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RESEARCH ARTICLE

J. Aguzzi · J. A. Cuesta · M. Librero · J. Toja

Daily and seasonal feeding rhythmicity of *Palaemonetes varians* (Leach 1814) from southwestern Europe

Abstract The feeding activity rhythm of *Palaemonetes varians* (Leach 1814) was studied by collecting stomachs over a 24-h cycle in four different seasons of 1996 and spring–summer of 1997 to assess a regulation of this behaviur dependent upon seasonal variations in photo-period length. A total of 6,692 stomachs were collected from a population reared in an extensive earthen pond located in the Guadalquivir Estuary salt marshes (Spain). Stomach fullness (*f*) classification was performed with a stereomicroscope by means of a four-point visual quali-tative scale. Results showed that a high proportion of stomachs were empty in all seasons considered and a great variability in the data occurred irrespective of the time of the day. The number of full stomachs at each catch were represented over 24-h for each sampling sea-son. Time series showed the occurrence of a feeding activity rhythm phased at day–night transitions. The sunset peak occurred in all months of sampling, while the sunrise one occurred in summer. Results are discussed in relation to available data on behavior, moulting, and reproduction of this and other species of the same genus.

J. Aguzzi (✉)
Neuroscience Institute, Morehouse School of Medicine,
720 Westview Drive, S.W. Atlanta,
GA 30310, USA

J. A. Cuesta
Instituto de Ciencias Marinas de Andalucìa (CSIC),
Avenida Republica Saharaui, 2-11510 Puerto Real (Cádiz),
Spain

M. Librero · J. Toja
Departamento de Ecología, Facultad de Biología de Sevilla,
Universidad de Sevilla, Apdo 1095,
41080 Sevilla, Spain

Present address: J. Aguzzi
Insitut de Ciencies del Mar (ICM-CSIC),
Passeig Maritim de la Barceloneta 37-49, 08003 Barcelona, Spain
E-mail: jaguzzi@cmima.csic.es

Introduction

The brackish water shrimp, *Palaemonetes varians* (Leach 1814), is present in salt marsh areas of north European coasts in Norway (Dolmen 1997), Scotland (e.g., Moyse and Smaldon 1990), and Portugal (Neves 1973), down to the Mediterranean basin, including southwestern Spain (García-Raso and Manjón-Cabeza 1996) and Morocco (Holthuis 1987). Individuals of this species inhabit inland coastal ponds, characterized by stagnant, highly turbid water, with broad seasonal variations in salinity and temperature (Healey 1995); hence they show a high tolerance of hypoxia (Nielsen and Hagerman 1998). In southwestern Spain this species is reared in extensive culture ponds due to its resistance to environmental stress and high economical value.

The ecological importance of the species for coastal ecosystems involves its feeding habits. Like all other species of the genus, *P. varians* eats a wide variety of aquatic foods. Because it is a detritivor, it contributes to the mechanical breakdown of refractory organic matter such as plant fibers, and at the same time, it is a primary and a secondary consumer (Escaravage and Castel 1990). Active predation is performed by assimilating microfauna (e.g., nematodes, polychaetes, motile mys-ids, and mosquito larvae) in the entire water column (Anderson 1985; Roberts 1995). Regarding its ecological role, the species is an important element in the trans-ference of nutrients and energy among various tropic levels of coastal ecosystems.

Up to date, only a few reports have been published on the behavioral rhythmicity of *P. varians*, indicating periods of activity at sunset and sunrise (Antheuisse et al. 1971; Bouchon 1991). Owing to its growing eco-nomical importance for aquaculture (e.g., Domingues et al. 2003) and ecotoxicology (e.g., Boisson et al. 2003), methods of population sampling should consider rhythmic behavior as a source of bias in an animal's capture. Captures may vary depending on the hour of

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the day and the day of the season. In the present study, *P. varians'* rhythmic behavior was studied in relation to its feeding activity. The change in stomach fullness was examined over a 24-h period in four different seasons to assess a regulation of feeding behavior upon variations in photoperiod length.

Materials and methods

Sampling

The studied population was located in an earthen pond of 1 km^2 area, belonging to the aquaculture enterprise Pesquerias Isla Mayor, S.A. (PIMSA) located at "Veta de la Palma" (Isla Mayor, Seville, Spain) (6°14′W 36°57′N). Ponds were provided by a system of side channels, allowing the renovation of water coming from the Guadalquivir estuary. However, hydrodynamism inside the pond was very low, but high turbidity in water occurred owing to the effect of wind. Marked seasonal variations in salinity (from 10–15 ppm in winter to 20–25 ppm in summer) and dissolved oxygen (PIMSA, unpublished data) were also recorded. These environmental conditions allowed the extensive culturing of *P. varians* as well as other species of fish of economical value (polyculture).

For the purpose of the present study, sampling was carried out by means of a hand net (100 μm mesh size) mounted on a 2-m stick. Samples were obtained by towing the hand net on bottom surface areas near the pond margins. We chose sampling areas of maximum commercial capture by creeling, since animals usually roam along margins to feed when they are active. Animals were collected at 1-h time interval over 24-h in months corresponding to four different seasons of 1996: in February (the 13th), in April (the 17th), in July (the 13th), and November (the 10th). Sampling was replicated focusing on the spring–summer months of the following year (1997), since during these seasons moulting and reproduction might affect feeding behavior (Bouchon 1991). Months of sampling were: April (the 18th), June (the 16th), and finally July (the 12th).

At each catch, almost 40 individuals were randomly selected. They were immediately dissected and their stomachs were removed, conserved into plastic vials and immediately frozen at −20°C and stored at that temperature until laboratory analysis.

Out of 6,692 stomachs analyzed in the present study, almost 960 were collected at each sampling season (see Table 1). Stomachs were dorsally opened and a degree of stomach fullness (*f*) was visually estimated with a stereomicroscope, following a four-rank qualitative scale: "empty" (*f* = 0–25%), "nearly empty" (*f* = 25–50%), "nearly full" (*f* = 50–75%) and "full" (*f* = 75–100%) (partially modified from Cartes 1993; Maynou and Cartes 1998; Bernárdez et al. 2000; Aguzzi et al. 2004c). The estimation of a degree in stomach fullness

Table 1 *Palaemonetes varians*, total number (N_{tot}) of stomachs analyzed at each sampling season over a 24-h cycle

	N_{tot}	N_d	N_n	Sunset	Sunrise
1996					
February	952	477	475	19:00	6:00
April	960	520	440	21:00	7:00
July	951	591	360	22:00	6:00
November	959	439	520	19:00	7:00
1997					
April	960	520	440	21:00	7:00
June	950	590	360	22:00	6:00
July	960	600	360	22:00	6:00

Sunset and sunrise timing is reported for each month of sampling. N_d; N_n, total numbers of stomachs analyzed during the day (N_d) and the night (N_n), respectively

by means of the *f*-scale relies on visual classification, thus presenting a certain intrinsic degree of subjectivity. To reduce to the minimum possible bias in measurements due to this subjectivity, all records were always taken by the same person (Aguzzi et al. 2004c). Additionally, it should be noted that the scale extremes could not be confused (Cartes 1993; Aguzzi et al. 2004c).

Feeding rhythmicity

The generalist feeding profile of the *Palaemonetes* species suggests that the feeding rhythmicity is usually difficult to estimate since stomach contents are mixed with variable augments of substrate particles, ingested at any time of the day (Anderson 1985). A preliminary data survey from all records by computing a fullness average at each catch did not show any discernible feeding rhythmicity, due to the high heterogeneity of data. Conversely, the binning of the number of stomachs of two adjacent *f*-ranks (i.e., 50–75% and 75–100%) at each catch allowed the definition of clearer feeding patterns, since this was based on more homogeneous data. Hence, time series as numbers of stomachs ranking into *f* = 50–100% per catch were represented over 24-h. A 2-h step moving average was superimposed onto time series plots to enhance the fluctuation pattern in time series of data.

Time series of data were plotted separately for each season, along with sunset and sunrise timings at the latitude of the study area, as approximated to the sampling interval of 1-h (see Table 1). The peak significance was assessed with the mesor (midline estimating statistic of rhythm) method. Mesor can be defined as the mean of the oscillation or the mean value of a rhythmic variable for equidistant data covering a 24-h period (e.g., Baskar et al. 2004). Per each time series, a 24-h mean in the number of 50–100% stomachs was computed. According to this method, a peak is made by a minimum of four consecutive catches in which the number of 50–100% stomachs

exceeds this mean value reported as a line on the plot (adapted from Hammond and Naylor 1977; Aguzzi et al. 2004a, b, 2005). To determine in which phase of the day–night cycle significant numbers of 50–100% stomachs generally occurred in all time series, their temporal frequency distribution was calculated per 2-h time intervals (adapted from Aguzzi et al. 2004a, b). That interval was chosen to allow better visualization of any temporal trend in that distribution.

Results

In the present study, high percentages of stomachs were assigned to the lowest fullness rank (0–25%) both at day and night, in all sampling seasons considered (Figs. 1a, 2a). Percentages in empty stomachs showed a seasonal trend: in 1996 (Fig. 1a) maximums were reported in winter (February) and summer (July) (i.e., 58% and 77%, respectively). Conversely, in these months percentages of full stomachs attained their minimum (i.e., 13% in February, and 6% in July). Percentages of full stomachs were high in spring and autumn (i.e., 28% in April and 25% in November). Also during 1997 (Fig. 2a), the percentage of empty stomachs increased from April (42%) to July (72%).

In both 1996 and 1997, time series presented a high data variability despite the binning at each catch in the number of stomachs of two adjacent f-ranks. On the basis of the chosen criterion for the determination of

Fig. 1 1996. Number of stomachs recorded per f-rank during each month of sampling (**a** *open square*, 0–25%; *filled square*, 25–50%; *grey shaded square*, 50–75%; *dotted square*, 75–100%) along with the corresponding feeding rhythmicity (**b** *line with diamonds*, time series of the numbers of 50–100% stomachs; *dashed line*, mesor; *black bar*, night phase; *solid line*, 2-h step moving average)
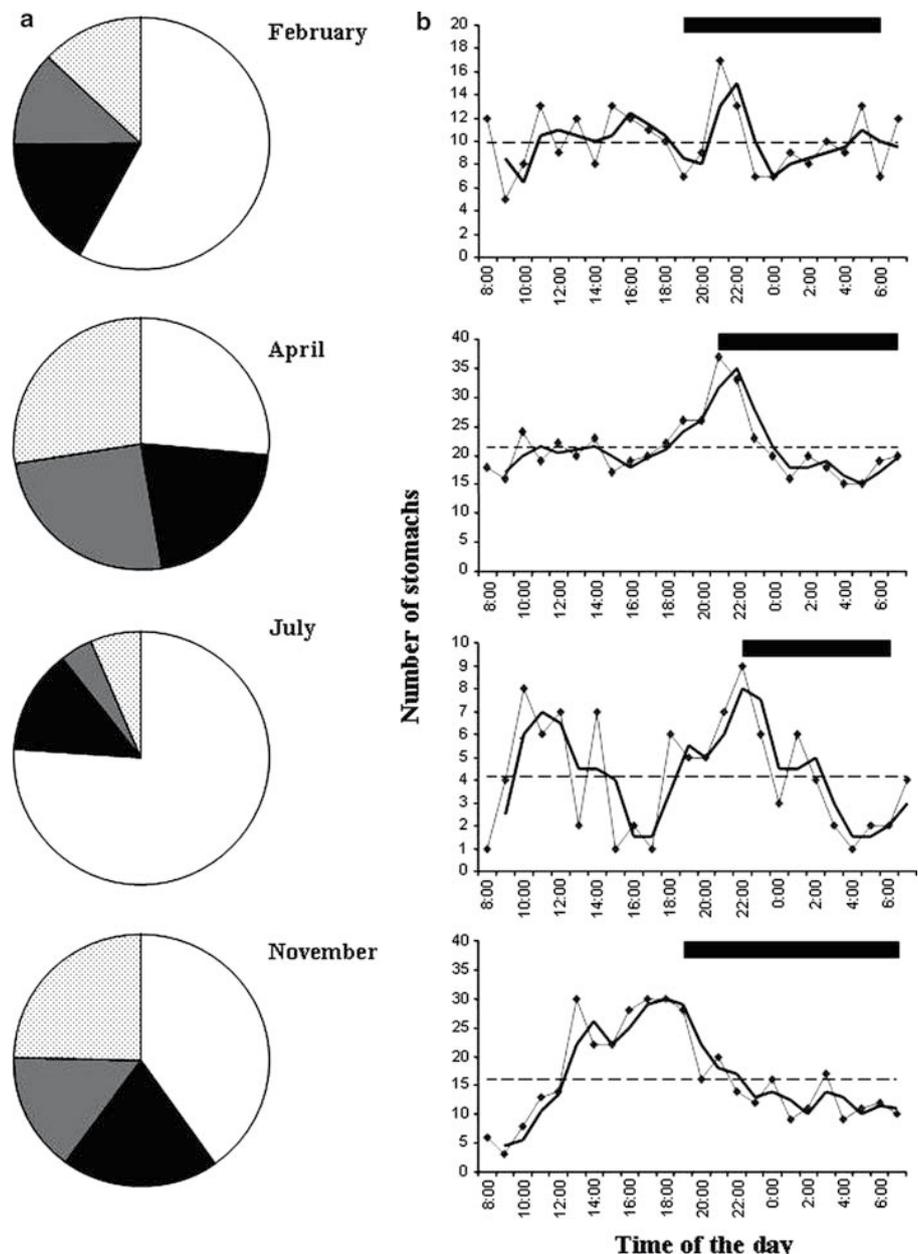
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Fig. 2 1997. Number of stomachs recorded per f-rank during each month of sampling (**a** *open square*, 0–25%; *filled square*, 25–50%; *grey-shaded square*, 50–75%; *dotted square*, 75–100%) along with the corresponding feeding rhythmicity (**b** *line with diamonds*, time series of numbers of 50–100% stomachs; *dashed line*, mesor; *black bar*, night phase; *solid line*, 2-h step-moving average)
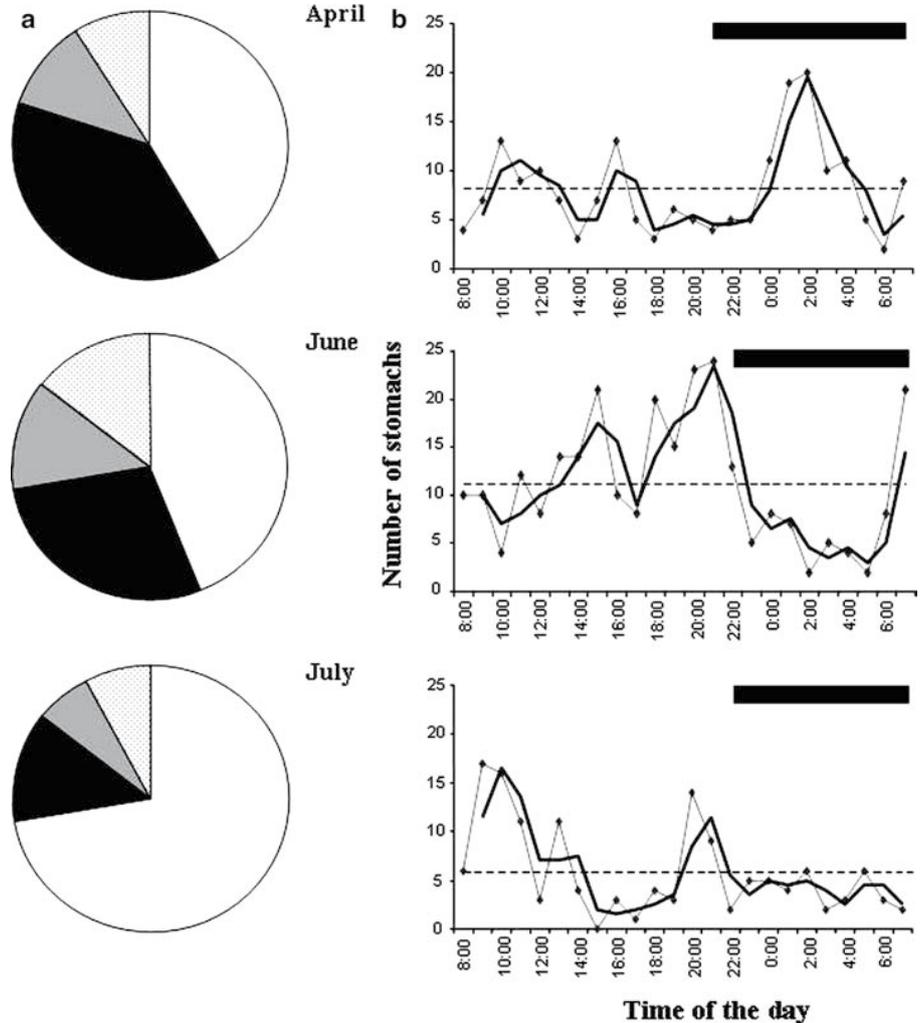
peak significance, marked feeding rhythms could be generally described for all sampling seasons, regardless of this data variability.

In 1996 (Fig. 1b), time series showed the following feeding pattern. In February no clear rhythmicity occurred. Several sparse points (from 11:00 to 17:00) exceeded the mean line without defining a peak. A more consistent increase occurred at night (from 21:00 to 22:00), but again, no peak was recognized at that time. In April, a marked peak was recorded closer to sunset time (i.e., from 18:00 to 23:00) with a maximum toward the night phase (at 21:00). Sparse values exceeded the mesor during central daylight hours, without defining a significant peak (i.e., from 10:00 to 14:00). In July, a weak bimodal rhythmicity occurred. A significant peak was recorded toward sunset (from 18:00 to 23:00, the maximum at 22:00), while a non-significant one took place after sunrise (from 10:00 to 12:00, the maximum at 10:00). Both the significant and the non-significant peak were followed by two temporally neighboring, but separated, points above the mesor (at 2:00 and 13:00, respectively). In November, a single wide peak was recorded from midday to sunset (from 13:00 to 21:00).

Three maximums were present: at 13:00, at 17:00 and at 18:00.

In 1997 (Fig. 2b), the April time series showed a major peak at night-time (from 00:00 to 4:00). Other sparse values appeared at daytime (from 10:00 to 12:00 and at 16:00) without defining a significant peak. In June, a weak bimodal feeding pattern took place. A significant crepuscular peak (from 18:00 to 22:00) was recorded along with a non-significant one at sunrise (a single point at 7:00). Other close but sparse values not integrating into the peak were recorded at daytime (at 11:00 and from 13:00 to 15:00). In July, the feeding activity showed a bimodal profile similar to the one recorded during 1996 for the corresponding season (Fig. 1b). Notwithstanding, following the chosen criterion for significance attribution, only one peak could be reported at daytime (from 8:00 to 11:00), the crepuscular one (from 20:00 to 21:00) being not significant. Both peaks were followed by sparse values above the mesor (at daytime, 13:00; at night-time, 2:00; and at sunrise, 5:00).

In order to analyze the modulation of the feeding rhythm upon seasonal photoperiod length variations, a phase analysis of the rhythmic time series was per-

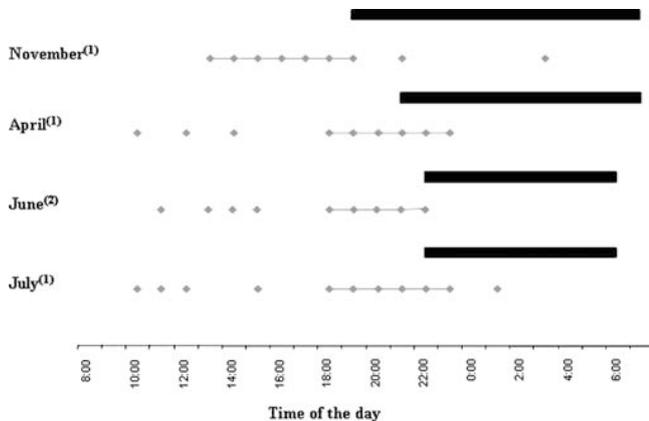Shrimp feeding behaviour.
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Fig. 3 Phase analysis of feeding rhythms as the temporal distribution of significant numbers of 50–100% stomachs (i.e., those exceeding the mesor) in time series of data of 1996 (*1*) and 1997 (*2*). *line with diamonds*, significant peaks; *diamond*, sparse significant values; *black bar*, night phase

formed. All the 50–100% stomachs, exceeding their 24-h mean in corresponding plots of 1996 (including June of 1997) were represented over 24-h with corresponding night durations (black bars) at the time of sampling (Fig. 3). This analysis showed the occurrence of photoperiodic regulation in the feeding activity rhythm. When the time series plots of November are compared with those of June and July, it is possible to appreciate how for a contraction of the night duration, a temporal shift in the occurrence of the sunset feeding peak takes place. Conversely, for an increment of the photophase duration, sparse values are recorded at sunrise and daytime, hence defining the occurrence of a second, yet seasonally variable, peak.

The temporal frequency distribution of significant numbers of 50–100% stomachs (Fig. 4) showed the highest values toward sunset (at 18–20, 28%, at 20–22, 34%) and after sunrise (10–12, 31%). Interestingly, the minimum was attained in the 6–8 time interval (3%).
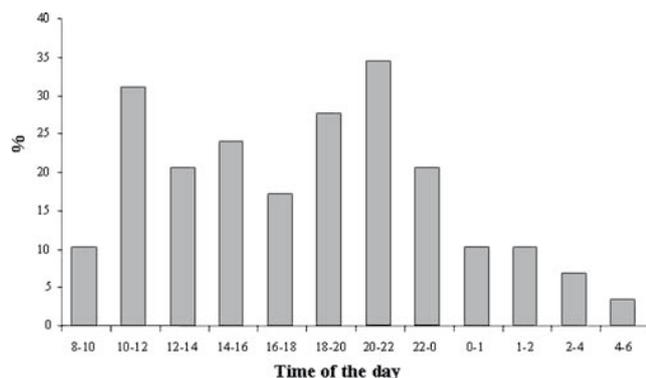

Fig. 4 Temporal frequency distribution of significant values in recorded time series of 50–100% stomachs as computed per time interval bin of 2 h

Discussion and conclusions

The present study addressed the question of the presence of a feeding rhythmicity in *P. varians* and its regulation upon seasonal variations in photoperiod length. Despite high percentages in empty stomachs and data variability, a bimodal feeding rhythmicity was characterized: a crepuscular peak was generally present in all sampling seasons, along with a second one appearing with evidence after sunrise only in spring–summer.

A peak in stomach fullness is generally present at the onset of the night phase; therefore, the temporal starting point in behavioral activity (i.e. swimming and walking) is defined in this species. In laboratory, *P. varians* require 2–3 h to completely evacuate the stomach contents when fed ad libitum (Cuesta, unpublished observation). Hence, it is possible to set the onset of behavioral activity related to feeding at around sunset. The presence of a similar feeding peak near the sunrise transition, during which the same environmental illumination probably takes place, suggests that the light intensity may play an important role as *zeitgeber* (i.e., entraining environmental agent) in the modulation of behavior. Sunset and sunrise optimum light intensity was proposed as the main environmental modulator of feeding rhythmicity of other decapods species such as *Nephrops norvegicus* shown similar feeding habits (Chapman et al. 1975; Oakley 1979; Aguzzi et al. 2004c). In *P. varians* direct evidence for biological clock regulation of behavior is still missing up to date, since no tests on walking or swimming were run in light–dark and constant darkness laboratory conditions. Anyway according to Bouchon (1991), the species possesses a circadian clock regulation in its behavior, relying upon photophase duration to adjust its ticking on a daily base (i.e., entrainment).

Laboratory studies on *P. argentinus* feeding behavior showed that animals increment their food intake up to complete stomach repletion for an increase in nourishment supply (Giri and Collins 2003). In this study, the majority of stomachs showed low level of fullness irrespective of the hour of the day and the day of the season. Interestingly, time series made by minority numbers of 50–100% stomachs at each catch defined a clear feeding pattern. This fact suggests that only a proportion of individuals fill up their stomachs when the environmental conditions like optimum light intensity stimulate the onset of behavioral activity. In that sense, *P. varians* may seek nourishment (possibly performing predation) during periods of swimming activity, as driven at dusk and dawn by the onset of optimum illumination, hence competing more actively for food resources. Food uptake may continue until the end of the optimum light intensity conditions, when all animals cease feeding independently of the quantity of ingested matter. This observation may explain why, despite the scarcity of full stomachs recorded in the present study, these could be used as indicators to define peaks in feeding activity.

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These data agreed with those presented in a previous study by Antheunisse et al. (1971). On that occasion, a bimodal pattern of swimming behavior was found in summer for populations located at Schiermonnikoog island salt marsh creeks (Netherlands). In this study, a bimodal feeding rhythmicity was clearly recorded in July (Figs. 1b, 2b). The presence of the diurnal peak is apparently linked to the photoperiod length variation from winter to summer, since it tends to disappear with a seasonal contraction of the photophase (Fig. 4). In *P. varians* reproduction is stimulated in the summertime by an increase of photophase duration (Bouchon 1991). For other species of the same genus, the proposed mechanism linking reproduction to season is based on the summer increase in UV-A radiation triggering a hormonal response (Valt et al. 2003). In *P. argentinus*, the transition from winter to summer induces an increment of moulting rate, with a consequent lowering of biomass incorporation and higher mortality (Díaz et al. 2003). Marked behavioral changes at the onset of sexual maturity have often been reported for coastal species of decapods such as *Maja squinado* and *Callinectes sapidus* (e.g., González-Gurriarán and Freire, 1994; Hines et al 1995). In *P. varians*, the seasonal transformation of feeding activity rhythms from unimodal into bimodal may be induced by an increase in metabolic requirements underlying reproduction and moulting in summer. An increase in the behavioral activity corresponding to both processes may force animals to actively feed twice a day to satisfy underlying metabolic requirements.

As seen in this study, a marked feeding rhythmicity takes place in *P. varians*, being regulated by day–night cycles. During the day, sparse rises in stomach fullness take place outside those temporal windows during which significant peaks are recorded. These sparse rises probably occur in response to organic matter inputs into the pond or to vertical migrations of prey species into the water column. Being detritivores, primary or secondary consumers, the Palaemonid species eat a wide variety of food items (Anderson 1985). As observed in one case (in April, Fig. 2b), an isolated nocturnal peak was present in the corresponding time series. This was due to a concomitant bloom of the mysid *Mesopodopsis slabberi* (Cuesta, personal observation). The occurrence of these sparse peaks in stomach fullness suggests the occurrence of a masking effect exerted by aliment presence on the true feeding rhythmicity of the species in agreement with its scavenging and opportunistic behavior (Anderson 1985).

When sampling is performed to capture live specimens for laboratory testing or market purposes, creeling may induce stress in decapods due to the high density of animals in the cage, as well as the presence of other not targeted species (e.g., Spicer et al. 1990; Schmitt and Uglow 1997). Studies on the decapods' behavioral rhythmicity are hence important to identify those hours of maximum efficiency in sampling and for fisheries. From the present results, we suggest to reduce these inconvenient stresses by sampling animals in a limited temporal window during the day. Sampling could be performed, for all seasons that were considered, during the hours around sunset when the crepuscular feeding peak takes place. Assuming that the feeding peak is the product of active swimming behavior, creel cages should be left in position for a period of time starting from 2-h before sunset and ending 2-h after it.

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