A COEXISTENCE MECHANISM FOR TWO FRESHWATER PRAWNS IN THE PARANÁ RIVER FLOODPLAIN, ARGENTINA

Pablo Agustín Collins

Instituto Nacional de Limnología (CONICET-UNL), José Maciá 1933, 3016 Santo Tomé Santa Fe Argentina.
Escuela Superior de Sanidad, Fac. Bioq. y Cs. Biol., Universidad Nacional del Litoral (pcollins@arnet.com.ar)

A B S T R A C T

This study examined the circadian feeding cycles of two sympatric decapod prawns, *Palaemonetes argentinus* (Nobili, 1901) and *Macrobrachium borellii* (Nobili, 1896), as a coexistence mechanism. The work was done in some shallow lakes of the alluvial valley of the Paraná River (Santa Fe, Argentina). Both prawns consume similar food items, but they differ in their feeding times. *Macrobrachium borellii* stomach fullness was greater during night than day, whereas *P. argentinus* foraging activity occurred by day. Trophic niche breadth was wide and similar in both species during the day but was expanded in *P. argentinus* at night when *M. borellii* feeding activity increased. Niche overlap fluctuated without a definite pattern. Adaptive modifications of circadian feeding rhythms play an important role in the coexistence of these species.

Many studies have recognized the difficulties in applying food web theories to empirical data (Closs and Lake, 1994; Warren and Spencer, 1996). Thus, it is important to identify connections in a food web and their variations. Species can coexist when, as competitors, they partition resources. This may be achieved by character displacement. Alternatively, species may not compete (Begon *et al.*, 1996). Against this background, interactions among individuals of different species promote interrelationships that might determine changes in temporal and spatial scales where the searching behaviour of predators constitutes unlike pathways (Ekschmitt and Breckling, 1994).

Competition for food is important, and foraging activity may occur throughout the day. However, its intensity can vary as a result of endogenous circadian rhythms or such exogenous factors as availability, intra- and interspecific competition, or threats from potential predators. Some organisms have adjusted their daily activities to these factors, and it is often thought that evolution has shaped these patterns in an optimal manner (Stenseth, 1983). In aquatic food webs, trophic spatial and temporal activity remains poorly studied. Little is known about trophic resource partitioning among omnivorous crustaceans.

In the Paraná River system (Santa Fe, Argentina) the commonest and most widely distributed palaemonids in the littoral communities of shallow lakes and streams of the floodplain (Boschi, 1981) are *Macrobrachium borellii* Nobili, 1896, and *Palaemonetes argentinus* Nobili, 1901. The food of adults is very similar, oligochaeta and insect larvae being the main items (Collins and Paggi, 1998; Collins, 1999). Here, their circadian foraging activity is considered.

MATERIALS AND METHODS

Study Area

The work was conducted in two shallow lakes that had similar densities of *P. argentinus* and *M. borellii* among sampling points, lakes, and time (i.e., 86.3 ± 22.30 vs. 82.0 ± 15.68 prawns/m^2 respectively; $t_{(2,107, 0.05)} = 0.67$; $P = 0.505$), but some different limnological characteristics. The two sampling points in each lake were close together in a surface of 50 m^2 approximately, with abundant aquatic plants (mainly *Eichhornia crassipes*).

Both environments have a small catchment area (Fig. 1), where fine sediments predominate. "Laguna N° 1" is an old meander scroll lake of "Los Sapos" island of the Salado River (31°39′S, 60°41′W) (total length 150 m; depth 1.5 m, area 4700 m^2). "Alejandra" lake lies adjacent to the Coronda River (31°45′S, 60°31′W), with a total length of 900 m, 1.8 m of depth, and an area of 675 m^2.

"Laguna N°1" changes its volume mainly depending upon the water input from the Salado, which has a high dissolved salt content (3200 μomhs/cm), while "Alejandra" is an oxbow lake of low dissolved salt content derived the Paraná River (220 μohms/cm). Populational densities in the communities of the lakes fluctuate considerably (Bonetto and Waiss, 1995) depending upon the lake volume, distance to river, amplitude–longitude of flooding pulse, and time of water residence (Paggi and Jose de Paggi, 1990).

Field Procedures

Diurnal foraging activities of *P. argentinus* and *M. borellii* were investigated during three nonconsecutive days in each lake in spring (October 1995, 1996, 1997). Prawns were collected with a trawl net (8 m long, 1 m wide; 1 mm mesh) at three-hour intervals (11:00; 14:00; 17:00; 20:00; 23:00; 02:00; 05:00; 08:00; 11:00). The trawled areas were 5 m^2, approximately, along the shorelines of the lakes having aquatic plants (mainly *E. crassipes* and *Nymphoides indica*). Prawns were immediately anaesthetised by cooling in a refrigerator with ice and preserved in 10% Formalin in the field.

Water temperature, dissolved oxygen, conductivity, and pH were measured simultaneously on each sampling occasion. Transparency was estimated using a Secchi disc.

Laboratory Procedures

Cephalothorax length (CL) was measured using callipers ($\pm$ 0.1 mm), and alimentary tracts were removed. Stomach fullness was estimated visually according to a subjective scale from 0 (empty) to 5 (full) (Collins and Paggi, 1998). In order to examine fluctuations in food items, adult prawns (CL > 6 mm for *P. argentinus* and CL > 9 mm for *M. borellii*) were randomly subsampled in four groups (Table 1), and in one group, the minimum number of stomachs was taken.

Extracted stomach contents were mounted in 50% glycerol. Consumed items were sorted into taxonomic groups, counted, and measured under a compound microscope at 150 × to 600 ×. Identified remains were classified into 16 categories: unicellular algae, filamentous algae, Euglenophyceae, Bacillariophyceae, Fungi, macrophyte remains, Rotifera, Nematoda, Cladocera, Copepoda Calanoida and Cyclopoida, Palaemonidae, Chironomidae larvae, other insect larvae, Oligochaeta, and Arachnida.

Data Analysis

Prawn densities and limnological parameters were compared between lakes with Student's *t*-test. Fifteen stomach-contents samples of each species,
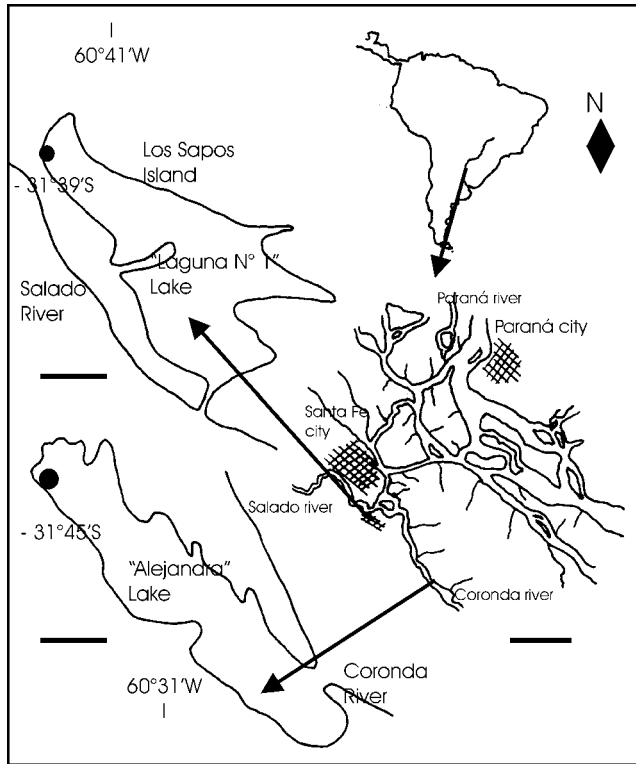
Fig. 1. Location of the study area. Black circle, sampled point. Scale: "Laguna N° 1" lake, bar ≅ 30 m; "Alejandra" lake, bar ≅ 150 m; Paraná river, bar ≅ 5 km.
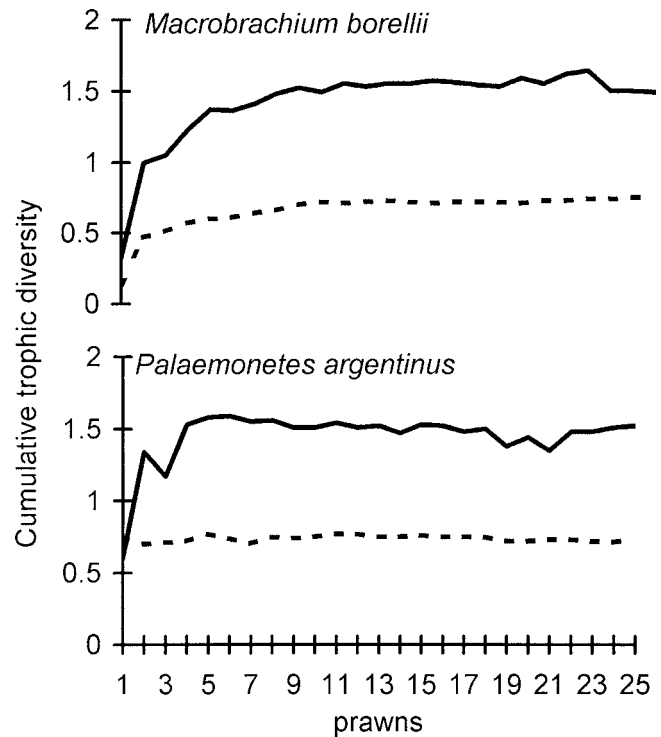

Fig. 2. Cumulative trophic diversity calculated after Shannon-Wiener (lower curve) and Simpson (upper curve) of *Palaemonetes argentinus* and *Macrobrachium borellii*.

sampling points, lakes, and time were analyzed. This minimum number was determined using the mean cumulative trophic diversity based on Shannon-Wiener and Simpson indexes (Legendre and Legendre, 1979) (Fig. 2); 180 stomachs of each species and time were observed.

In each sample, the comparison of the average size of prawn species was assessed with a one way analysis-of-variance (ANOVA). Differences were tested using Tukey HSD test according to Zar (1996).

Standard methods available for the evaluation of variation in feeding intensity involved the determination of the fullness index, which was calculated according to the expression $FI = (NF \cdot NT^{-1}) \, 100$, where NF is the number of full stomachs, and NT is the total number of stomachs. The fullness index homogeneity among sites and day sample was calculated with a Cochran C test, in which the hypothesis is that the variances are equal. To establish the importance of each item, food volumes were calculated by approximation to regular geometric shapes or converted to volume data of weight from literature (Edmonson and Winberg, 1971; Dumont *et al.*, 1975; Ruttner-Kolisko, 1977).

Niche breadth was estimated for each species at each sampled hour, using the equation of Ricklefs (1979):

$$B = \left(\sum_{i=1}^{n} p_i^2 \right)^{-1}$$

where (p_i) is the proportion of individuals found using resource *i*. Values of niche breadths were standardized on a scale of 0 to 1 (Pianka, 1973). Percentage of similarities for both prawn species in their feeding cycles were calculated using the niche-overlap index C_m following Pianka (1973).

The changes in food items were analyzed by means of the Index of Relative Importance, $IRI = (C_v + C_n) \, F_o$ (Pinkas *et al.*, 1971), where C_v is the volumetric content of prey, C_n is the numeric content of prey, and F_o is the frequency of occurrence of a prey item.

Table 1. Mean size (CL) of specimens examined. PA: *Palaemonetes argentinus*, MB: *Macrobrachium borellii*. In parentheses: standard deviation. All measurements in mm. (90 prawns of each species, lakes, and times. Total prawns: 3240).

Day time	N° 1		Alejandra	
	CLMB	CLPA	CLMB	CLPA
11:00	11.1 (1.51)	7.4 (0.75)	12.1 (1.32)	7.7 (1.07)
14:00	10.6 (1.49)	7.1 (0.70)	11.6 (1.59)	7.4 (1.70)
17:00	11.8 (2.67)	7.8 (0.84)	12.8 (2.76)	8.1 (1.85)
20:00	11.0 (2.06)	6.9 (1.33)	12.0 (2.60)	7.4 (1.75)
23:00	11.3 (2.58)	7.1 (1.51)	12.3 (2.48)	7.6 (1.25)
02:00	11.8 (1.63)	7.8 (0.78)	12.1 (1.56)	8.7 (1.07)
05:00	12.4 (1.73)	7.4 (0.98)	11.4 (1.37)	8.2 (1.74)
08:00	12.6 (2.71)	6.8 (1.27)	12.6 (2.77)	7.7 (2.57)
11:00	13.1 (2.33)	7.5 (1.17)	14.3 (2.53)	8.5 (2.11)

RESULTS

Mean values of conductivity (3205 and 220 μohms/cm), pH (7.7 and 6.9), transparency (26.5 cm and 38.7 cm), and dissolved oxygen (7.7 and 6.9 mg/L) differed between "Laguna N°1" and "Alejandra" lakes, although daily variations were similar. Temperatures oscillated between 16.8° (05:00 h) to 21.2°C (17.00 h) in N° 1 lake and 17.8° (02:00 h) to 21.3°C (14:00 h) in Alejandra lake and were similar between both ponds ($P = 0.205$).

The number of prawns captured was different throughout the day in both lakes and for both species (ANOVA, *P. argentinus* $F_{(5,53, \, 0.05)} = 7.18$, $P = 0.0039$; *M. borellii*, $F_{(5,53, \, 0.05)} = 3.64$, $P = 0.0355$). Lowest catches of the latter species (48 ± 10.9 prawns) were at midday (Tukey, $P < 0.05$). *Palaemonetes argentinus* was more abundant than *M. borellii* (ANOVA, $F_{(1,107, \, 0.05)} = 9.56$, $P = 0.004$) (93 ± 19.9 vs. 75 ± 17.3 prawns).
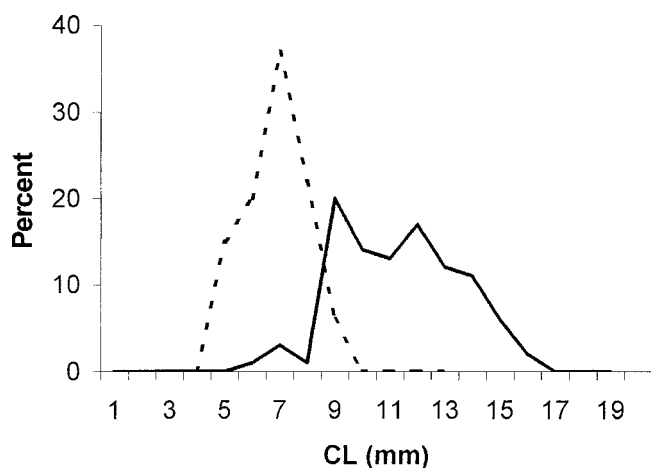
Fig. 3. Distribution of cephalothorax length of *Palaemonetes argentinus* (dashed line) and *Macrobrachium borellii* (solid line). Total prawns subsampled = 3240; *P. argentinus* = 1620; *M. borellii* = 1620.
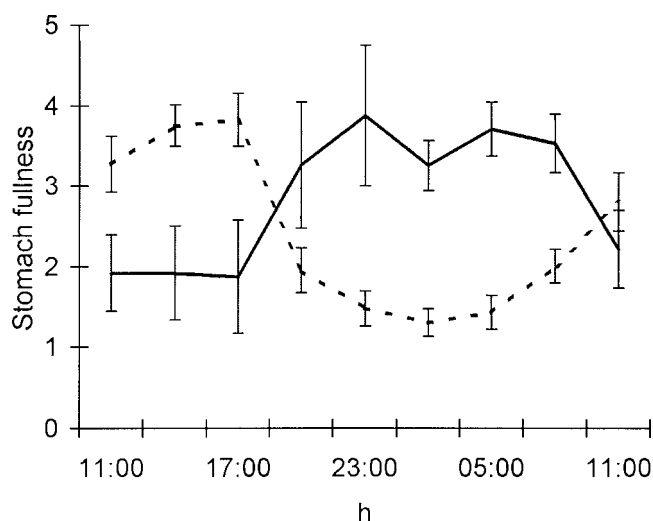

Fig. 4. Mean stomach fullness index of *Palaemonetes argentinus* (dashed line) and *Macrobrachium borellii* (solid line) in a circadian cycle (bar: standard deviation).

In both cases, size comparisons did not reveal a great difference in size-frequency distribution in daily cycles among sites and day samples (ANOVA, *P. argentinus*, $F_{(8,5022, 0.05)} = 1.06$, $P = 0.3759$; *M. borellii*, $F_{(8,3970, 0.05)} = 0.93$, $P = 0.4495$), but size-frequency distribution was significantly different between the two species, with *M. borelli* the larger (ANOVA, $F_{(1,8893, 0.05)} = 11.27$, $P = 0.00008$). Subsampled adult prawns had a mean CL size of 7.3 ± 1.08 mm for *P. argentinus* and 11.8 ± 2.19 mm for *M. borellii*, and the size range of the two species is shown in Fig. 3.

Stomach fullness variances were not significantly different among lakes and day samples in each species (Cochran C test$_{(5, 0.05)}$, *P. argentinus* = 0.29, $P = 0.1042$; *M. borellii* = 0.18, $P = 0.8601$). This index showed that feeding occurred during the whole day for both prawns, but foraging activity differed in intensity at different times (Fig. 4). In *P. argentinus*, stomach fullness was greatest during the day, but in *M. borellii*, during the night. Few stomachs were empty, $8.7 \pm 2.32\%$ for *P. argentinus* between 23:00 and 05:00 h and $1.2 \pm 0.98\%$ for *M. borellii* between 12:00 and 17:00 h.

In both species food items were very damaged, but most were identifiable (Table 2). Organic debris could not be accurately quantified and was discarded from later analysis.

The frequency of occurrence of unicellular algae, filamentous algae, macrophyte fragments and fungi fluctuated throughout the day without distinct rhythms for both prawns. However, unicellular algae (mainly *Scenedesmus* sp., *Ankistrodesmus* sp., and *Staurastrum* sp.) were more heavily grazed at sunrise by *P. argentinus* (IRI values 4162.83) than during the rest of the day (Fig. 5). Bacillariophyceae and fungi were found only in *P. argentinus*. The former (mainly *Gyrosigma* sp., *Fragillaria* sp., and *Bacillaria* sp.) were more frequent during the day and the latter during the night (Fig. 5). Euglenophyceae were consumed by *M. borelii* without a definite cycle (Fig. 5). For this prawn, unicellular algae occasionally occurred, and filamentous algae (mainly *Oedogonium* sp., *Ulotrix* sp., and *Microsporas* sp.) were only eaten in any quantity around

20:00 and 08:00 h (greatest IRI values 3500.95). Macrophyte fragments appeared during the whole day in *M. borellii*.

Cladocerans, calanoid and cyclopoid copepods were abundantly preyed upon with greater consumption by day than by night in *P. argentinus*, except for Cladocerans which peaked at 23:00 h. All these items were consumed by *M. borellii* more frequently by night (Fig. 5). Rotifera were found only in *P. argentinus*, with high IRI values except at sunrise.

The greatest differences of daily items consumed by both prawns were recorded mostly among benthic prey.

Macrobrachium borellii ingested mostly prey associated with the benthos or aquatic plant areas. Chironomid larvae, other insect larvae (e.g., Ephemeroptera, Trichoptera) and Oligochaeta (*Pristina* sp. and *Dero* sp.) occurred mainly during the night (maximum IRI values: 9708.76 for Oligochaeta, 4862.08 for chironomid larvae). In contrast, *P. argentinus* had a daytime consumption of benthic items (maximum IRI values: 8637.14 for Oligochaeta, 2118.96 for chironomid larvae) (Fig. 5). Palaemonidae and Arachnida were only found in *M. borellii* and mainly at night (Fig. 5).

Both prawns had similar trophic niche breadths during the day (from 08:00 to 17:00 h) and different ones at night (20:00–05:00 h). Niche breadth values were more constant in *M. borellii* than in *P. argentinus*, being greater at night (Fig. 6). Niche overlap values fluctuated throughout a day without a definite cycle. The lower C_m values corresponded to 05:00, 23:00, and 14:00 h (Fig. 7).

Overall, foraging activity increased during the night in *M. borellii* and decreased in *P. argentinus*, but the latter utilised more diverse food items.

DISCUSSION

The timing of feeding activity is influenced by the day/night cycle and shows various patterns of synchronization with this cyclical factor, depending on the species. Moreover, differences in physiology, foraging, behaviour, and predation

Table 2. Food items recorded from stomach contents of *Macrobrachium borellii* (M.b) and *Palaemonetes argentinus* (P.a).

	M.b	P.a
ALGAE		
Euclorophiceae		
Coelastrum sp.	x	x
Pediastrum sp.	x	x
Volvox sp.	x	x
Scenedesmus sp.	x	x
Ankistrodesmus sp.	x	x
Euglenophiceae		
Euglena sp.	x	–
Trachelomonas sp.	x	–
Zygophiceae		
Staurastrum sp.	x	x
Zignema sp.	x	x
Cosmarium sp.	x	x
Euastrum sp.	x	–
Closterium sp.	x	x
Pleurotaemiun sp.	–	x
Micrasterias sp.	–	x
Arthrodesmus sp.	x	–
Spirogyra sp.	–	x
Bacillariophiceae		
Gomphonema sp.	–	x
Gyrosigma sp.	–	x
Navicula sp.	–	x
Chaetoceros sp.	–	x
Fragillaria sp.	–	x
Bacillaria sp.	–	x
Nitzchia sp.	–	x
Ulothricophiceae		
Basicladia sp.	–	x
Oedogonium sp.	–	x
Ulotrix sp.	x	x
Schizogonium sp.	–	x
Micrpsporas sp.	x	x
Protosiphon sp.	–	x
Rizoclonium sp.	–	x
FUNGI (hifas)	–	x
MACROPHYTES (pieces)	x	x
NEMATODA	–	x
ROTIFERA		
Brachionus sp.	–	x
Keratella sp.	–	x
Polyarthra sp.	–	x
Bdelloidea	–	x
Others	–	x
OLIGOCHAETA		
Pristina proboscina	x	x
P. yenkina	–	x
Pristina sp.	x	x
Dero dero nivea	x	x
D. dero furcatus	–	x
Dero sp.	x	x
CRUSTACEA		
Cladocera		
Diaphanosoma birgei	x	x
Latonopsis sp.	x	x
Moina micrura	–	x
M. minuta	–	x
Moinodaphnia macleyii	x	x
Bosminopsis deitersi	x	x
Bosmina sp.	x	–
Macrothrix sp.	x	x
Chydorus pubescens	x	–

Table 2. Continued.

	M.b	P.a
Chhydorus sp.	x	x
Euryalona occidentalis	x	x
Camptocercus sarsi	x	x
Copepoda Cyclopoida		
Acanthocyclops sp.	x	x
Macrocyclops sp.	x	–
Eucyclops sp.	–	x
Copepodids	–	x
Copepoda Calanoida		
Notodiaptomus spiniger	–	x
Notodiaptomus sp.	–	x
Diaptomus sp.	–	x
Bockella bergi	–	x
Copepodids	–	x
Nauplii	–	x
Decapoda		
Palaemonidae	x	–
INSECTA		
Ephemeroptera	x	x
Hemiptera	x	–
Corixidae	x	–
Trichoptera	x	x
Diptera		
Chironomus sp.	x	x
Parachironomus sp.	–	x
Pseudochironomus sp.	–	x
Tanypodinae	x	x
ARACHNIDA		
Pisauridae	x	–

suggest a mechanism for habitat segregation as a light-dark response to selective pressures (Englund and Krupa, 2000).

Both prawns are omnivores with dual roles as predators and processors of organic matter, with *M. borellii* being the more aggressive (Collins and Paggi, 1998; Collins, 1999). The feeding behaviour of both prawns depends directly on the nature of the food. They utilize sediment, periphitic and planktonic communities, grasp surfaces, and hunt in the water column or sediment, using one or both chelae of the first pereiopods assisted by the second and third pairs (Williner and Collins, 2000; Giri and Collins, 2003). Food items in both prawn stomachs during the day were similar to those in an annual cycle for the same species (Collins and Paggi, 1998; Collins, 1999). New additions to the known diet include Arachnida for *M. borellii* and Fungi for *P. argentinus*. Similar diets were also observed in other species of prawns in freshwater and marine environments (Collart, 1988; Jayachandra and Joseph, 1989; Guerao, 1995; Guerao and Ribera, 1996).

Trophic niche breadth was wide and similar for both species during the day. It was expanded by night in *P. argentinus* when *M. borellii* increased its feeding activity. Niche overlap oscillated without a definite pattern, indicating that the fullness and trophic breadth indexes varied mainly because of an increase in the consumption of several items, e.g., *P. argentinus* ate Oligochaeta and insect larvae with greater intensity during the day, when *M. borellii* diminished its foraging activity.
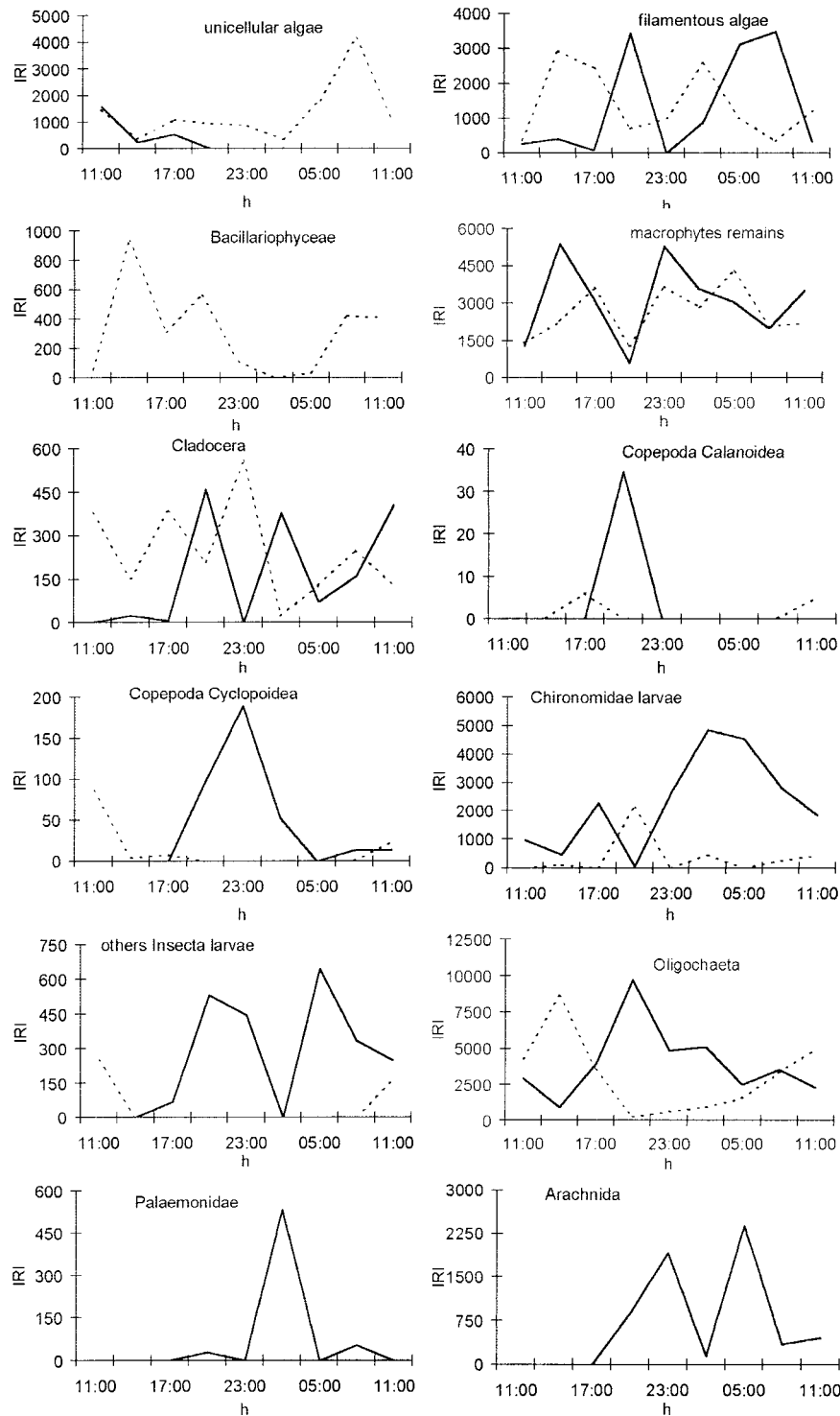
Fig. 5. IRI (Importance Relative Index) for main food items of *Palaemonetes argentinus* (dashed lines) and *Macrobrachium borellii* (solid line) in a circadian cycle.

The study of feeding chronology may provide valuable information on trophic ecology. By far the commonest items eaten by *P. argentinus* and *M. borellii* are plants, which are collected during the whole day without systematic variations. Small animal prey are consumed between 11:00 and 02:00 h by *P. argentinus* and between 20:00 to 08:00 h by *M.*

borellii. Although some plant and animal items are very small, they may play a significant nutritional role for decapods (Fryer, 1977; Kennish, 1996). On the theory of optimal feeding strategies, animals may favour feeding under certain weather conditions or times in order to minimize metabolic costs of feeding activity (Schoener, 1971).
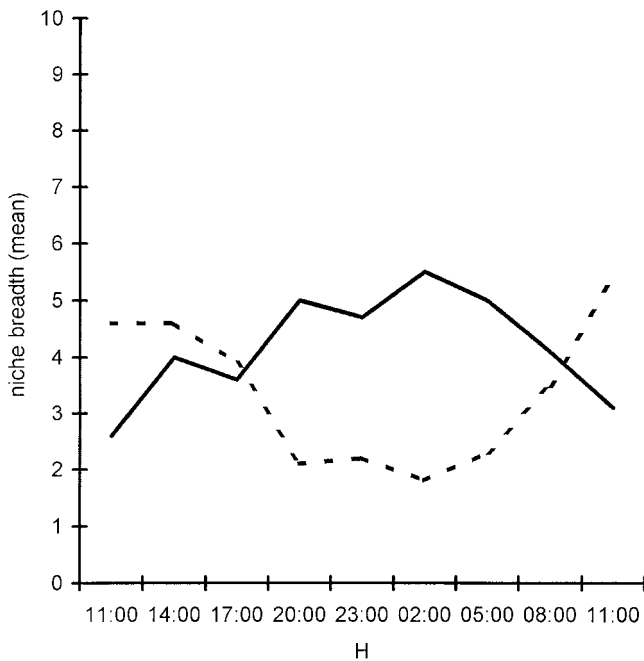
Fig. 6.   Food niche breadth (B) of *Palaemonetes argentinus* (dashed line) and *Macrobrachium borellii* (solid line) in a circadian cycle.

Fig. 8.   Food web model based in the stomach data of *Palaemonetes argentinus* and *Macrobrachium borellii*. The least (dashed lines) and the most (solid lines) important food items are indicated.

Macrobrachium borellii and *P. argentinus* have similar roles in the food web, but their main food sources, e.g., insect larvae (chironomids, Ephemeroptera, Trichoptera) and Oligochaeta, were used at different times (Fig. 8). Feeding activity patterns are reflected in the IRI values and the frequency occurrence of food items.

Several authors (Inyang, 1978; Vance, 1992) have proposed a pattern of high night activity for crustaceans, when habitat use may be related to a decrease in fish and bird predation. However, this study showed a daytime activity for *P. argentinus* what would favour exploitation of its main food resources, Oligochaeta and Diptera larvae. The daily patterns of prawns seem to be primarily controlled by photoperiod and other environmental factors.
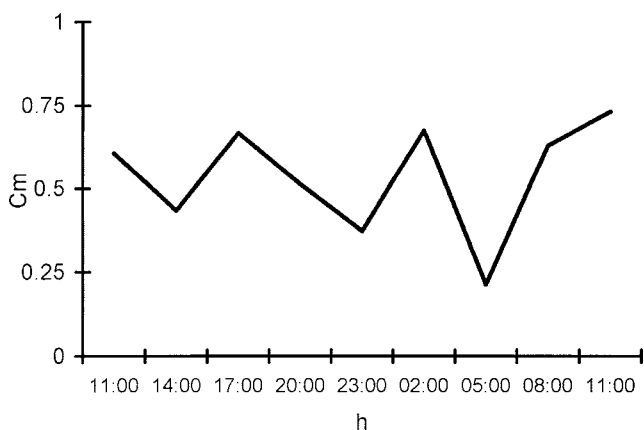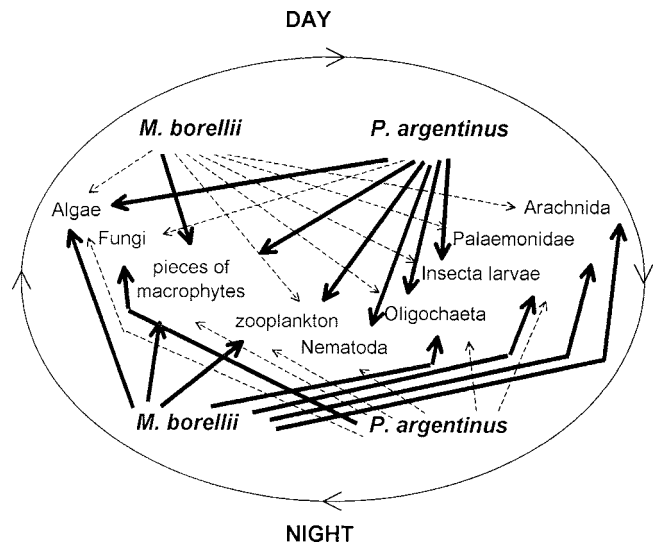
Segregation by feeding times between two species is expected to arise if there is enough food available and a possible enemy is active at different times of the day.

The two co-existing species have different circadian rhythms of feeding; *P. argentinus* seems to be a diurnal feeder, whereas *M. borellii* is nocturnal. However, if *P. argentinus* is left alone or without a nocturnal predator, it could feed with a great intensity during the night, changing its feeding rhythm. This speculation could be attributed to a competitive force—predation or injury risk caused by the more aggressive species (*M. borellii*) (Williner and Collins, 2000). Thus, adaptive modifications of circadian feeding rhythms play a role in the coexistence of these species in the Paraná River.

Fig. 7.   Food niche overlap (C$_m$) between *Palaemonetes argentinus* and *Macrobrachium borellii* in a circadian cycle.

LITERATURE CITED

Begon, M., M. Mortimer, and D. J. Thompson. 1996. Population Ecology. A Unified Study of Animals and Plants. Blackwell Science, London. 247 pp.

Bonetto, A. A., and I. R. Wais. 1995. Southern South American streams and rivers. Pp. 257–293 *in* C. E. Cushing, K. W. Cummins, and G. W. Minshall, eds. Ecosystems of the World. 22: River and Stream Ecosystems. Elsevier Press, Amsterdam.

Boschi, E. E. 1981. Decapoda Natantia. Serie Fauna de Agua Dulce de la República Argentina, Buenos Aires. 60 pp.

Closs, G. P., and P. S. Lake. 1994. Spatial and temporal variations in the structure of an intermittent-stream food web.—Ecological Monographs 64: 1–21.

Collart, O. O. 1988. Aspectos ecológicos do camarão *Macrobrachium amazonicum* (Heller, 1862) no baixo Tocatins (Pa-Brasil).—Memoria de la Sociedad de Ciencias Naturales La Salle 48, (Supl): 341–353.

Collins, P. 1999. Feeding of *Palaemonetes argentinus* (Nobili) (Decapoda: Palaemonidae) in flood valley of river Paraná Argentina.—Journal of Crustacean Biology 19: 485–492.

———, and J. Paggi. 1998. Feeding ecology of *Macrobrachium borellii* (Nobili) (Decapoda: Palaemonidae) in flood valley of river Paraná Argentina.—Hydrobiologia 362: 21–30.

Dumont, H. J., I. van de Velde, and S. Dumont. 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters.—Oecologia 19: 79–97.

Edmonson, W. F., and G. G. Winberg. 1971. A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters. Blackwell Scientific Publications, Oxford. 358 pp.

Ekschmitt, K., and B. Breckling. 1994. Competition and coexistence: the contribution of modelling to the formation of ecological concepts.—Ecological Modelling 75/76: 71–82.

Englund, G., and J. J. Krupa. 2000. Habitat use by crayfish in stream pools: influence of predators, depth and body size.—Freshwater Biology 42: 75–83.

Fryer, G. 1977. Studies on the functional morphology and ecology of the atyid prawns of Dominica.—Philosophical Transactions of the Royal Society of London, B, Biological Science 277: 57–128.

Giri, F., and P. Collins. 2003. Evaluación de *Palaemonetes argentinus* (Decapoda, Natantia) en el control biológico de larvas de *Culex pipiens* (Diptera, Culicidae) en condiciones de laboratorio.—Iheringia Série Zoologia 93: 237–242.

Guerao, G. 1995. Locomotor activity patterns and feeding habits in the prawn *Palaemon xiphias* (Crustacea: Decapoda: Palaemonidae) in Alfacs Bay, Ebro delta (Northwest Mediterranean).—Marine Biology 122: 115–119.

———, and C. Ribera. 1996. Locomotor activity patterns and feeding habits in the prawn *Palaemon serratus* (Pennant, 1777) (Decapoda, Palaemonidae) in the Alfacs Bay, Ebro delta, Spain.—Crustaceana 69: 101–112.

Inyang, N. M. 1978. Notes on food of the Baltic palaemonid shrimp *Palaemon adspersus* var. *fabricii* (Rathke) in Kiel.—Meeresforschung 26: 42–46.

Jayachandra, K. V., and N. Y. Joseph. 1989. Food and feeding habits of the slender river prawn, *Macrobrachium idella* (Hilgendorf, 1898) (Decapoda, Palaemonidae).—Mahasagar 22: 121–129.

Kennish, R. 1996. Diet composition influences the fitness of the herbivorous crab *Grapsus albolineatus*.—Oecologia 105: 22–29.

Legendre, L., and P. Legendre. 1979. Ecologie Numerique T.2. Ed Masson, Paris. 247 pp.

Paggi, J. C., and S. Jose de Paggi. 1990. Zooplankton of the lotic and lentic environments of the Middle Paraná River.—Acta Limnologica Brasiliensia 3: 685–719.

Pianka, E. R. 1973. The structure of lizard communities.—Annual Review of Ecology and Systematics 4: 53–74.

Pinkas, L., M. S. Olipham, and I. L. K. Iversor. 1971. Food habits of albacore, bluefin tuna and bonito in California waters.—Fisheries Bulletin (U.S.) 152: 1–105.

Ricklefs, R. E. 1979. Ecology. Chiron Press, New York.

Ruttner-Kolisko, A. 1977. Suggestions for biomass calculation of plankton rotifers.—Archiv für Hydrobiologie 8: 71–76.

Schoener, T. W. 1971. Theory of feeding strategies.—Annual Review of Ecology and Systematics 2: 369–404.

Stenseth, N. 1983. A coevolutionary theory for communities and food web configurations.—Oikos 41: 487–495.

Vance, D. J. 1992. Activity patterns of juvenile penaeid prawns in response to artificial tidal and day-night cycles: a comparison of three species.—Marine Ecology Progress Series 87: 215–226.

Warren, P. H., and M. Spencer. 1996. Community and food-web responses to the manipulation of energy input and disturbance in small ponds.—Oikos 75: 407–418.

Williner, V., and P. Collins. 2000. ¿Existe jerarquización en las poblaciones de Palemónidos del valle aluvial del Río Paraná?.—Natura Neotropicalis 31: 53–60.

Zar, J. H. 1996. Biostatistical Analysis.—Prentice Hall, New Jersey.