Field estimation of daily ration in deep-sea shrimp *Aristeus antennatus* (Crustacea: Decapoda) in the western Mediterranean

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ABSTRACT: Estimates of the daily ration consumed by the deep-sea shrimp *Aristeus antennatus* were obtained from 18 h of continuous trawl sampling conducted over the mid-slope (between 610 and 710 m depth) of the Catalan Sea (NW Mediterranean). This deep-sea environment is characterized by constant and relatively warm temperature ($13 \pm 0.5°C$) throughout the year. Two independent daily-ration estimates were produced: First, an actual daily ration was obtained by computing the weight of the fresh food items, yielding a value of 2.588 g wet food weight per 100 g shrimp wet weight. Second, the daily ration was estimated by the models of Eggers and Elliot & Persson. Daily rations for *A. antennatus* computed from these models ranged between 1.666 ($\pm$1.193) and 2.315 ($\pm$0.924) g wet food weight per 100 g shrimp wet weight, or between 0.130 ($\pm$0.115) and 0.223 ($\pm$0.091) g dry food weight per 100 g shrimp wet weight. The results of the 3 daily-ration models were compared and tested by bootstrapping; they did not differ significantly. Our results are compared with daily rations reported for other marine organisms. The feeding ecology of *A. antennatus* is discussed in relation to the food-limited deep-sea environment which this shrimp inhabits.

KEY WORDS: Daily ration · *Aristeus antennatus* · Feeding ecology · Deep-sea ecology

INTRODUCTION

In the last 2 decades, models based on the daily-ration concept have been used to determine the amount of food consumed by marine organisms, especially fish, in natural conditions (Durbin et al. 1983, Worobec 1984, Macpherson 1985, Pakhomov et al. 1996). This methodology has seldom been applied to crustaceans in the field (Pakhomov & Perissinotto 1996, Perissinotto & Pakhomov 1996) or in the laboratory (Yamashita et al. 1984, Sardà & Valladares 1990). The results derived from these studies are of interest in the fields of trophic ecology and in autoecological studies, such as predation pressure on prey species or impact of environmental modifications (Héroux & Magnan 1996). The daily-ration models were developed in fish species and these have been the subject of most studies available in the literature. The only works addressing food consumption and evacuation rates in decapod

crustaceans (Hill 1976, Sardà & Valladares 1990) were conducted in laboratory conditions.

Despite the general consideration that food availability is the main limiting factor in deep-sea environments (Gage & Tyler 1991), quantitative studies on food consumption at bathyal and abyssal depths are non-existent, probably due to the difficulty in obtaining near-continuous samples in deep-sea environments. Only Macpherson (1985) in the field and Sardà & Valladares (1990) in the laboratory have worked on deep-water species dwelling on the upper slope, a depth stratum still strongly influenced by surface primary production. Estimates 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.

Attempts to estimate daily rations in decapod crustaceans in the field have not been undertaken until now. Here we assess the applicability of daily-ration models to the deep-water shrimp *Aristeus antennatus*, the widely dominant decapod crustacean species in

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the mid- to lower-slope megabenthic communities in the Catalan Sea (NW Mediterranean) (Cartes & Sardà 1992, Cartes et al. 1994). In this area, both studies on the depth distribution of megabenthic biomass (Stefanescu et al. 1992, Cartes & Sardà 1992), and detailed studies on dietary preferences in the dominant decapod species (Cartes in press) have been performed.

The biology and ecology of *Aristeus antennatus* have been studied in detail (Sardà & Demestre 1987, Demestre 1990, Cartes 1994) in relation to depth, size composition and seasonality. Results from feeding ecology studies reveal that *A. antennatus* feeds on highly diverse prey and has higher stomach fullness indices than other decapods in the bathyal environment (Cartes in press), indicating that it is a highly predatory and active species, feeding continuously (Cartes 1993). This study complements quantitatively other studies on the feeding ecology of this important species.

MATERIALS AND METHODS

Sea sampling. Sampling was performed over an 18 h period in the Catalan Sea (NW Mediterranean) over the mid-slope depth stratum. Five trawl locations were selected in the vicinity of 41° 07' N, 02° 03' E, at depths varying from 610 to 710 m on commercial fishing grounds. Trawling started at 17:30 h on 13 July 1989 and ended at 11:05 h of the following day. Previous studies indicate that the maximum feeding activity in *Aristeus antennatus* occurs towards dusk and at night (Lagardère 1972, Cartes 1993), thus our 18 h cycle probably approximates a 24 h cycle. Temperature in Mediterranean deep waters is constant and relatively high throughout the year: $13 \pm 0.5°C$ below 200 m depth (Hopkins 1985).

A total of 311 individuals were caught in the 5 trawl hauls (between 60 and 70 individuals per haul). Cephalothorax length (CL) and wet weight of individuals were measured. Size varied from 17.2 to 59.9 mm CL, although practically all individuals were adults (sexual maturity is reached at CL between 21 and 26 mm; Demestre 1990). Between 30 and 36 individu-

als were randomly selected from each sample and prepared for stomach contents analysis, amounting to a total 165 stomachs analysed (Table 1). Stomachs were removed and their wet weight after blotting measured. The stomachs were later taken to the laboratory and dried in an oven at 100°C for 24 h to obtain dry weight. The gut fullness index is expressed in 2 ways, for comparative purposes, throughout this article: as g wet food weight per 100 g shrimp wet weight (%BW Wet) and as g dry food weight per 100 g shrimp wet weight (%BW Dry). The stomach fullness index was computed for each individual as (Héroux & Magnan 1996):

%BW Wet = (g stomach wet weight/
          g shrimp wet body weight) × 100

%BW Dry = (g stomach dry weight/
          g shrimp wet body weight) × 100

The diet composition was analysed in the remaining stomachs in each sample (complete results in Cartes 1993). The wet weight of the non-digested prey items in each stomach was calculated using data from parallel samplings of macrofauna (suprabenthos and infauna) collected in the same area. For each prey taxon, a sufficient number of prey items corresponding to those size classes preyed upon by *Aristeus antennatus* were selected and weighed after blotting for 20 min. The sum of all non-digested prey in %BW Wet was used as an estimate of the food consumed during the sampling period. In this study, we term this independent estimate of the actual food consumed over the study period the 'actual daily ration'.

Models of daily ration. The methods and models for the determination of daily ration in fish are reviewed in Héroux & Magnan (1996). At present, the exponential model of food evacuation is well established and justified in the literature, although other models have been proposed (Macpherson et al. 1989, Bromley 1994).

Models of daily ration require an estimate of R, the gastric evacuation rate. The value of R can be obtained in the field under certain conditions or by starvation experiments in the laboratory (Hill 1976, Sardà & Valladares 1990, Héroux & Magnan 1996). For *Aristeus antennatus*, and for most species of deep-sea animals,

Table 1. Trawl samples of *Aristeus antennatus* retained for food consumption analysis between 13 and 14 July 1989 in the Catalan Sea (NW Mediterranean). N: number of individuals analysed

Haul ID	Depth (m)	Start time (h GMT)	End time (h GMT)	N	Size range (mm CL)	Sex ratio (% males)	Mean weight (g)
dn1/1	651–710	17:30	19:45	33	25.2–59.9	21.5	29.892
dn1/2	641–706	21:43	23:51	33	20.4–54.1	44.1	17.386
dn1/3	637–655	01:35	03:46	30	20.1–54.1	30.6	17.466
dn1/4	675–728	05:23	07:26	33	17.2–44.5	37.6	14.816
dn1/5	610–646	08:40	11:05	36	19.6–53.9	32.4	18.752

it is impossible to undertake this kind of experiment in the laboratory. Thus, an independent estimate of R must be obtained. Drawing from conclusions by other authors (Elliott & Persson 1978, Bromley 1994), R is unaffected by predator or prey size, meal size and feeding frequency, whereas it is affected by the composition of food prey but mainly by water temperature (Elliott & Persson 1978). A number of empirical equations for relating temperature (T) and R in fishes can be found in the literature (Durbin et al. 1983, Worobec 1984, Pakhomov et al. 1996). With $T = 13°C$, the exponential relation of Durbin et al. (1983, their Eq. 3) yielded $R = 0.172$ h^{-1}, the linear relation of Worobec (1984, her Fig. 1) yielded $R = 0.183$ h^{-1}, and the power relation of Pakhomov et al. (1996, their Table 2) yielded $R = 0.192$ h^{-1}. The experimental value of R recalculated from data in Sardà & Valladares (1990) in their study of *Nephrops norvegicus*, at $T = 13°C$, was $R = 0.179$ h^{-1}, which is well within the range of the other estimates. We took this last value as appropriate in our computations of daily-ration estimates because *N. norvegicus* is, like *A. antennatus*, a species feeding on a wide variety of prey (Lagardère 1977), dwelling in similar environmental conditions, and sometimes coexisting with *A. antennatus*, and subject to the same temperature regime.

An attempt to estimate R from our experimental data set following the method used to obtain R_{max} in Héroux & Magnan (1996) failed because we could not meet the assumptions of identifying a period of minimum or no feeding in *Aristeus antennatus*.

The 3 more widely used models to compute the daily ration in fish are the Eggers (1977, 1979) and Elliott & Persson (1978) models, briefly summarized as follows (see also Eggers 1977, 1979, Elliott & Persson 1978, Bromley 1994, Héroux & Magnan 1996).

– *Eggers (1977)*:

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

where $C_{(24E)}$ is the daily-ration estimate, and F_{24} is the mean stomach fullness index over a 24 h period, in %BW Wet or %BW Dry. This model assumes that the weight of the stomach contents does not change between the beginning and the end of the study period.

– *Eggers (1979)*: When the last assumption cannot be met, Eggers (1979) proposed the corrected model:

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

where $C_{(24EC)}$ is the corrected daily-ration estimate, and $F_{t=24}$ and $F_{t=0}$ are the values of the stomach fullness index at the end and at the beginning of the sampling period, respectively.

– *Elliott & Persson (1978)*: The food consumed during the time interval t_i is:

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

and the daily ration estimate, $C_{(24E\&P)}$, is the sum of Eq. (3) over the K time intervals considered:

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

The assumptions of the Elliott & Persson model is that food evacuation is exponential and that the rate of food consumption within each sampling interval is constant. Both assumptions are probably met in *Aristeus antennatus*, but should be checked for other crustaceans, especially those showing marked feeding peaks.

We used the stomach fullness index F (as %BW Wet or %BW Dry) after verifying that stomach weight varies isometrically with body weight (see discussion in Héroux & Magnan 1996).

Following Héroux & Magnan (1996) we used bootstrap simulations to approximate the standard error of each daily-ration estimate ($C_{(24E)}$, $C_{(24EC)}$ and $C_{(24E\&P)}$). For each of the 3 models, values of F (%BW Wet and % BW Dry) were selected at random with replacement a large number of times (10 000) to generate a distribution of each daily-ration estimate, following Eqs (1) to (4). The standard deviation of the 10 000 simulated values are a close approximation to the daily-ration estimate's standard error (Manly 1991, 1992). In addition, the bootstrap procedure was used to generate the distribution of differences between $C_{(24E)}$ and $C_{(24EC)}$, between $C_{(24E)}$ and $C_{(24E\&P)}$, and between $C_{(24EC)}$ and $C_{(24E\&P)}$. Then the observed difference between any pair of estimates was tested against the distribution of differences, by the approximate 2-sided t-test described in Manly (1991, 1992). Two estimates of daily ration were considered significantly different ($\alpha < 0.05$) if their difference laid outside the central 95% values of the generated distribution of differences (Manly 1991, 1992). An alternative way to compute the standard error of the Elliott & Persson model, not employed in the present work, is the δ-method approximation, given in Worobec (1984).

RESULTS

Mean fullness (in %BW Wet and %BW Dry) for each haul is given in Table 2. A t-test of difference between each consecutive pair of hauls was not significant for any pair of samples in %BW Wet or %BW Dry. Thus, although fullness (% BW Wet) is highest for the second haul sample it is not different from the first and third sample (Table 2), indicating that the slight dusk-night transition feeding peak does not invalidate the basic assumptions of the daily-ration models considered here. However, the difference in fullness between the

Table 2. Mean stomach fullness (F) in g wet food weight per 100 g shrimp wet weight (%BW Wet) and g dry food weight per 100 g shrimp wet weight (%BW Dry). SD given in parentheses

Haul ID	F (%BW Wet)	F (%BW Dry)
dn1/1	0.587 (0.266)	0.066 (0.024)
dn1/2	0.639 (0.330)	0.056 (0.028)
dn1/3	0.571 (0.311)	0.052 (0.034)
dn1/4	0.442 (0.285)	0.037 (0.027)
dn1/5	0.376 (0.199)	0.031 (0.024)
All hauls	0.540 (0.303)	0.052 (0.030)

first and the fifth samples (Table 2) was significant (t-test, p < 0.01 for both %BW Wet and %BW Dry).

The composition of the undigested food items consumed by *Aristeus antennatus* is summarized in Table 3. The diverse prey items are pooled into 5 broad categories, in relation to their taxonomic position, size and soft/hard structure. For more detailed results see Cartes (1993). The total prey consumed in the study period was projected to an actual daily ration of 2.588 %BW Wet.

The daily-ration estimates along with standard errors computed by the models discussed in the 'Material and methods' section are given in Table 4. The estimates by Eggers' (1977) model are higher than the estimates by Eggers' (1979) model, and these in turn are higher than the estimates by Elliott & Persson's (1978) model, both for %BW Wet and %BW Dry. However, the differences in the estimates are not significant (p > 0.05) by the approximate t-test on the distribution of differences generated by bootstrapping.

DISCUSSION

A considerable number of studies using daily-ration models were based on data obtained in the laboratory, and this is particularly the case in decapods (Hill 1976,

Sardà & Valladares 1990). Studies based on field samplings have the advantage of working in the same environmental conditions in which the species lives. Field samplings also allow estimates of daily rations based on natural diets, which are difficult to replicate in the laboratory for deep-sea species or species feeding on a variety of prey items.

Daily-ration models are adequate and applicable to decapod crustaceans for field determination of food consumption. The choice of the model (Eggers 1977, Eggers 1979 or Elliott & Persson 1978) seems to have little relevance with regard to the results, as shown in this study or in Héroux & Magnan (1996). Furthermore, our estimate of actual daily ration, computed from the weights of undigested prey items in the stomachs, lies well within the confidence intervals of the daily-ration estimates by the 3 models employed. On the other hand, the models of Eggers (1979) and Elliott & Persson (1978) are satisfactory for a continuously feeding species, such as *Aristeus antennatus*, but for other species of decapod crustaceans with marked feeding rhythms (e.g. Pasipheidae or *Plesionika martia* in our study area) other models might be more adequate, such as the model of Diana (1979), as discussed in Macpherson (1985).

Comparing our results of food consumption in *Aristeus antennatus* with daily rations for other species reported in the literature (summarized in Table 5) some aspects are worth noting. The maximum daily ration of *Nephrops norvegicus* (2.5 %BW Wet, recalculated from Sardà & Valladares 1990), a slow-moving decapod species of the upper slope, is within the range of daily-ration estimates computed for *A. antennatus*. However, that value is probably an overestimation of the natural food consumption in *N. norvegicus*, as the experiments were performed in the laboratory under excessive food supply and the animals were fed a diet far from their natural diet. Natural food consumption in *N. norvegicus* (and other Nephropidae) must be considerably lower than the value reported by Sardà & Valladares (1990), considering the high proportion of

Table 3. Fresh food items (in g) consumed by *Aristeus antennatus* (165 individuals) over the study period. Large crustaceans include chiefly *Calocaris macandreae* and natantian decapods. Most small crustaceans are the isopod *Cirolana* and to a lesser extent, Gammaridean amphipods. Molluscs are composed mainly of the bivalve *Abra*. Total %BW Wet for the 18 h sampling period and projected for 24 h are shown

Haul ID:	dn1/1	dn1/2	dn1/3	dn1/4	dn1/5	All hauls Total 18 h	Total 24 h
Polychaetes	0.728	0.028	–	–	–		
Large crustaceans	–	0.447	0.354	0.654	0.746		
Small crustaceans	3.104	1.961	1.051	1.028	0.578		
Molluscs	0.139	0.356	0.279	0.080	0.063		
Fish remains	0.362	–	–	0.362	0.362		
Total (g)	4.333	2.792	1.684	2.124	1.749		
Total (%BW Wet)	0.439	0.487	0.321	0.434	0.259	1.941	2.588

Table 4. Comparison of daily-ration estimates in *Aristeus antennatus* by 3 different models: $C_{(24E)}$ (Eggers 1977), $C_{(24EC)}$ (Eggers 1979), $C_{(24E\&P)}$ (Elliott & Persson 1978); ± 1 SE in parentheses. Estimates are not significantly different (p > 0.05) by the approximate *t*-test discussed in the 'Materials and methods'. $R = 0.179\ h^{-1}$ (recalculated from Sardà & Valladares 1990). Values of *C* are in g wet weight per 100 g shrimp wet weight (%BW Wet) and g dry weight per 100 g shrimp wet weight (%BW Dry). The values of *C* in %BW Wet are to be compared with the estimate of actual ration 2.588 %BW Wet (Table 3)

Model	%BW Wet	%BW Dry
$C_{(24E)}$	2.315 (±0.924)	0.223 (±0.091)
$C_{(24EC)}$	2.034 (±1.024)	0.177 (±0.102)
$C_{(24E\&P)}$	1.666 (±1.193)	0.130 (±0.115)

empty stomachs reported by different authors from field samplings (Lagardère 1977, Wassenberg & Hill 1989, Mytilineou et al. 1992, authors' unpubl. data) and by the ability of *N. norvegicus* to survive extended periods of starvation in captivity (Farmer 1975).

As a representative of a faunal type adapted to a food-limited environment (Gage & Tyler 1991), *Aristeus antennatus* is probably atypical among deep-water decapods and is probably a species with one of the highest daily rations within the benthic bathyal decapod communities in the Mediterranean. The remaining co-existing decapod species (e.g. *Plesionika martia*, *Plesionika acanthonotus*, *Acanthephyra eximia*) show clearly higher proportions of empty stomachs (Cartes in press). However, a low proportion of empty stomachs is generally found in other deep-water Penaeoidean shrimps, such as *Solenocera membranacea* and *Parapenaeus longirostris* (Cartes 1995), indicating probably high daily rations for this group. The high metabolic rates demonstrated for *A. antennatus* (Company 1995) could be a source of evidence for this.

Our results yielded daily-ration estimates higher than those reported by Macpherson (1985) for piscivorous demersal fish over the upper slope off Namibia at $T = 8.0$ to 10°C (Table 5). Our results are comparable to the daily-ration estimates by Worobec (1984) for winter flounder in a southern New England (USA) salt pond at temperatures varying from 6.5 to 22.0°C within an annual cycle (Table 5). It is interesting to note that the diet composition of winter flounder (small crustaceans, polychaetes, and to a lesser extent, tunicates and molluscs) has a similar diversity of prey categories as our shrimp species (Cartes 1993). Our estimates of daily ration were lower than the estimates by Tudela & Palomera (1995) for European anchovy ($T > 20$°C), both in %BW Wet and %BW Dry, or Héroux & Magnan (1996) for brook charr in an oligotrophic lake ($T = 17.8$ to 19°C) in Quebec, Canada (Table 5). The daily rations for the Antarctic amphipod *Themisto gaudichaudi* computed by Pakhomov & Perissinotto (1996) under laboratory conditions and from field estimates ($T < 10$ °C) are 1 to 2 orders of magnitude higher than ours (in %BW Dry; Table 5).

Ignoring the uncertain influence of temperature at which these estimates were obtained, and bearing in mind the limitations of the data set presented here, a global comparison of the daily-ration estimates available can be advanced. We hypothesize that epi- and mesopelagic species, with clear migratory and feeding diel cycles, have higher daily rations than benthic (and nektobenthic) species. In the same way, species lower on the trophic chain (amphipods and anchovy feeding on mesozooplankton) would have higher daily rations (in relative terms to body weight) than predators higher on the trophic chain. Thus, *Aristeus antennatus* would be positioned at an intermediate level, as a benthic but mobile species that preys on detritivores or small predators occupying a lower position in the benthopelagic food chain.

Table 5. Comparison of daily-ration estimates for *Aristeus antennatus* with daily rations obtained in other species. Sources: 1: Sardà & Valladares (1990); 2: recalculated from Pakhomov & Perissinotto (1996); 3: Héroux & Magnan (1996); 4: Worobec (1984); 5: recalculated from Tudela & Palomera (1995); 6: Macpherson (1985)

	%BW Wet	%BW Dry	Source
Aristeus antennatus (actual ration)	2.588	–	This study
A. antennatus (range of daily–ration models)	1.666–2.315	0.130–0.223	This study
Nephrops norvegicus (maxiumum food consumption)	2.5	–	(1)
Themisto gaudichaudi (field estimates)	–	4.5	(2)
T. gaudichaudi (laboratory experiments)	–	5.2–13.4	(2)
Brook charr	–	0.42–0.62	(3)
Winter flounder (range for 1 yr)	1.27–3.31	–	(4)
European anchovy	3.70–3.92	0.58–0.61	(5)
Coelorhynchus fasciatus (range for 2 yr)	0.55–1.30	–	(6)
Helicolenus dactylopterus (range for 2 yr)	0.07–0.46	–	(6)
Lophius upsicephalus (range for 2 yr)	0.55–1.60	–	(6)

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