørboe and Tiselius, 1987; Dam and Peterson,1988), amphipods (Pakhomov and Perissinotto, 1996) or euphausids

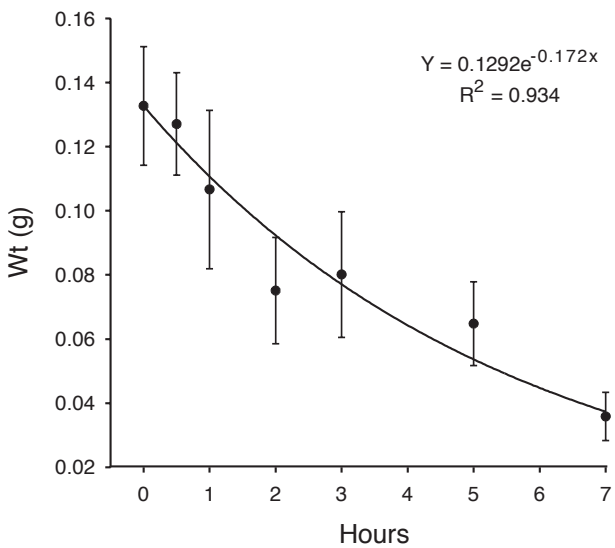

FIG. 3 – Laboratory experiment. Exponential curve of decrease in the mean stomach contents (g) and standard errors over time in *Nephrops norvegicus*.

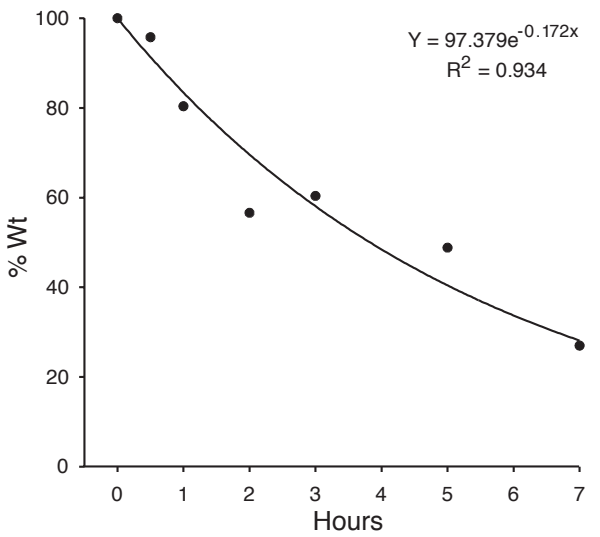

FIG. 4 – Laboratory experiment. Exponential curve of the percentage of the mean stomach contents as a function of the initial content over time in *Nephrops norvegicus*.

TABLE 3. – *Nephrops norvegicus*. Comparison of gut evacuation rates for different crustacean species (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.

	GER	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)

(Clarke *et al*, 1988; Perissinotto and Pakhomov, 1996). An alternative method for estimating 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 may have negligible effects on the 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 Magnan, 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 practically identical, suggesting that these are realistic values for the temperature considered (14ºC) (Elliott, 1972). In fact, both values must be considered as instantaneous evacuation rates for diets based on crustaceans, since for softer prey species this value can be higher (Sardà and Valladares, 1990)

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

From data collected in previously published studies on fish, Worobec (1984) and Pakhomov *et al*. (1996) established equations relating temperature T with gut evacuation rates R; For T = 14ºC, the same temperature at which these experiments were conducted, both Worobec's linear model (1984) and the power relation of Pakhomov *et al*. (1996) give R = 0.20 h^{-1}.

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