

Morphology and histology of *P. argentinus* (Crustacea, Decapoda, Caridea) digestive tract

LILIANA SOUSA¹ AND ANA MARÍA PETRIELLA^{1,2}

¹ Depto. de Ciencias Marinas, Facultad de Ciencias Exactas y Naturales, UNMP. Mar del Plata, Argentina.

² CONICET.

Keywords: Crustacea, Caridea, morphology, histology, digestive tract

ABSTRACT: This work describes the morphology and histology of the *P. argentinus* digestive tract. The foregut comprises the mouth, oesophagus, and stomach and is lined by a simple cylindrical epithelium overlain by cuticle. There are tegumental glands in the oral region and in the first portion of the oesophagus and of the hindgut. The cardiac stomach is an oval dorsal sac in the cephalothorax and has no calcified structures. The pyloric stomach comprises an upper chamber and a lower gland filter. The filter consists of an outer row of elongated setae and an inner row of dorsally curved setae forming longitudinal channels 16-18µm wide. The midgut runs from the dorsal chamber of the pyloric stomach to the sixth abdominal somite without caeca. The hindgut runs from the sixth abdominal somite to the ventral anus. The mid-gut epithelium comprises dominant cylindrical cells and small undifferentiated cells in the first portion. The hindgut wall presents longitudinal folds, conspicuous muscular bundles, and a folded cuticle. The digestive tract of *P. argentinus* is basically similar to that of most of decapods. The absence of calcified structures in the stomach and the width of the longitudinal channels in the filter are related to the predominantly detritivorous diet.

Introduction

There is a large body of information about decapods digestive tract particularly concerning economically important species such as palinurids (Cox and Bruce, 2003; Cox and Johnston, 2003, 2004), thalassinids (Pinn *et al.*, 1998) and scyllarids (Johnston and Alexander, 1999). The gut of decapods is essentially a tube opening anteriorly at the mouthparts and posteriorly at the anus; the foregut

and hindgut are ectodermally derived and are lined by cuticle, and the midgut with a glandular epithelium is derived from endoderm (Icely and Nott, 1992).

Caine (1975) investigated the alimentary behaviour of *Procambarus* species, concluding that there are two basic methods to obtain food: the detritivorous mechanism and the manipulation of big pieces of food. In crustacean, the mouth parts and the gastric mill show different adaptations in relation to the diet (Lin, 1996). Macrophagous decapods have a well developed and calcified gastric mill, while detritivorous evidence a reduced structure (Icely and Nott, 1992). In spite of this, there is evidence that the anatomy of the foregut may be modified in closely related species with similar feeding habits (Icely and Jones, 1978). Morphology and histological structure of the digestive tract can be also altered by external factors such as environmental

Address correspondence to: Dra. Liliana Sousa. Dpto. de Ciencias Marinas, Facultad de Ciencias Exactas y Naturales, UNMP. Funes 3350. B7602AYL. Mar del Plata, ARGENTINA.
E-mail: lgsou@mdp.edu.ar

Received on June 30, 2005. Accepted on April 12, 2006.

contamination (Meyers and Hendricks, 1985; Vogt, 1987).

Palaemonetes argentinus is one of the most widely distributed decapods in the littoral region of Argentina, Paraguay, Uruguay and southern Brazil (Morrone and Lopreto, 1995). This prawn plays an important trophic role in the littoral communities and inhabits from fresh-water to brackishwater lakes and streams (Spivak, 1997). Some of the waterbodies in which this prawn can be found receive direct discharges of chemicals from terrestrial ecosystems and the individuals accumulate important amounts of organochlorine pesticides in their tissues (Gonzalez Sagrario *et al.*, 1998; Miglioranza *et al.*, 2002). The hepatopancreas of *P. argentinus* was previously studied (Sousa and Petriella, 2000; Sousa *et al.*, 2005) and the organ undergoes histological and histochemical modifications in response to different physiological demands (moult, reproduction) (Sousa and Petriella, 2001) and environmental changes such as salinity and pollution (Sousa, 2003).

This work aims to describe the morphology and histology of the *P. argentinus* digestive tract, as part of a project which focuses to detect possible histological

alterations in different organs of this species, such as gills, hepatopancreas and the rest of the digestive tract as a consequence of pesticides action.

Materials and Methods

Adult individuals of both sexes, at sexual rest, of initial weight between 0.100 and 0.200g were collected from Sotelo stream, tributary of Mar Chiquita lagoon (Argentina, 38°S 55°W). This stream is a shallow creek where pesticide concentrations are below toxic levels and are not related to adverse biological effects (Menone, 1999; Miglioranza *et al.*, 2002).

For macroscopic observation of the digestive tract, some individuals fixed in formalin 5% were observed under a stereoscopic microscope.

For histological description, the cephalothorax and abdomen of 24 individuals in intermoult were fixed for 24 h in Davidson fluid (ethanol, formol, acetic acid and water) (Bell and Lightner, 1988), dehydrated in increasing concentration of ethanol, butyl alcohol (two changes of 24 h), butyl-paraffin 50:50 (for 24 h) and finally

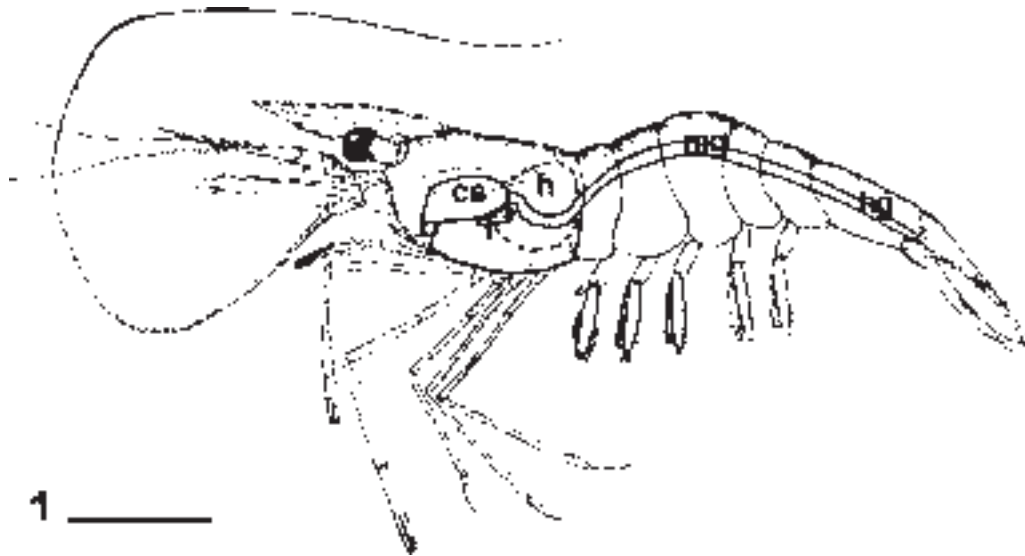


FIGURE 1. Schematic view of the digestive tract of *Palaemonetes argentinus*. cs: cardiac stomach; f: pyloric filter; h: hepatopancreas; hg: hindgut; mg: midgut; o: oesophagus. Scale bar: 5 mm.

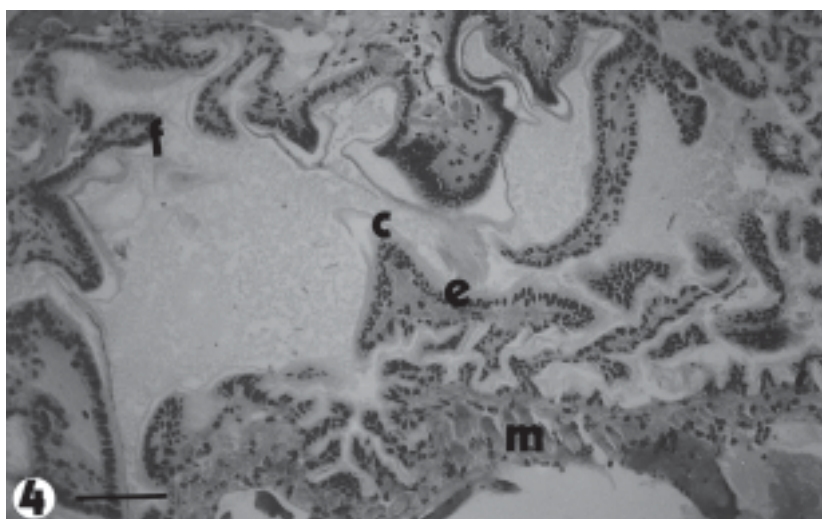
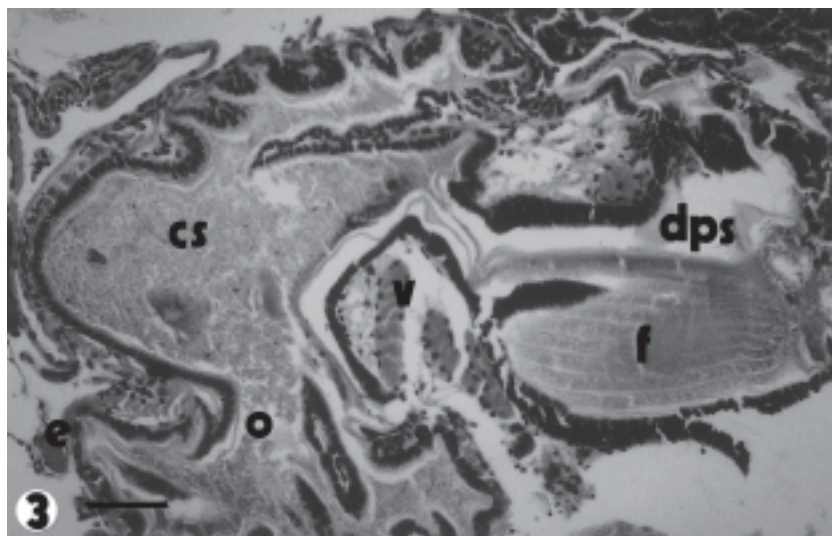
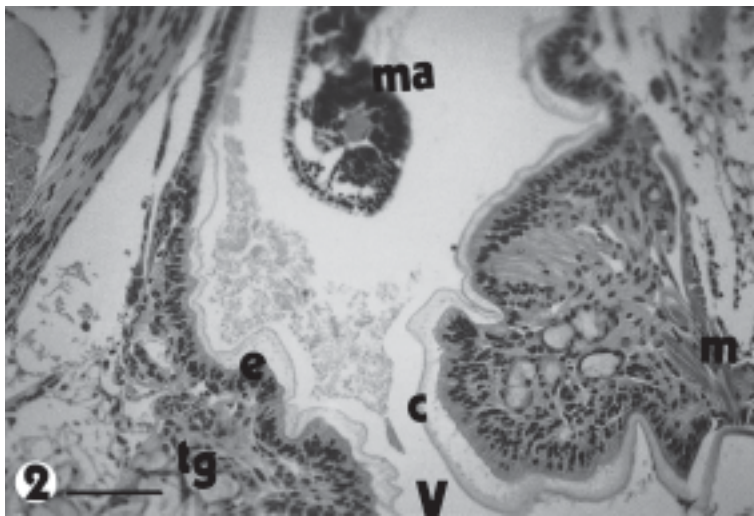


FIGURE 2. Longitudinal section of the oral region. c: cuticle; e: epithelium; m: muscle; ma: mandible; tg: tegumental gland; V: ventral. H&E. Scale bar: 25 μ m.

FIGURE 3. Longitudinal section of *P. argentinus*' foregut. cs: cardiac stomach; dps: dorsal chamber of the pyloric stomach; e: epithelium; f: pyloric filter; o: oesophagus; v: cardiopyloric valve. H&E. Scale bar: 150 μ m.

FIGURE 4. Detail of the cardiac stomach. Note the irregular folds of the wall. c: cuticle; e: epithelium; f: fold; m: striated muscle. H&E. Scale bar: 50 μ m.

embedded in paraffin. Sections (3µm) were stained with haematoxylin-eosin, Mallory's triple stain, PAS and Toluidine Blue.

The moult stage was determined by microscopic examination of the setae of the uropods exopodite, following the criteria established by Díaz *et al.* (1998).

Results

1. Morphology and anatomical relations

The foregut comprises the mouth, oesophagus, and stomach. The mouth is situated on the ventral side of the cephalic region, bounding laterally by robust mandibles. The oesophagus is a short vertical structure which connects the mouth with the stomach (Fig. 1).

The cardiac stomach is dorsal in the cephalothorax and looks like an oval sac; it leads into the pyloric stomach, which is situated in a ventro-posterior position in relation to the cardiac stomach. The pyloric stomach is reduced in size, elliptically shaped and comprises two chambers: an upper chamber leading into the midgut, and a lower chamber or gland filter. Externally, the filter looks like two lateral pouches with longitudinal grooves, opening into the hepatopancreatic ducts. The hepatopancreas occupies much of the cephalothoracic cavity and is twice as big as the cardiac stomach. The hepatopancreatic lobes are dorsally located and surround completely the midgut.

The midgut runs from the dorsal chamber of the pyloric stomach to the sixth abdominal somite, curving downwards between the hepatopancreatic lobes; and in the abdomen it curves upwards adopting a dorsal position. The midgut has neither anterior nor posterior caeca, and is the longest part of *P. argentinus*' digestive tract.

The hindgut runs from the sixth abdominal somite to the ventral anus and has no caeca (Fig. 1).

2. Histology

The oral region (Fig. 2) is lined by a simple cylindrical epithelium overlain by cuticle. The epithelial cell nuclei are at different heights giving a pseudo-stratified aspect. In the labrum, a dense connective tissue can be observed with Mallory's triple stain, with abundant connective cells, and longitudinal striated muscular fibres. In the paragnatha, the connective tissue is spongy. Tegumental glands are scattered throughout the oral region and their cells stain metachromatically with Toluidine Blue.

The oesophagus comprises a simple cylindrical epithelium overlain by cuticle, both the epithelium and the cuticle share similar characteristics to those of the oral region. The connective tissue is scarce and the striated muscle is well developed. The oesophagus wall presents deep infoldings along its length (Fig. 3) and tegumental glands in the first portion, which are similar to those observed in the oral region.

The cardiac stomach is lined by a simple cylindrical epithelium, whose height varies in the different zones; nuclei are at different heights in the cells (at medial and basal zones). The epithelium is underlain by a thin layer of dense connective tissue and surrounded by circular and longitudinal striated fibres. A serrated cuticle lays on the epithelium. The stomach wall forms many small folds projecting into the lumen, whose number and size vary according to distension degree (Figs. 3, 4). In some zones where the folds are bigger, the epithelium shows a stratified aspect and the connective tissue is well developed with big haemolymphatic lagoons. The cardiac stomach is separated from the pyloric one by the cardiopyloric valve, which is a fold of the ventro-posterior wall of the cardiac stomach extending dorsally and leaving a narrow canal towards the pyloric stomach (Fig. 3).

The pyloric stomach (Fig. 3) is small comparing with the cardiac one. The wall histology is similar to that of the cardiac stomach, but the striated muscle is better developed (Fig. 5). In the upper chamber the epithelium shows numerous deep folds that reduce the lumen (Figs. 5, 6). In the lower chamber the cuticle forms the double structure of the filter (Fig. 5). The filter consists of an outer row of elongated setae and an inner row comprising dorsally curved setae where each seta overlaps the next (Figs. 5, 7). The inner row of filtration setae form longitudinal channels of 16-18µm wide (Fig. 7). In the filter zone the epithelium is underlined by scarce connective tissue.

The midgut in *P. argentinus* has a simple epithelium which is cubical or cylindrical in relation to the content volume. One cellular type is dominant and extends from the basal lamina to the lumen (Fig. 8). These cells have central nuclei, small subapical vacuoles and a well developed brush border; some of them have a basophilic cytoplasm and are secreting actively (Fig. 9). In the first portion, small undifferentiated cells can be observed on the basal lamina (Fig. 8). Mucopolysaccharides are evidenced by Toluidine Blue stain in the apical region of the cells, in the brush border and in the lumen. The basal lamina is well developed and is strongly PAS positive, while the brush border was

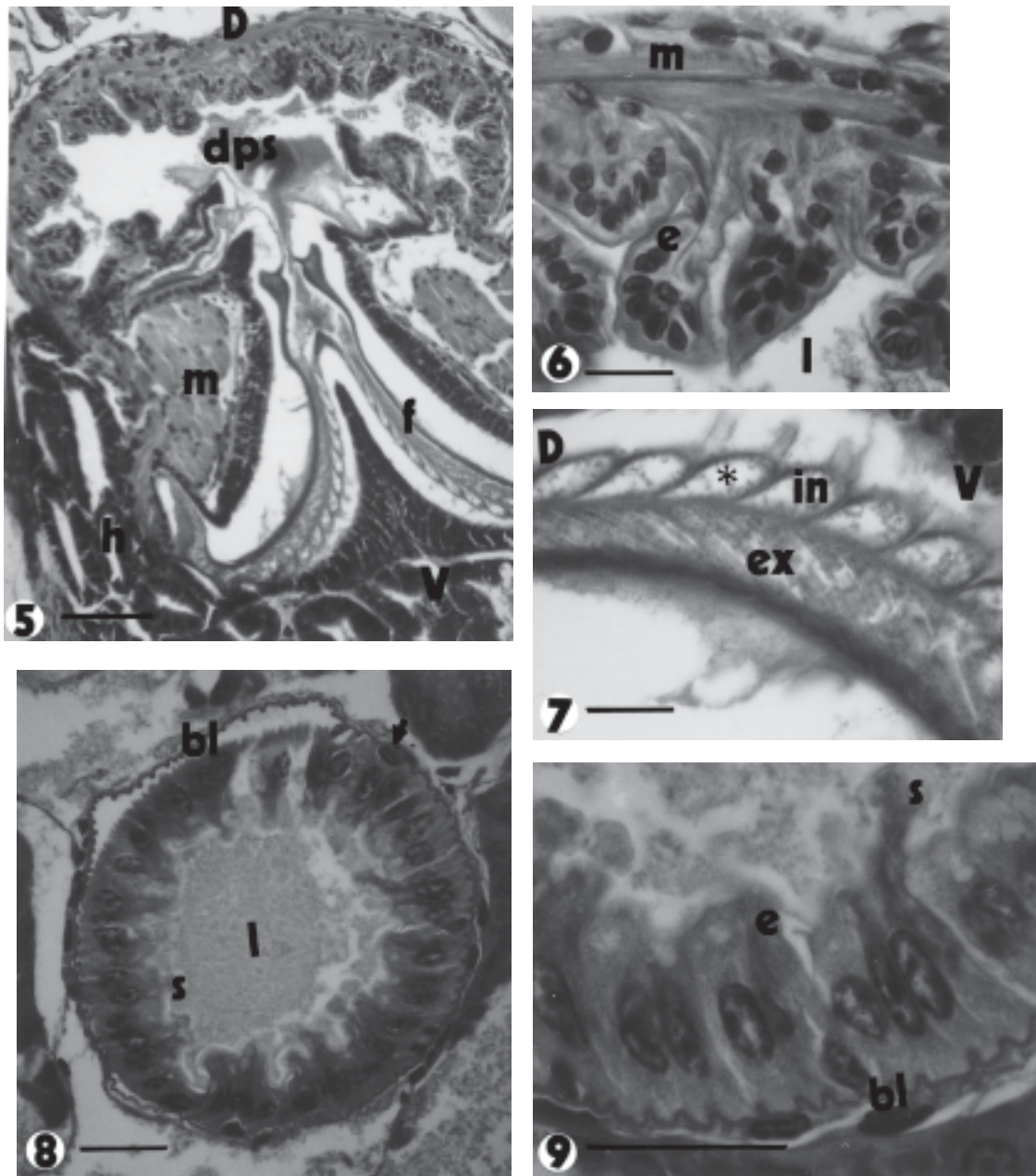


FIGURE 5. Pyloric stomach. Note the dorsal chamber and the ventral filter. D: dorsal; dps: dorsal chamber; f: filter; h: hepatopancreas; m: muscle; V: ventral. PAS. Scale bar: 100 μ m.

FIGURE 6. Pyloric stomach, detail of the dorsal chamber. e: epithelium; l: lumen; m: muscle. PAS. Scale bar: 25 μ m.

FIGURE 7. Detail of the double structure of the pyloric filter. Note the longitudinal channels formed by the dorsally curved setae (*). D: dorsal; ex: external elongated setae; in: inner setae; V: ventral. PAS. Scale bar: 25 μ m.

FIGURE 8. Cross section of the midgut showing the cylindrical epithelium and the basal cells (arrow). bl: basal lamina; l: lumen; s: secretion. H&E. Scale bar: 25 μ m

FIGURE 9. Detail of the midgut epithelium. bl: basal lamina; e: epithelium; s: secretion. H&E. Scale bar: 25 μ m.

weakly PAS positive. Beneath the basal lamina are bands of circular and longitudinal muscle. The epithelium and the basal lamina form longitudinal folds.

The hindgut is lined by a simple cylindrical epithelium with central nuclei; the thin basal lamina is underlain by spongy connective tissue. The hindgut wall presents deep longitudinal folds and conspicuous bundles of striated longitudinal and circular muscle; the cuticle is thicker than in the midgut and presents small folds. In the anterior portion, there are numerous tegumental glands that share similar characteristics with those of the oral region and of the oesophagus. The posterior portion shows a great development of striated circular muscle towards the anus.

Discussion

The main features of *P. argentinus* digestive tract are coincident with the general plan of decapods; however, it presents certain particular characteristics. The oesophagus is a simple muscular tube which drives the food into the cardiac stomach. The wall folds permit to change the distension degree in relation to the size and amount of ingested food. Contrasting with that observed in big Decapoda (Barker and Gibson, 1978; Factor, 1995) and in Mysidacea (De Jong and Casanova, 1997), no oesofagic valve was observed. This fact suggests that non ingested food could be regurgitated. The absence of this valve was also mentioned for some braquiurans such as *Menippe rumphii* (Erri Babu *et al.*, 1982).

The cardiac stomach of *P. argentinus* is a simple sac without calcified structures in the interior, which is quite common in caridean prawns (Boschi and Angelescu, 1962; Icely and Nott, 1992). Yet, the cardiac chamber of the caridean prawn *Macrobrachium borelli* has calcified elements in the anterior wall (Boschi, 1981). The reduction of the gastric mill in *P. argentinus* is compensated by the presence of complex and quitinized mandibles, with enough rigidity to reduce in size big pieces of food (Boschi, 1981). As other palaemonids, this species triturates the food with its powerful mandibles before entering the mouth parts and being mixed with the mucus (Collins, 1999). Coincidentally, Pathwardan (1935) suggested that the gastric mill efficiency is inversely correlated to the mandibles efficiency. The gastric mill reduction and the wall folds make *P. argentinus* cardiac stomach to be an extensible sac, which would permit food storage. Muscular development in the stomach wall suggests that, as in other species, contractions of the wall contribute to mix food with

digestive enzymes from the hepatopancreas and make possible the mechanical action of the serrated cuticle.

P. argentinus pyloric stomach shares similar general characteristics with other decapods (Icely and Nott, 1992). The double structure of the filter ensures that only the smallest particles pass into the hepatopancreas, increasing the filter efficiency. The outer filter setae press the finest particles towards the inner filter and also eliminate the big particles towards the midgut (Kunze and Anderson, 1979; Lin, 2000). The width of the longitudinal channels is approximately 16-18µm in *P. argentinus* and this width is within the range found in species feeding on fine particles. In coincidence, Lin (2000) indicated that the width of longitudinal channels in *Penaeus monodon* and *Metapenaeus ensis* is 16-18µm at different body lengths. However, in macrophagus species the longitudinal channels width is about 30µm (Schaefer, 1970). In coincidence, Caine (1976) observed that the space between setae has a direct correlation with diet, with spacing increasing with increased macrophagy.

In the midgut, the final phases of the digestive cycle take place: digestion of products coming from the cardiac stomach, absorption and processing of digestive products, and removal of residual wastes that will form the faeces (Icely and Nott, 1992). The midgut epithelium is considered an active epithelium that regulates water flux and ion transport (Icely and Nott, 1992). In the present study, the midgut epithelium comprises mainly one cell type, and little basal cells appear scattered between the others. These characteristics are coincident with that described for other decapods (Pillai, 1960; Icely and Nott, 1992). The predominant cells were observed at different phases of secretory activity. Some authors suggests that the basal cells function as replacement elements; however, Mycles (1979) found that cell division was confined to the distal end of the gut caeca. On the other hand, the origin of replacement cells is unknown in species lacking midgut caeca (Icely and Nott, 1992), such as *P. argentinus*; in this study the basal cells were not observed in mitosis, for this fact they can not be affirmed as replacement elements.

The passage of solid materials into the midgut produces a volume increment that is accommodated by the epithelium and basal lamina folds. The mucopolysaccharides detected on the epithelium and lumen may lubricate the indigestible food bolus as it passes towards the hindgut. In agreement with this, the presence of these macromolecules has been mentioned for several decapod species, and they seem not to be associated to digestive processes (Lovett and Felder, 1990; Johnston and Alexander, 1999).

P. argentinus hindgut shares similar histological features with the rest of decapods, and is involved in defecation which is facilitated by contractions of the wall muscles (Barker and Gibson, 1978; Icely and Nott, 1992; Factor, 1995; Johnston and Alexander, 1999). The wall folds permit to resist great volume changes; the thick cuticle and the secretion of the tegumental glands that lubricate the surface protect the epithelium from abrasion. In some decapods, the hindgut epithelium is lined by spines projected posteriorly to prevent back flow of material (Hopkin and Nott, 1980; Johnston and Alexander, 1999). In contrast, these spines were not observed in *P. argentinus*. As in other species, the well developed circular muscle around the anus of *P. argentinus* is probably involved in constricting the lumen to force the faeces through the anus to the exterior (Johnston and Alexander, 1999).

The general features of *P. argentinus* digestive tract are similar to those of most of decapods. As a special feature, the lack of a well structured gastric mill can be mentioned, which as in some other carideans would be reduced to numerous wall folds and a serrated cuticle. On the other hand, many Caridea and all the Penaeoidea have complex gastric mills and mandibles (Felgenhauer and Abele, 1985). Some studies showed that the digestive tract morphology depends primarily on the species phylogeny; however, other factors such as dietary preferences can modify its anatomy (Suh, 1990; Icely and Nott, 1992; De Jong, 1996). Collins (1999) studied the natural feeding of *P. argentinus* determining that it is an omnivorous / detritivorous species with the predominant presence of phytoplankton and benthic microinvertebrates in the diet. Consequently, the reduction of the gastric mill and the width of the longitudinal channels in the inner valve of the pyloric filter are related to the predominantly detritivorous diet.

Several authors described important pathological changes in the hepatopancreas, gills, midgut, oesophagus, stomach and hindgut of different decapod crustaceans exposed to pesticides and heavy metals (Nimmo and Blackman, 1972; Doughtie and Rao, 1984; Meyers and Hendricks, 1985). Further work, particularly, chemical and histological studies on the digestive tract of *P. argentinus* will be carried out to detect the effect of pesticides on the functional cytology of the different organs.

Acknowledgements

The present work was supported by a grant from Universidad Nacional de Mar del Plata (2003-2005) and

is part of a project financed by Consejo Nacional de Investigaciones Científicas y Técnicas (PIP N° 2882/2000).

References

- Barker PL, Gibson R (1978). Observations on the structure of the mouthparts, histology of the alimentary tract, and digestive physiology of the mud crab *Scylla serrata* (Forskål) (Decapoda: Portunidae). *J Exp Mar Biol Ecol* 32: 177-196.
- Bell TA, Lightner DV (1988). A handbook of normal Penaeid shrimp histology. World Aq. Soc. Allen Press, Inc. (USA). 144pp.
- Boschi EE (1981). Decapoda Natantia. In: Fauna de agua dulce de la República Argentina. Vol. 26. FECIC, Buenos Aires, 61 pp.
- Boschi EE, Angelescu V (1962). Descripción de la morfología externa e interna del langostino con algunas aplicaciones de índole taxonómica y biológica, *Pleoticus muelleri* (Bate), Crustacea, familia Penaeidae. *Bol Inst Biol Mar* 1:1-73.
- Caine EA (1975). Feeding and masticatory structures of six species of the crayfish genus *Procambarus* (Decapoda: Astacidae). *Forma et Functio* 8: 49-66.
- Caine EA (1976). Relationship between diet and the gland filter of the gastric mill in hermit crabs (Decapoda, Paguridae). *Crustaceana* 31: 312-313.
- Collins PA (1999). Feeding of *Palaemonetes argentinus* (Decapoda: Palaemonidae) from an oxbow lake of the Paraná River, Argentina. *J Crust Biol* 19(3): 485-492.
- Cox SL, Bruce MP (2003). Feeding behaviour and associated sensory mechanisms of stage I-III phyllosoma of *Jasus edwardsii* and *Jasus verreauxi*. *J Mar Biol Ass UK* 83: 465-468.
- Cox SL, Johnston JD (2003). Developmental changes in the structure and function of mouthparts of phyllosoma larvae of the packhorse lobster, *Jasus verreauxi* (Decapoda: Palinuridae). *J Exp Mar Biol Ecol* 296: 35-47.
- Cox SL, Johnston JD (2004). Developmental changes in foregut functioning of packhorse lobster, *Jasus (Sagmariasus) verreauxi* (Decapoda: Palinuridae), phyllosoma larvae. *Mar Freshw Res* 55: 1-9.
- De Jong L (1996). Functional morphology of the foregut of *Lophogaster typicus* and *L. spinosus* (Crustacea, Mysidacea, Lophogastrida). *Cah Biol Mar* 37: 341-347.
- De Jong L, Casanova B (1997). Comparative morphology of the foregut of three *Eucopeia* species (Crustacea, Mysidacea, Lophogastrida). *J Nat Hist* 31: 389-402.
- Diaz AC, Petriella AM, Sousa LG (1998). Setogenesis and growth of the freshwater prawn *Palaemonetes argentinus* (Decapoda, Caridea, Palaemonidae). *Iheringia Sér Zool* 85: 59-65.
- Doughtie DG, Rao KR (1984). Histopathological and ultrastructural changes in the antennal gland, midgut, hepatopancreas, and gill of grass shrimp following exposure to hexavalent chromium. *J Inv Pathol* 43(1): 89-108.
- Erri Babu D, Shyamasundari K, Hanumantha Rao K (1982). Studies on the digestive system of the crab *Menippe rumphii* (Fabricius) (Crustacea: Brachyura). *J Exp Mar Biol Ecol* 58: 175-191.
- Factor JR (1995). The digestive system. In: Biology of the lobster *Homarus americanus*. Academic Press, New York. pp. 395-440.
- Felgenhauer BE, Abele LG (1985). Feeding structures of two atyid shrimps with comments on caridean phylogeny. *J Crust Biol* 5: 397-419.

- González Sagrario MA, Aizpún de Moreno JE, Moreno VJ, Escalante AH (1998). Dynamics of organochlorine compounds in different trophic levels of Los Padres Pond in Argentina. I. Pesticides. *Environ Sci* 6(3): 153-170.
- Hopkin SP, Nott JA (1980). Studies on the digestive cycle of the shore crab *Carcinus maenas* (L) with special reference to the B-cells in the hepatopancreas. *J Mar Biol Ass UK* 60: 891-907.
- Icely JD, Jones DA (1978). Factors affecting the distribution of the genus *Uca* (Crustacea: Ocypodidae) on an East African shore. *Est Coast Mar Sci* 6: 315: 325.
- Icely JD, Nott JA (1992). Digestion and absorption: digestive system and associated organs. In: *Microscopic anatomy of invertebrates: Decapod, Crustacea*. Vol. 10. F.W. Harrison and A.G. Humes, Eds. Wiley-Liss Inc., N.Y., pp 147-201.
- Johnston DJ, Alexander CG (1999). Functional morphology of the mouthparts and alimentary tract of the slipper lobster *Thenus orientalis* (Decapoda: Scyllaridae). *Mar Freshw Res* 50: 213-223.
- Kunze JC, Anderson DT (1979). Functional morphology of the mouthparts and gastric mill in the hermit crab *Clibanarius taeniatus* (Milne Edwards), *Clibanarius virescens* (Krauss), *Paguristes squamosus* McCulloch and *Dardanus setifer* (Milne Edwards) (Anomura: Paguridae). *Aust J Mar Freshw Res* 30: 683-722.
- Lin FY (1996). Structure of the gland filters in the pyloric stomach of *Penaeus japonicus* (Decapoda: Penaeidae). *J Crust Biol* 16(3): 515-521.
- Lin FY (2000). Scanning electron microscopic observations on the gland filters of the pyloric stomach of *Penaeus monodon* and *Metapenaeus ensis* (Decapoda, Penaeidae). *Crustaceana* 73(2): 163-174.
- Lovett DL, Felder DL (1990). Ontogenetic changes in enzyme distribution and midgut function in developmental stages of *Penaeus setiferus* (Crustacea, Decapoda, Penaeidae). *Biol Bull* 178: 160-174.
- Menone M (1999). Evaluación de la contaminación por plaguicidas y bifenilos policlorados en la Albufera Mar Chiquita. Tesis. Facultad de Ciencias Exactas y Naturales, Univ. Nac. Mar del Plata. 148 pp.
- Meyers TR, Hendricks JD (1985). Histopathology. In: *Fundamentals of aquatic Toxicology*. Rand GM, Petrochelli SR, Eds. McGraw Hill Int. Book Co, Johannesburg, pp. 283-331.
- Miglioranza KS, González Sagrario MA, Aizpún de Moreno JE, Moreno VJ, Escalante, AH, Osterrieth ML (2002). Agricultural soil as a potential source of input of organochlorine pesticides into a nearby pond. *Environ Sci Poll Res* 9(4): 250-256.
- Morrone JJ, Lopreto EC (1995). Parsimony analysis of endemism of freshwater Decapoda (Crustacea: Malacostraca) from Southern South America. *Neotropica* 41: 3-8.
- Mycles DL (1979). Ultrastructure of alimentary epithelia of lobsters, *Homarus americanus* and *H. gammarus*, and crab *Cancer magister*. *Zoomorphology* 92: 201-215.
- Nimmo DR, Blackman RR (1972). Effects of DDT on cations in the hepatopancreas of penaeid shrimp. *Trans Am Fish Soc* 101(3): 547-549.
- Pathwardan SS (1935). On the structure and mechanism of the gastric mill on Decapoda. II. A comparative account of the gastric mill in Brachyura. *Proc. Indian. Acad. Sci.* Vol 1B. p 359-375.
- Pillai RS (1960). Studies on the shrimp *Caridina laevis* (Heller). 1. The digestive system. *J Mar Biol Assoc India* 2: 57-74.
- Pinn EH, Atkinson RYA, Rogerson A (1998). The diet of two mudshrimps, *Calocaris macandreae* and *Upogebia stellata* (Crustacea: Decapoda, Thalassinidae). *Ophelia* 48: 211-223.
- Schaefer N (1970). The functional morphology of the foregut of three species of decapod Crustacea: *Cyclograpsus punctatus* Milne-Edwards, *Diogenes brevirostris* Stimpson, and *Upogebia africana* (Ortmann). *Zoologica Africana* 5: 309-326.
- Sousa LG (2003). Estudio sobre las modificaciones tisulares del camarón *Palaemonetes argentinus* (Crustacea, Decapoda, Caridea). Su empleo como indicadores de contaminación. Tesis. Facultad de Ciencias Exactas y Naturales, Univ. Nac. Mar del Plata. 138 pp.
- Sousa LG, Petriella AM (2000). Histology of the hepatopancreas of the freshwater prawn *Palaemonetes argentinus* (Crustacea, Caridea). *Biocell* 24(3): 189-195.
- Sousa LG, Petriella AM (2001). Changes in the hepatopancreas histology of *Palaemonetes argentinus* (Crustacea, Caridea) during moult. *Biocell* 25(3): 275-281.
- Sousa LG, Cuartas EI, Petriella AM (2005). Fine structural analysis of the epithelial cells in the hepatopancreas of *Palaemonetes argentinus* (Crustacea, Caridea). *Biocell* 29(1): 25-31.
- Spivak ED (1997). Life history of a brackish-water population of *Palaemonetes argentinus* (Decapoda: Caridea) in Argentina. *Ann Limnol* 33: 179-190.
- Suh HL (1990). Morphology of the gastric mill of the genus *Thysanopoda* (Euphausiacea). *J Crust Biol* 10: 479-486.
- Vogt G (1987). Monitoring of environmental pollutants such as pesticides in prawn aquaculture by histological diagnosis. *Aquaculture* 67:157-164