

# Ecological constraints and life history strategies of palaemonid prawns in Amazonia

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## Introduction

A species' life history strategy represents a combination of various co-adapted characteristics, such as morphology, physiology, behaviour and demography, which together represent possible responses to a determined situation (BARBAULT 1991).

Amazonian palaemonid prawns present very similar morphologies (HOLTHUIS 1952, KENSLEY & WALKER 1982), low size-range variation, large dietary overlap and similar habitat utilization (KENSLEY & WALKER 1982). However, they have developed a very large diversity of reproductive strategies that range from complete metamorphosis with eclosion of thousands of planktonic zoea larvae to abbreviated development of a few large eggs (MAGALHÃES 1985, 1986 A, 1986 B, 1988 A, 1988 B, 1989, MAGALHÃES & WALKER 1988).

Interspecific competition models for limiting resources, usually food and sometimes habitat, have been frequently used to explain patterns in resource utilization, spatial distribution and population growth. Other factors like spatial patchiness, predation, parasitism, seasonal cycles and weather disturbances generally maintain population densities low enough to prevent resource depletion and exploitation competition (STRONG 1984). Fresh water invertebrate communities are primarily influenced by the hydrological and physico-chemical characteristics of the aquatic environment related to flow regime and river basin geological features (WELCOMME 1985).

In this study, we summarize research with reproductive strategies in prawns from different aquatic environments in Amazonia, and suggest that discharge variations and plankton production represent the main ecological constraints for the diversity of adaptive lines and community evolution.

## Methods

Prawn reproduction strategies were analyzed considering population size structure, species fecundity, size and number of eggs, larval development, periods of gonad ripening and population reproduction intensity.

The study involved laboratory rearing of the larvae of *Macrobrachium amazonicum* (HELLER 1862), *M. nattereri* (HELLER 1862), *Palaemonetes carteri* GORDON 1935, *Pseu-*

*dopalaemon chryseus* KENSLEY & WALKER 1982, *Emyrrhynchus amazoniensis* TIEFENBACHER 1978, *E. burchelli* CALMAN 1907 and *E. wrzesniewskii* MIERS 1877. Ovigerous females of *M. Amazonicum* were collected in floodplain lakes of the Solimões River, while those of *P. carteri* came from Lago Cristalino, a small floodplain lake located in the right bank of the lower Rio Negro; all the other species were captured in small forest streams in the vicinities of Manaus. In the laboratory, the newly-hatched larvae were reared individually until metamorphosis. Measurements and morphological data on each larval stage, as well as its duration, were taken for all species. Procedures for rearing larvae, dissecting and preparing specimens for illustration are reported in MAGALHÃES (1985, 1988 a).

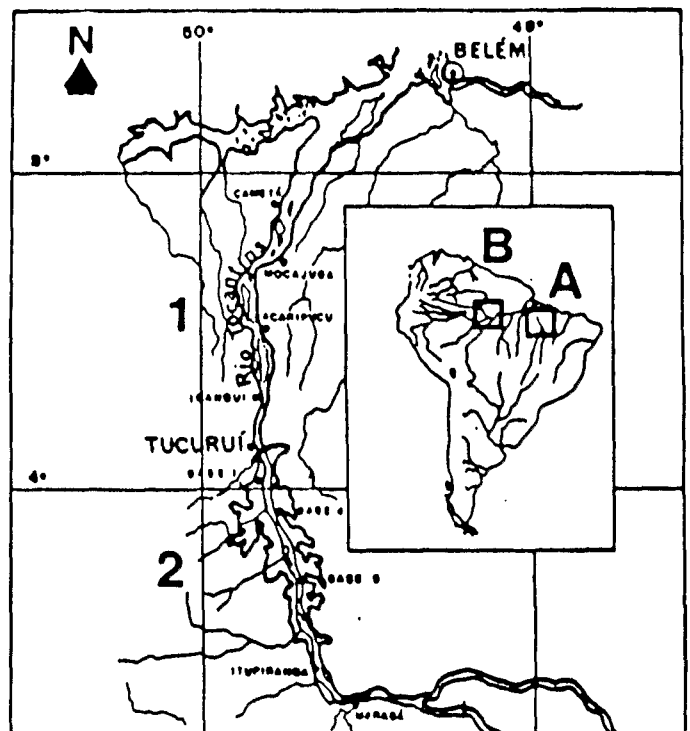


Fig. 1. Map of the study area showing the location of the sampling sites in Eastern Amazonia (A): in the Lower Rio Tocantins (site 1 = Cameta, Acaripucu, Içangui, Tucuruí) and in the Tucuruí reservoir (site 2 = Bases 1, 4 and 5).

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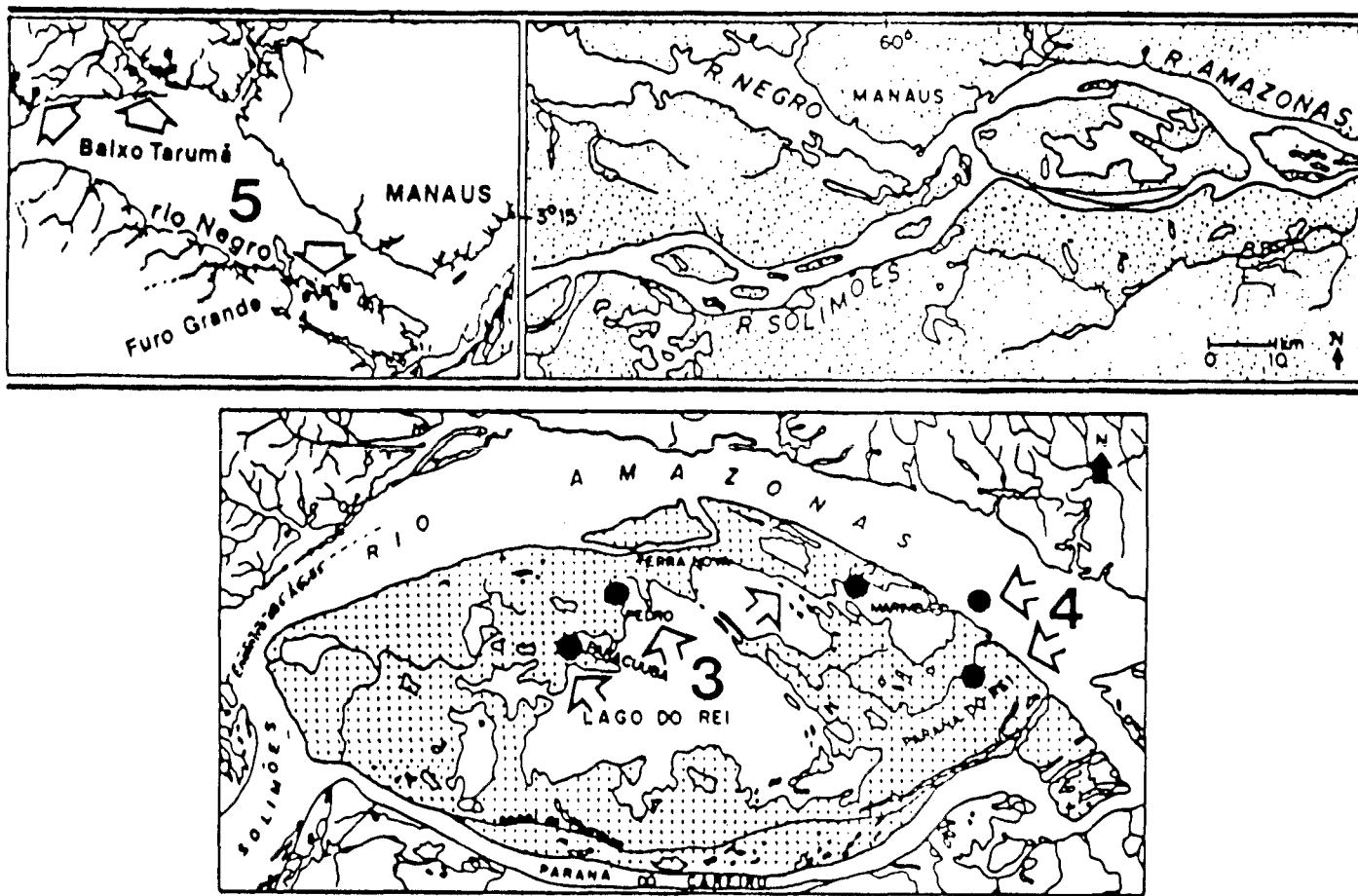


Fig. 2. Map of the study area showing the location of the sampling sites in Central Amazonia (B): in the várzea lake of Ilha do Careiro (site 3), in the Solimões River outside the island (site 4) and in small forest streams near the Rio Negro (site 5).

Field collections were realized in Eastern and Central Amazonia. Monthly samplings were conducted in 1985, in the lower Rio Tocantins downstream from Tucuruí Dam (Fig. 1), at Cameté (referred to as site 1), and in 1986 in four reservoir stations (site 2). Studies in Central Amazonia were carried out close to Manaus (Fig. 2). Bi-monthly samples were collected from April 1986 to August 1987 in Lago do Rei, a floodplain lake on Careiro Island (site 3), and in the Amazonas River near the island (site 4). Monthly collections were carried out from January 1989 to May 1990 in small forest streams (site 5) in the proximity of the Rio Negro.

Monthly records of water level were obtained for all areas. Collections were carried out with traditional shrimps traps at sites 1, 2, 3 and 4, set close to the river bank with dried powdered fruits of the palm tree *Orbynia speciosa* as bait (ODINETZ COLLART 1987, 1991a, 1991b). At site 5, prawns were collected with small hand nets, after removing the submerged litter from 30–40cm below the water surface. Prawns were counted, sexed, measured and ovigerous females noted. Carapace length (Clmm) was measured from the posteriormost margin of the orbit to the posterior edge of the cephalothorax.

### Study areas

The Tocantins River, the last tributary of the Amazon before it reaches the Ocean, discharges into the south arm of the estuary just upstream of Belém. The Araguaia and Tocantins Rivers drain a 767,000 km<sup>2</sup> basin, joining about 500 km from Belém to form the Lower Tocantins, where the fourth largest dam in the world, Tucuruí Dam, was recently built. The discharge of the Tocantins varies seasonally by a factor of 10, and the average annual difference between low water in September and high water in February–March is 10 m. The Tocantins carries "clear water" during the dry season and "white water" during the rain season. Total suspended solids vary from 5 to 250 mg · l<sup>-1</sup> and pH between 6 and 8 (SANTOS 1983). Tucuruí Dam was closed in September 1984 creating a 2430 km<sup>2</sup> reservoir with an average depth of 15 m and a three month flushing rate.

Lago do Rei is connected year-round to the Amazon and covers almost 100 km<sup>2</sup> of Careiro Island during high water. Limnological features depend on the main river water regime, and thus on the rainfall affecting the upper Amazon Basin (ODINETZ COLLART & MOREIRA 1989). Surface water temperature averages 29.3 °C ±

1°C in marginal areas. Dissolved oxygen supersaturation (10–12 mg · l<sup>-1</sup>) occurs during both low and high water. Conductivity varies between 46 to 80 μ · S · cm<sup>-1</sup> and pH between 5.2 and 7.1, in relation respectively with inflow and outflow from the lake, and photosynthesis activity.

The different forest streams sampled at site 4 are all part of the Rio Negro drainage network and have very similar chemical properties: low conductivity (8.9–10 μ · S · cm<sup>-1</sup>), low pH (4.5–5.0) waters, dominance of alkali metals (57%), high proportions of trace elements (especially Fe and Al) accounting for 32% of the total metals and a very low percentage of alkali earth ions Ca and Mg (11%) (FURCH 1984).

## Results

Six species were collected in sufficient abundance to investigate their reproductive strategy. *Macrobrachium amazonicum* was extremely abundant at sites 1, 2, 3 and 4. *M. surinamicum* HOLTHUIS 1948 occurred only at site 1. *M. nattereri* and *Palaemonetes carteri* were present all year-round at all stations around site 5. *Euryrhynchus amazoniensis* was more abundant than *E. burchelli* at site 5, the only location where both species were collected.

### Populations size structure

The sampling method was size selective. Traditional shrimp traps collected individuals above 6 mm carapace length; hand nets collected prawns

above 2 mm carapace length. Table 1 summarizes distribution, occurrence and size characteristics of the different prawn species. *M. amazonicum* populations showed different mean sizes depending on sampling site. Bigger prawns of both sexes occurred more in flowing waters than in lacustrine areas in Eastern Amazonia (sites 1 and 2; t test = 26.62; P < 0.05) and in Central Amazonia (sites 3 and 4; t test = 65.8; P < 0.05). In the lower Tocantins, populations of *M. amazonicum* and *M. surinamicum* showed similar mean sizes but different length frequency distributions when considering only ovigerous females (males are bigger than females in *M. surinamicum* and the opposite occurs in *M. amazonicum*). Small forest streams were characterized by small-sized prawns. Ovigerous females of *P. carteri*, *E. amazoniensis* and *E. burchelli* had overlapping size ranges.

### Fecundity, clutch size and larval development

Table 2 summarizes clutch size and fecundity characteristics of the prawn species. *M. amazonicum* and *M. surinamicum* carry a large number of small-sized eggs. Clutch size is significantly related to ovigerous female size (Table 2). The larval development period consists of several free-swimming larval stages, with *M. amazonicum* having as many as 11 stages of zoea before metamorphosis, which can take as long as 33 days to be completed.

Table 1. Occurrence and size structure characteristics of the Amazonian prawn species: (N) abundance; minimum and maximum size values; mean population size.

Prawn species	Sites	Population (N) and mean size	Male max., (N) and mean size	Female max., (N) and mean size	Ovigerous females min. max. (N) and mean size
<i>M. amazonicum</i>	1	(22,475) 12.2 ± 2.8	28.0 (9,970) 11.8 ± 2.8	26.0 (12,505) 12.46 ± 2.8	9.0–25.0 (805) 16.0 ± 3.3
<i>M. amazonicum</i>	2	(4,745) 11.0 ± 2.4	18.0 (743) 10.3 ± 2.7	18.0 (4,002) 11.2 ± 2.3	7.0–18.0 (339) 12.2 ± 2.4
<i>M. amazonicum</i>	3	(30,186) 10.7 ± 1.6	17.0 (3,952) 9.3 ± 1.9	18.0 (26,234) 10.9 ± 1.5	7.0–18.0 (15,618) 10.9 ± 1.5
<i>M. amazonicum</i>	4	(4,532) 12.5 ± 2.4	19.0 (946) 11.1 ± 1.9	22.0 (3,586) 12.9 ± 2.4	10.0–21.0 (767) 14.9 ± 1.9
<i>M. surinamicum</i>	1	(665) 11.9 ± 2.2	20.0 (268) 13.8 ± 2.1	15.0 (397) 10.7 ± 1.3	8.0–14.0 (298) 10.6 ± 1.1
<i>M. nattereri</i>	5	(1,648) 8.2 ± 2.6	17.0 (673) 9.1 ± 2.8	14.1 (975) 7.4 ± 2.6	8.0–13.3 (143) 10.5 ± 1.1
<i>P. carteri</i>	5	(4,418) 4.6 ± 0.8	5.4 (1,718) 4.1 ± 0.2	7.1 (2,696) 4.9 ± 0.8	2.3–7.1 (1,054) 5.5 ± 0.2
<i>E. amazoniensis</i>	5	(976) 4.4 ± 1.0	7.2 (438) 4.9 ± 1.1	6.4 (338) 4.1 ± 0.8	3.2–7.1 (157) 4.1 ± 0.7
<i>E. burchelli</i>	5	(432) 3.2 ± 0.5	3.7 (46) 2.7 ± 0.5	4.3 (386) 3.2 ± 0.4	2.6–4.2 (223) 3.3 ± 0.3

Table 2. Clutch size and fecundity characteristics of the Amazonian prawn species: (N) number of analyzed females; r = correlation between ovigerous females' carapace length and clutch size.

Prawn species	Sites	Ovigerous female range size, (N)	Clutch size	Egg mean size	Larval stages	correlation
<i>M. amazonicum</i>	1	9 - 25 (31)	258 - 5,706			r = 0.90***
	2	7 - 12 (23)	146 - 617			r = 0.81***
	3-4	10 - 19 (24)	365 - 2,850			r = 0.92***
	lab.		289 - 2,259	1.05 × 0.77	11	
<i>M. surinamicum</i>	1	9 - 12.2 (15)	894 - 2,503			r = 0.80***
<i>M. nattereri</i>	5	8.7 - 13.3 (68)	12 - 48			r = 0.42****
	lab.		34 - 150*	2.58 × 2.14	3	
<i>P. carteri</i>	5	5 - 6.3 (300)	5 - 39			r = 0.23****
	lab.		12 - 43	2.31 × 1.49	3	
<i>P. chryseus</i>	lab.	30.9 (20)**	14 - 43	1.86 × 1.29	3	
<i>E. amazoniensis</i>	5	3.1 - 6.1 (121)	4 - 27			r = 0.43****
	lab.		9 - 30	1.68 × 1.03	1	
<i>E. burchelli</i>	5	2.9 - 4.6 (200)	8 - 26			r = 0.45****
	lab.		14 - 23	1.36 × 0.85	1	
<i>E. wrzesniowskii</i>	lab.	13.1 (7)**	8 - 19	1.60 × 0.99	1	

\* After RODRÍGUEZ (1982); \*\* Mean total length; \*\*\*  $P < 0.05$ ; \*\*\*\*  $P > 0.05$ .

Larvae show simple morphological features on hatching. Growth and morphological transformations are gradual. Newly-hatched larvae are relatively small (mean 2.81 mm total length) when compared to female mean size (63.5 mm TL) and have yolks. Mouth parts are rudimentary, becoming functional after the third stage, when the larvae begin to feed on exogenous food. Only five thoracic appendages are present, the pereopods 1-2, 3 and 4 appear first as biramous rudimentary buds and become functional, respectively, in the second, fourth and fifth zoea, being primarily used for swimming. The sixth abdominal somite and telson are fused together. Pleopod buds 1-5 are present from the eighth stage on. The uropods appear in the third zoea, being both endopod and exopod setaceous only from the fourth zoea stage on, but fully formed after metamorphosis. The telson has a broadly triangular shape and 7+7 plumose setae.

*M. nattereri*, *Palaemonetes carteri* and *Pseudopalaemon chryseus* all carry only a few, large eggs and go through three, benthic, larval stages. Larvae hatch with more advanced features and morphological changes are more pronounced. These species have larger, yolk-rich first instar larvae (mean > 4.5 mm TL). Their mouth parts are rudimentary throughout the larval period since larvae do not feed until metamorphosis is complete. All five pairs of pereopods are present on hatching. Chelipeds remain non-functional during the larval pe-

riod. Pereopods 3-5 are rudimentary buds in the first instar of *M. nattereri* and *P. carteri*, becoming functional thereafter. In *P. chryseus* they are already fully formed and functional from the first instar on. The sixth abdominal somite and telson are clearly separated. Pleopods 1-5 occur as more or less advanced buds on hatching. They can be fully formed and functional by the second stage, as in *P. chryseus*. The uropods appear in the third stage, although the endopod is still rudimentary. The telson is roughly paddle-like, with 7+7 plumose setae in *M. nattereri* to 12+12 in *P. chryseus*.

Clutch size and larval development of *Euryrhynchus amazonienis*, *E. burchelli* and *E. wrzesniowskii* are similar. Both lay few, yolk-rich eggs. The newly-hatched benthic forms show advanced morphological features, resembling an adult in almost every structure, except for the absence of free uropods and, in *E. amazoniensis*, the presence of non-setaceous mouth parts. Other structures, like chela, walking legs and pleopods are fully developed and functional on hatching. It takes them only one instar to attain complete adult morphology.

#### Reproductive pattern

*M. amazonicum* showed different reproductive patterns depending on the sampling site. Occurrence of ovigerous females was highly seasonal in the lower Tocantins with a reproduction peak

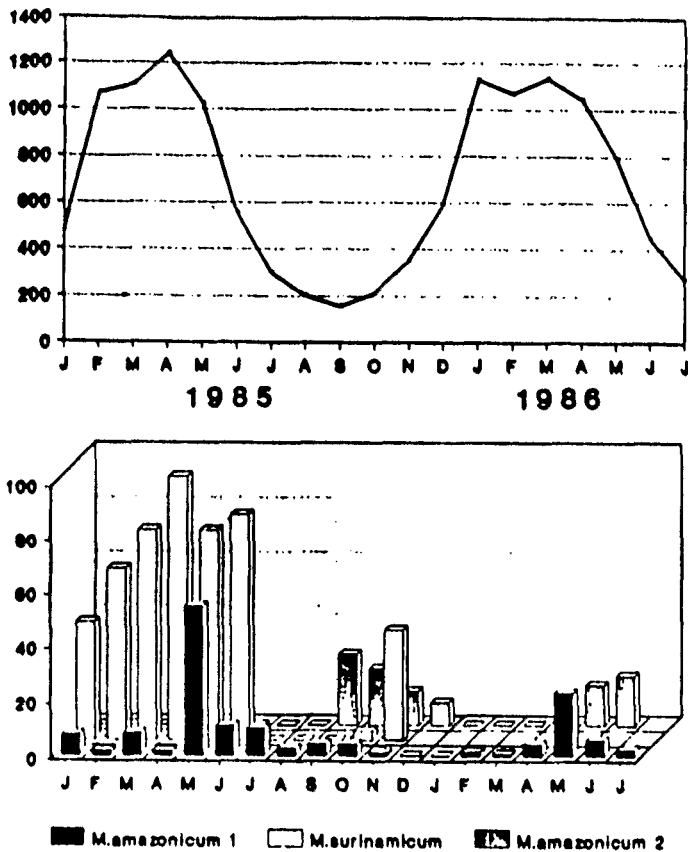


Fig. 3. Seasonal variation of: (A) monthly water level of the Tocantins River; percentage of ovigerous females of (B) *M. amazonicum* and *M. surinamicum* in the Lower Tocantins and (C) *M. amazonicum* in the Tucuruí Reservoir.

during mid-falling waters. The reproductive period was more extended for *M. surinamicum* as well as for *M. amazonicum* populations in the reservoir (Fig. 3). Lacustrine populations of *M. amazonicum* (site 3) were characterized by continuous reproductive activity. However, comparing observed percentages of ovigerous females to theoretical values that consider fecundity as only a size-dependant relation, three well-marked periods of massive gonad ripening were identified (Fig. 4 A & 4 B) during mid-falling, low and mid-rising waters. Reproductive intensity was computed considering ovigerous females abundance and size structure as well as species fecundity. A significantly higher number of eggs were released during rising waters (Fig. 4 C).

Forest stream species showed a similar seasonal pattern of reproduction with breeding restricted to rising and high waters (Fig. 5). However, a two months shift in reproductive periods occurs between similar sized species: *P. carteri* breeds later than *M. nattereri* during rising water and ovigerous females in *E. burchelli* occur during falling wa-

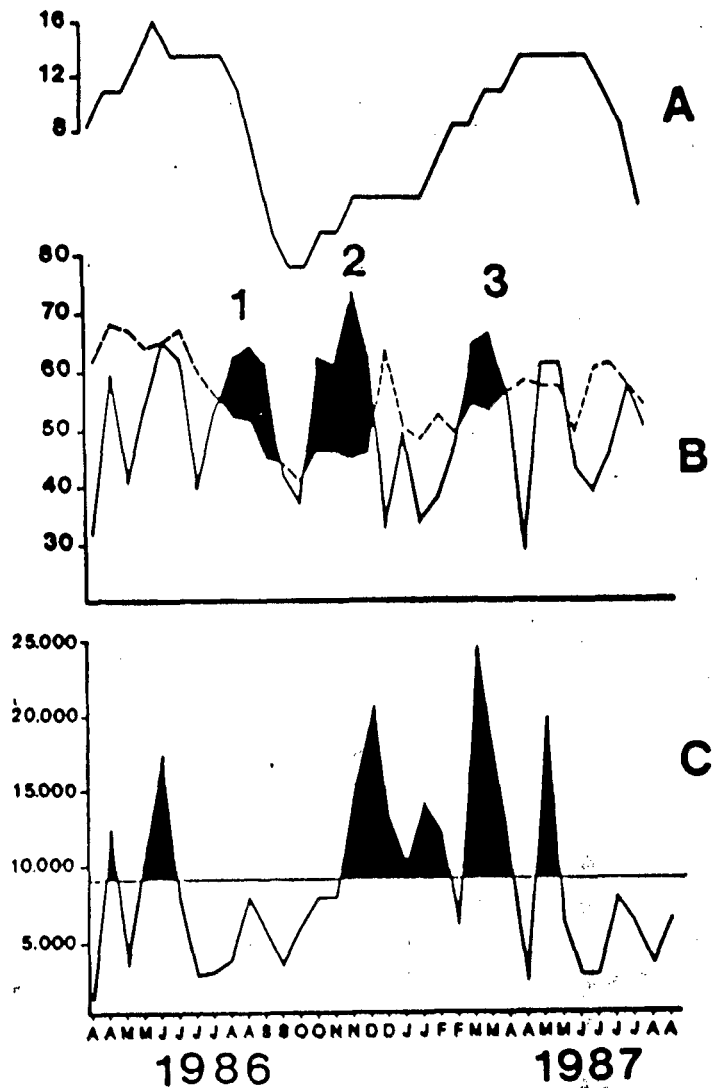


Fig. 4. Seasonal variations of: (A) monthly water level of the Rio Negro River in 1986–1987; percentage of ovigerous females (B) of *M. amazonicum* in the varzea lake observed values — and - - - - theoretical values considering fecundity as a females' size dependent relation.

ters while they are restricted to rising waters in *E. amazoniensis*.

### Discussion

Larval development of palaemonid prawns has been related to habitat characteristics. Extended metamorphosis is common in brackish and littoral fresh waters, with high primary production, while abbreviated development is often found in nutrient-poor forest streams (IHERING 1897, SOLLAUD 1923, SHOKITA 1973, MAGALHÃES & WALKER 1988). In the Amazon region, *M. amazonicum* is known to have extended development with several planktonic larval stages. Other continental species, i.e. species that complete their entire life cycle independent of the estuaries (RODRIGUEZ

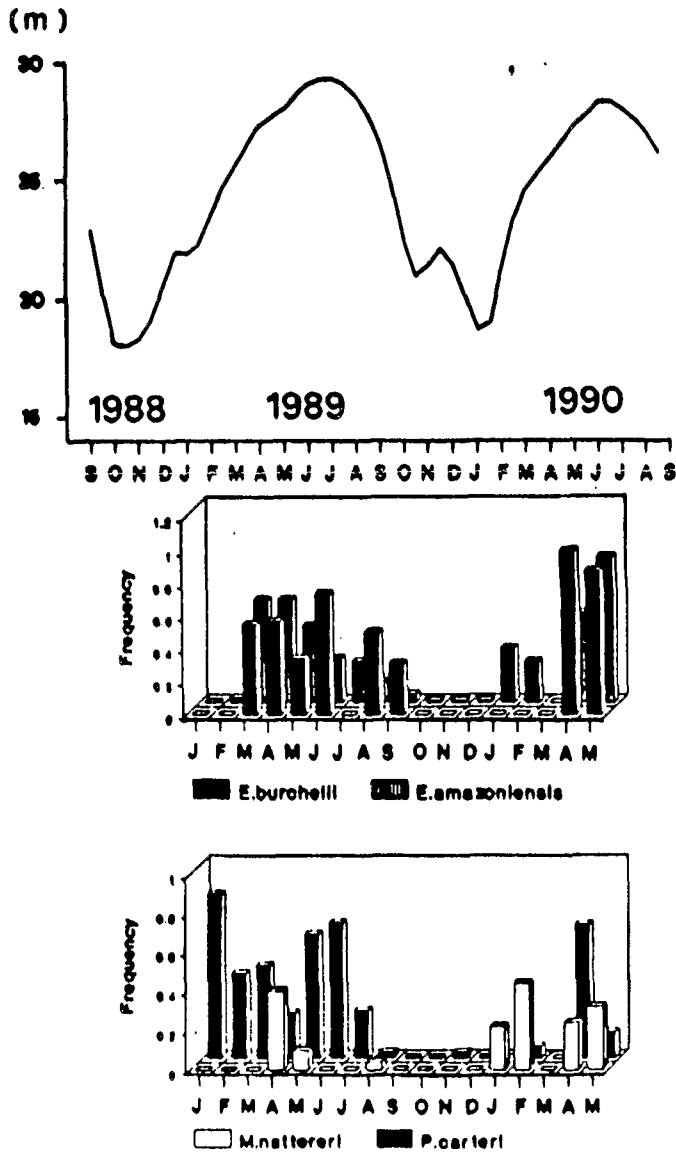


Fig. 5. Seasonal variation of: (A) monthly water level of Rio Negro in 1989–1990; percentage of ovigerous females of (B) *P. carteri* and *M. nattereri*; and (C) *E. amazonensis* and *E. burchelli*.

1981), like *M. nattereri*, *Pseudopalaemon chryseus*, *Palaemonetes carteri*, *Euryrhynchus* spp., usually reach metamorphosis after at most three stages of benthic lecithotrophic larva. *M. amazonicum* inhabits the nutrient-rich waters of the Amazonian várzea where planktonic production is high enough to support its planktotrophic larvae. In black water river systems and small shadowy forest streams planktonic preys are scarce and the main food sources are in the submerged litter (WALKER & FERREIRA 1986). RABALAI & GORE (1985) suggested several reasons for the partial or total suppression of pelagic larval stages in Decapoda. It is likely that the scarcity of planktonic resources in Amazonian freshwater habitats created an important selective pressure for the develop-

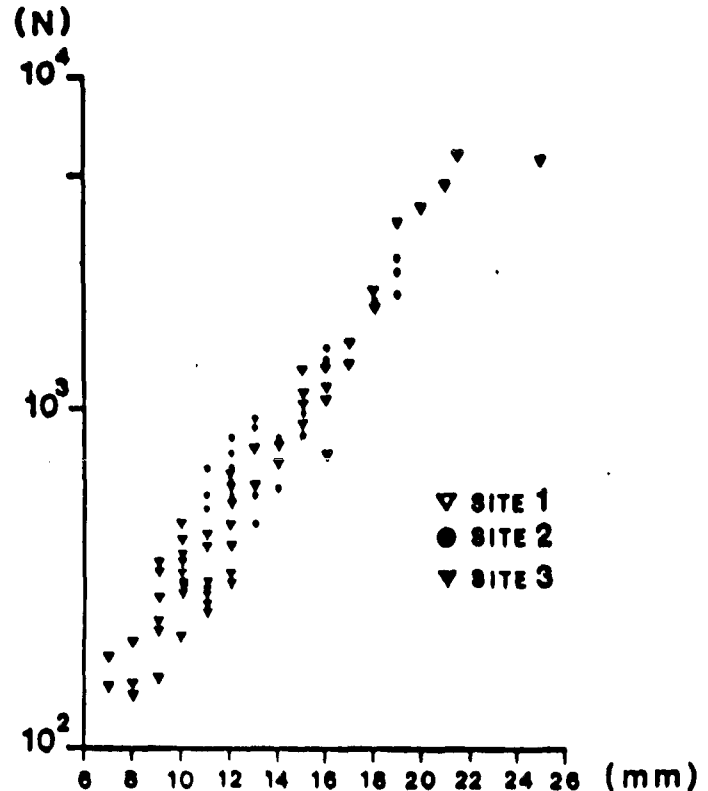


Fig. 6. Relation between clutch size and ovigerous females' carapace length in *M. amazonicum* from (▽) site 1, (●) site 2 and (▼) sites 3 and 4.

ment of an abbreviation of the larval development. That this adaptation in freshwater prawns could be related to the availability of food resources has already been suggested by SHOKITA (1973), WALKER & FERREIRA (1985), MAGALHÃES & WALKER (1988) and WONG (1989).

The significant correlation between clutch size and female length in *M. amazonicum* and *M. surinamicum* suggests that ontogenetic constraints are the main factors controlling individual fecundity in littoral species. Central Amazonian populations of *M. amazonicum* display different breeding patterns, but all the ovigerous females follow the same fecundity relation (Fig. 6). In contrast, clutch size is not size-dependent in species with abbreviated development like *M. nattereri*, *P. carteri*, *E. amazoniensis* and *E. burchelli*. In the nutrient-poor forest streams, ecological factors such as food availability controls not only larval development but also individual fecundity.

Most palaemonid prawns show seasonal reproductive patterns. In littoral species, breeding occurs during 4 to 5 months, with a well marked peak, the same female being able to produce several clutches (TRUESDALE & MERMILLIOD 1979, MARIOGHAE 1982, INYANG 1984, DONATTI 1986). In temperate waters, gonad ripening is mainly af-

fectured by temperature or/and photoperiod (FAVARETTO 1975, BOND & BUCKUP 1982, COELHO 1963, LITTLE 1968, DONATTI 1986, TRUESDALE & MERMILLIOD 1979, LOBÃO et al. 1978). In tropical waters, gonad ripening and breeding pattern are mainly controlled by flow regime, through physical-chemical factors or current velocity. In the Tocantins River, the breeding peak of *M. amazonicum* correlates with maximum water discharge during rising waters. Reproduction during rising water or rainy season provides two favourable adaptations for littoral species. The higher water levels facilitate larval dispersion in brackish estuarine areas and also allow for higher primary production and food availability for larvae downstream.

In floodplain lakes of Central Amazonia, phytoplankton production is highest during low waters (SCHMIDT 1973). Two factors may be related to gonad ripening in *M. amazonicum* at site 3: 1) maximum flow during both rising and falling waters, and 2) plankton production. Maximum breeding intensity for this species occurs during rising water levels. WALKER & FERREIRA (1985) showed that palaemonid species display a seasonal breeding pattern restricted to rising waters in small forest streams which are flooded seasonally by the main river, while in permanent forest streams, prawns are breeding year round (KENSLEY & WALKER 1982).

For WISE (1984), "high or low niche overlap can be evidence for or against competition, depending upon the assumptions made about the relative importance of exploitation and interference competition and the relevance of this evidence to evolutionary versus ecological time scales". Freshwater ecosystems are rarely resource-limited in the humid tropics. Palaemonid prawns from submerged forest litter show low size-range variation, large dietary overlap (KENSLEY & WALKER 1982) and similar reproductive strategies. However, congeneric or closely related species display small differences in breeding patterns. Natural experiments are not appropriate for testing null hypotheses that involve manipulation of species densities. However, they provide hypotheses and indirect evidence (WISE 1984). The breeding pattern in palaemonid prawns has been shown to be controlled mainly by environmental factors. Fluctuations in reproductive periods of forest stream prawns are apparently independent responses of non-competitive coexisting species to environmental disturbances due to in and outflow.

Breeding during rising waters is a wide-spread reproductive strategy in many tropical freshwater

species that increases larval dispersion downstream to estuarine areas or laterally to floodplain waters (WELCOMME 1985). This reproductive pattern appears to be an adaptive response to water level fluctuations. Colonizing an expanding habitat reduces intra-specific competition and consequently increases individual fitness within a species.

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