Braz. J. Vet. Res. Anim. Sci.,
São Paulo, v. 35, n. 1, p. 32-36, 1998.

Food passage time through the alimentary tract of a brazilian teleost fish, *Prochilodus scrofa* (Steindachner, 1881) using radiography

Tempo de trânsito alimentar no trato digestivo de um teleósteo brasileiro, *Prochilodus scrofa* (Steindachner, 1881) com o uso da radiografia

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SUMMARY

Food passage time through the digestive tract of a detritivorous freshwater fish (*Prochilodus scrofa*) was determinate by radiographic techniques using barium sulfate as a contrast medium. The fish were kept in tanks at a constant temperature of 23.5ºC and received by an oral catheter a mixture of 2.5 parts of ground ration and 1 part of oral suspension of contrast medium (Celobar). Radiographs were taken at intervals of 3 hours. Immediately after the introduction of the mixture the stomach was outlined by the contrast. A sphincter was observed between the cardiac and the muscular stomachs. After 3 hours, 80 per cent of the proximal intestine was filled. After 6 hours the contrast reached the proximal, medial and distal portions of the intestine. After 9 hours 70 per cent of the distal intestine was filled and after 12 hours, the rectum segment was still marked (25 per cent of the distal portion of the intestine).

UNITERMS: Intestine; Digestive system; Radiography; Fish.

INTRODUCTION

The interest in fish culture in Brazil has increased considerably during the last years. Lack of nutrition data and food management of the native species are among the difficulties found by our breeders, turning their production objectives towards non native species, which already have technology developed in these areas.

Prochilodus scrofa is among the native species with good performance for fish culture, exhibiting high rusticity in management and high fertility[38], besides being an excellent nutritive source, with energetic values similar to those showed by other fish with high protein level[26].

For this species, the available literature contains a number of works related to its farming, reproduction, histophysiology and anatomy of digestive tract[1,10,12,22,23,25,30,31].

The determination of food income of a population in its habitat is a recurrent problem in ecological studies of fish. This determination provides the basis for research related to development and productive effectiveness, as well as for the calculation of energetic stocks. The time between ingestion and evacuation or the food passage time through the digestive tract is a parameter particularly useful in the calculation of food consumption[17,42,43]. The knowledge of gastric emptying time and the food passage time through the intestinal duct constitute important parameters for the determination of fish nutrition management. Ricker[36] recognizes the gastric emptying time as an important parameter for the determination of the ration amount to be offered. Magnuson[27] points out the relevance of this item, specifying the relationships between the stimulus for feeding and the appetite, the feeding activity and the amount of food in the stomach. Elliott[7,9] establishes the relationship of gastric emptying time to the maximum stomach capacity for food consumed in different temperatures and Pandian[33,34] establishes this relationship for food conversion.

A number of techniques has been used in the determination of the gastric emptying rate and the food passage time through the digestive tract in fish. Among them we can find: dissection[5], emetics[19], stomach suction[8,40], radioactive labeled food and radioisotopes[35,39], monitoring feces production[21], artificial food[13] and radiography[3,11,18,41,42]. This last method provides great advantages in studying non osseous structures, like elucidating aspects of functional activity in fish, besides being a non invasive method of enormous convenience[3].

An important aspect to be considered in this species is its iliophagous and detritivorous feeding habit, i.e., the ingestion of food with low protein, fat, carbohydrate and energetic levels[24]. This could force this fish to feed continuously in order to satisfy its nutritional needs, filling completely its digestive tract[1].

This work has for its objective the investigation of food passage time through the alimentary channel in *P. scrofa*, using radiographic techniques and barium sulfate as a contrast medium.

We should still consider the lack of works monitoring food traffic, using radiography (or other techniques) in teleosteans of similar physiology and food habits.

MATERIAL AND METHOD

This assay was taken with a homogeneous group of fish (mean weight = 103.75 g, mean length = 19.1 cm), which were kept in tanks (2,000 liters) at the Instituto de Pesca (Fishery Institute), with continuous air and water flows, at a constant temperature (23.5ºC) kept by thermostat. There was a 4 month period for the adaptation of fish to captivity conditions before the beginning of the experiment.

During this period, assays were made in order to determine the ideal intervals between radiographs, as well as the kilovoltage (40 kV) and milliamperage (6 mAs) of the radiograph equipment (CGR - Chenon C. Paux, model G.T. - 300), besides improving the used techniques.

The population density in tanks did not exceed 5 fishes per aquarium. There was no change in photoperiod, because the tanks were located near windows, allowing penetration of diurnal light.

Before the beginning of the experiment, the fish were fed daily *ad libitum* with pattern fish food, produced by the Instituto de Pesca.

For the experiment, *P. scrofa* was submitted to a starvation period of 72 hours in order to ensure the complete emptying of the digestive tract, and after that, they were transferred to test tanks where they were anaesthetized (Benzocaine - 40 ppm).

The fish received simultaneously, directly into the cardiac stomach through a canule coupled to a syringe, ground and siftened ration, added with contrast medium in the proportion of 2.5 parts of ration by 1 part of contrast medium (CELOBAR - barium sulfate/ carboximetilcellulose sodic - oral suspension - BEECHAM), being after that returned to the initial tanks. This procedure is essential to ensure precisely the amount of food and the time of ingestion. At each 3 hour interval, 4 fish were collected, anaesthetized and had their radiographs obtained. The experiment was taken in periods of 3, 6, 9 and 12 hours after the administration of the mixture ration/contrast. One radiograph was obtained immediately after the inoculation.

According to the morphometrical analysis developed by Leite *et al.*[23], for the determination of the relationship of the stomach volume/fish weight, it was possible to establish the ideal amount of mixture to be administered to each fish, approximately 1 ml.

In this paper the anatomical topographic patterns described by Barbieri *et al.*[1] (Fig. 1 and 2) were used for the recognition of the intestinal segments radiographically marked by the food mixture.

Gastric emptying was considered complete with the disappearance of the residues of the contrast from the cardiac and pyloric stomachs. The intestinal emptying was determinated by the arrival of the food mixture to the last intestinal segment, more precisely the rectum segment.

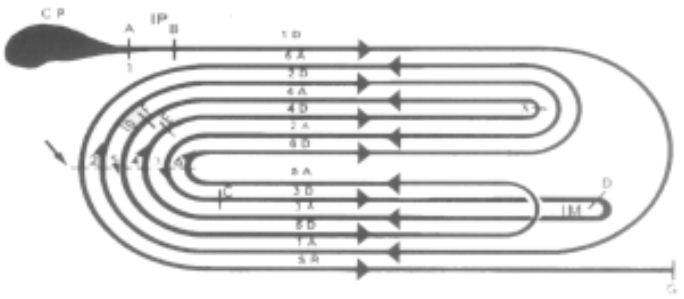

Figure 1
Scheme of the tangle of the intestinal segments of *P. scrofa*. The arrows indicate the direction in which the food flows through the intestine: 1...6 indicate the segments, A and D inform if the segment is ascending or descending. IP = Proximal intestine, IM = Medial intestine, ID = Distal intestine. The bigger arrow indicates the point where the rectum segment begins.

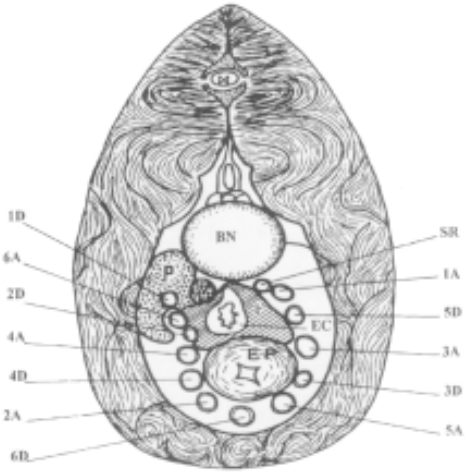

Figure 2
P. scrofa in transversal section at dorsal fin level showing the gastrointestinal organs in their normal position inside the abdominal cavity. 1...6 indicate the segments, A and D inform if the segment is ascending or descending. SR = Rectum segment. (EC = cardiac stomach, EP = pyloric stomach, P = pyloric caeca, BN = bladder, F = liver).

RESULTS

It can be observed in Fig. 3, which is the radiograph obtained immediately after the introduction of the food mixture, that there is a complete filling of the cardiac and pyloric stomachs. At this point there can be observed the presence of a site between the cardiac and the pyloric stomachs that was not filled by the contrast. When the image is overlaid onto the anatomical scheme of the stomach (Fig. 4), it can be seen that the non-contrasted site corresponds to the small caecal segment, described by Hernandez-Blazquez *et al.*[16], which remains empty.

The obtained results showed that 3 hours after the introduction of the food mixture, *P. scrofa* still presented full cardiac and pyloric stomachs, with 80 per cent of the proximal intestinal portion now full, represented by the segments 1D, 1A, 2D and 2A (Fig. 5A, B).

After 6 hours, the complete gastric emptying and the filling of the intestinal proximal, medial and distal portions (segments 1, 2, 3, 4, 5, and 6) were observed (Fig. 6A, B).

After 9 hours (Fig. 7A, B), only 70 per cent of the distal portion were filled (5D, 5A, 6D, 6A and rectum segments) and after 12 hours (Fig. 8) the partial fulfillment (25 per cent) of the distal intestinal portion was observed, more precisely the rectum segment.

DISCUSSION

The anatomy of the digestive tract of *P. scrofa* is complex, with a composed stomach (cardiac, caecal and pyloric), besides a pyloric caeca and an enormously tangled intestine. This aspect is very common in herbivorous fish and in those that ingest food that is difficult to digest, probably in order to increase the absorption area[1,23]. Although the anatomical aspect of the composed stomach was studied by Hernandez-Blazquez *et al.*[16], the caecal stomach functions are not yet well defined. From the images obtained immediately after the introduction of the contrast mixture (Fig. 3), we can conclude that the composed stomach is divided in two compartments joined by the caecal stomach, which plays the role of a sphincter, isolating the cardiac stomach from the pyloric (muscular) one, avoiding the reflux of the food that would be produced by smooth muscle under intraluminal pressures.

It is important to emphasize that many factors can change the gastric emptying time and the food traffic through the intestine in fish, e.g. the water temperature, the period of starvation before the experiment, the stress caused by handling, the force feeding, the composition of the food and the fish size[6,11,17,29,37].

It is necessary to distinguish that, for this last parameter, Elliott[8] has not detected any effect of fish size on the gastric emptying time in *Salmo trutta*, like Hofer *et al.*[17] for the adult carp, *Rutilus rutilus* (12-18 cm of total length and 30-100 g of total weight) over the food passage time through the intestine. Jobling *et al.*[20], consider that the indication related to the effect of the fish size is controversial.

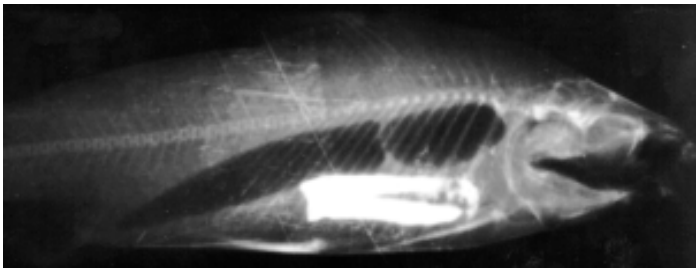

Figure 3
Radiograph obtained immediately after the introduction of the food mixture. The complete filling of the cardiac and pyloric stomachs can be observed, with a negative image of the sphincter that exists between the two stomachs.

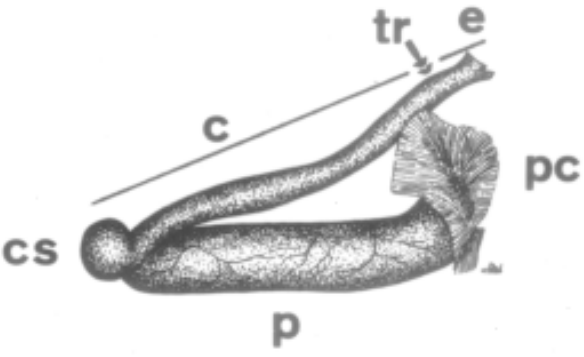

Figure 4
Esophagus and stomach of *P. scrofa* in right lateral view. Esophagus (E), transition site (*arrow*), cardiac stomach (C), caecal stomach (CS), pyloric stomach (P), pyloric caeca (CP).

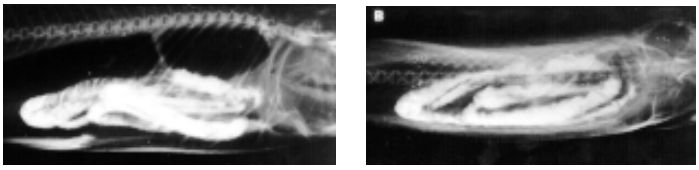

Figure 5
Radiographs of *P. scrofa* in lateral (A) and dorsal (B) view, 3 hours after the introduction of the alimentary mixture, when there was the filling of the cardiac and pyloric stomachs, besides the two first intestinal circumvolutions.

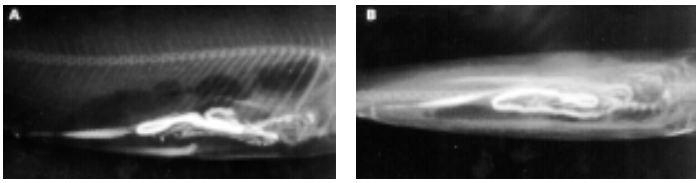

Figure 6
Radiographs obtained in lateral (A) and dorsal (B) views of *P. scrofa*, where the filling of the proximal, medial and distal portions of the intestine, can be observed after 6 hours.

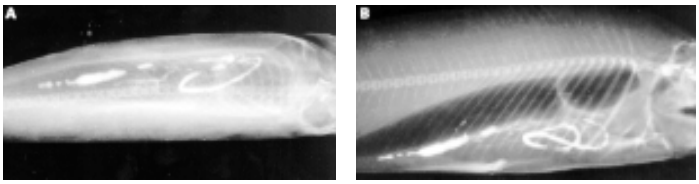

Figure 7
9 hour interval after the beginning of the experiment, showing that the mixture was filling the 5th and the 6th intestinal circumvolutions, besides the rectum segment. (A = Dorsal View; B = Lateral View).

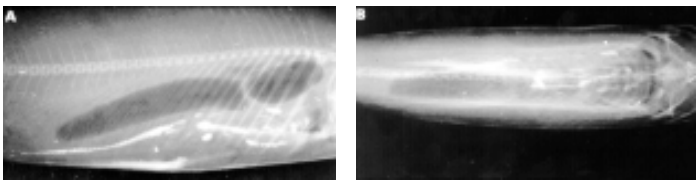

Figure 8
Lateral (A) and dorsal (B) views of *P. scrofa* and we can observe the partial filling (25 per cent) of distal portion of intestine, more precisely the rectum segment, 12 hours after.

In addition, concerning the factor of food composition, this investigation was performed with a mixture of ration/contrast, in order to avoid a greater interference in food passage time, this way providing a closer approach to natural conditions. The addition of barium sulfate to the food does not affect significantly the gastric emptying time, when compared to food without the addition of a contrast medium[20].

In our experiment, the following parameters were standardized and kept unchanged: food composition, ratio of food/ contrast, period of starvation, water temperature and fish size.

The data of the food passage time through the gastrointestinal tract obtained in this experiment are similar to those reported by Maliyenko[28] - 9:25 h - with juveniles *Rutilus rutilus* (2.0 - 10.4 cm) and those related by Opuszynski; Shireman[32] - 7.1 - 12.8 h - with *Aristichtys nobilis* (13 cm of total length).

Our results corroborate the thesis that *P. scrofa* has for its feeding habit the continuous ingestion of food, since the complete gastric emptying occurred 6 hours after the ingestion and 9 hours after being fed, 72 per cent of the digestive tract was found to be empty. Gastric emptying plays the main role in control of appetite in fish[4]. Gwither; Grove[15] connected the gastric emptying to the return of the appetite, and Magnuson[27], Beamish[2] and Grove *et al.*[14] demonstrated that hunger was determined by the amount of food present in the stomach.

Although some mechanisms involved in the mechanical function and in the control of food traffic by the digestive tract of *P. scrofa* are still unknown, it is proposed that in similar conditions to those verified in this study, the return of the appetite can occur within 6 hours after feeding, and 24 hours of starvation can assure the complete emptying of the digestive tract of *P. scrofa*.

ACKNOWLEDGMENTS

The authors are grateful to Dr. Massuka Y. Narahara, Chairwoman of Aquatic Biology Section of the Instituto de Pesca, for the facilities in the obtainment of most of the material used in this experiment.

We are also grateful to the Technicians José Plaza, from the Instituto de Pesca and Paulo G. G. Marin and Jorge L. Sepatini, from the Radiological Service - Clinical Surgery - Veterinary Medicine College - University of São Paulo, for their cooperation during the experiment.

Our special thanks to Dr. Alison Colquhoun, from the University of Oxford, for her helpful hints in the English revision.

RESUMO

O tempo de passagem de alimentos através do trato digestivo do peixe detritívoro de água doce *Prochilodus scrofa* foi determinado com o uso de técnicas radiográficas e de sulfato de bário como meio de contraste. Os peixes foram mantidos em tanques com temperatura constante de 23ºC e receberam via oral, através de um cateter, uma mistura de 2,5 partes de ração peletizada moída e 1 parte de suspensão oral do meio de contraste (Celobar). As radiografias foram obtidas em intervalos de 3 horas. Imediatamente após a introdução da mistura, visualizou-se o preenchimento gástrico pelo contraste. Foi observado um esfíncter existente entre os estômagos cárdico e pilórico. Após 3 horas, 80 por cento do intestino proximal estava repleto. Após 6 horas, o contraste atingiu as porções proximal, média e distal do intestino. Após 9 horas, 70 por cento do intestino distal estava repleto, e após 12 horas, havia a marcação do segmento do reto (25 por cento da porção distal do intestino).

UNITERMOS: Intestino; Sistema digestivo; Radiografia; Peixes.

REFERENCES

1- BARBIERI, R.L.; LEITE, R.G.; HERNANDEZ-BLAZQUEZ, F.J. Morphologie du tract digestif du curimbatá, *Prochilodus scrofa*. I. Anatomie Intestinale. **Ciência e Cultura**, v.41, n.1, p.61-70, 1989.

2- BEAMISH, F.W. Ration size and digestion in large mouth bass, *Micropterus salmoides* Lacépède. **Canadian Journal of Zoology**, v.50, n.1, p.153-64, 1972.

3- BELL, G.R.; BATEMAN, J.E. Some radiographic observations on the gastro-intestinal and urinary systems of anesthetized pacific salmon (ONCHORHYNCUS). **Canadian Journal of Zoology**, v.38, n.1, p.199-202, 1960.

4- BRETT, J.R.; HIGGS, D.A. Effect of temperature on the rate of gastric digestion in fingerling sockeye salmon, *Onchorhynchus nerka*. **Journal of the Fisheries Research Board of Canada**, v.27, n.3, p.1767-79, 1970.

5- COLLINS, M.R. The feeding periodicity of stripped mullet *Mugil cephalus* L., in two Florida habitats. **Journal of Fish Biology**, v.19, n.2, p.309-15, 1981.

6- EDWARDS, D.J. Effect of temperature on rate of passage of food through the alimentary canal of the plaice *Pleuronectes platessa* L. **Journal of Fish Biology**, v.3, n.2, p.433-9, 1981.

7- ELLIOTT, J.M. Number of meals in a day, maximum weight of food consumed in a day and maximum rate of feeding for brown trout *Salmo trutta* L. **Freshwater Biology**, v.5, n.2, p.294-303, 1975b.

8- ELLIOTT, J.M. Rates of gastric evacuation in brown trout *Salmo trutta*. **Freshwater Biology**, v.2, n.1, p.1-18, 1972.

9- ELLIOTT, J.M. Weight of food and time required to satiate brown trout, *Salmo trutta* L. **Freshwater Biology**, v.5, n.2, p.287-93, 1975a.

10- FENERICH-VERANI, N.; GODINHO, H.M.; NARAHARA, M.Y. The size composition of the eggs of curimbatá, *Prochilodus scrofa* Steindach. 1881, induced to spawn with human chorionic gonadotropin (HCG). **Aquaculture**, v.47, n.1, p.37-41, 1984.

11- FLOWERDEW, M.W.; GROVE, D.J. Some observations of the effects of the body weight, temperature, meal size, and quality on gastric emptying time in the turbot *Scophtalmus maximus* (L.) using radiography. **Journal of Fish Biology**, v.14, n.1, p.229-38, 1979.

12- GODINHO, H.M.; ROMAGOSA, E.; CESTAROLLI, M.A.; NARAHARA, M.Y.; FENERICH-VERANI, N. Reprodução induzida de curimbatá, *Prochilodus scrofa*, Steind. 1881, sob condições de cultivo experimental. **Revista Brasileira de Reprodução Animal**, Belo Horizonte, v.8, n.2, p.113-9, 1984.

13- GROVE, D.J.; CRAWFORD, C. Correlation between digestion rate and feeding

frequency in the stomachless teleost, *Blennius pholis* L. **Journal of Fish Biology**, v.16, n.3, p.235-47, 1980.

14- GROVE, D.J.; LOZOIDES, L.; NOTT, J. Satiation amount, frequency of feeding and gastric emptying rate in *Salmo gairdneri*. **Journal of Fish Biology**, v.14, n.2, p.539-46, 1978.

15- GWITHER, D.; GROVE, D.J. Gastric emptying in *Limanda limanda* (L.) and the return of appetite. **Journal of Fish Biology**, v.18, n.2, p.245-9, 1981.

16- HERNANDEZ-BLAZQUEZ, F.J.; FERREIRA, N.; CARVALHO, A.A.F. de; FERRI, S. Morphological Aspects of the Esophagus and Stomach of a Freshwater Iliophagous Fish under Scanning Electron Microscopy. **Gegenbaurs morphologisches Jahrbuch**, v.136, n.1, p.119-225, 1990.

17- HOFER, R.; FORSTNER, H.; RETTENWANDER, R. Duration of gut passage and its dependence on temperature and food consumption in roach *Rutilus rutilus* L.: Laboratory and field experiments. **Journal of Fish Biology**, v.20, n.3, p.289-99, 1982.

18- HOLMEGREEN, S.; GROVE, D.J.; FLETCHER, D.J. Digestion and control of gastrointestinal motility. *In*: RANKIN, J.C.; PITCHER, T.J.; DUNCAN, R. (Eds). **Control processes in fish physiology**. London : Croom Helm, 1983. p.23-40.

19 - JERNEJCIC, F. Use of emetics to collect stomach contents of walley and largemouth bass. **Transactions of the American Fishery Society**, v.98, n.2, p.698-702, 1969.

20- JOBLING, M.; GWITHER, D.; GROVE, D.J. Some effects of temperature, meal size and body weight on gastric evacuation time in the dab *Limanda limanda* (L.). **Journal of Fish Biology**, v.10, n.1, p.291-8, 1977.

21- LANE, T.H.; JACKSON, H.M. Voidance time for 23 species of fish. **Investigations Fishery Control**, v.33, p.1-29, 1969.

22- LEITE, R.G. **Análise quantitativa do comportamento do curimbatá, *Prochilodus scrofa*, Steindachner, 1881 (CHARACIFORMES - PROCHILODONTIDAE) em tanque com adubação orgânica**. São Carlos, 1987. 63 p. Dissertação (Mestrado) – Departamento de Ciências Biológicas, Universidade Federal de São Carlos.

23- LEITE, R.G.; BARBIERI, R.L.; HERNANDEZ-BLAZQUEZ, F.J. Morfologia do trato digestivo do curimbatá, *Prochilodus scrofa*. II Morfometria. **Boletim do Instituto de Pesca**, v.15, n.2, p.221-7, 1988.

24- LEITE, R.G.; SILVA, M.S. Determinação da composição centesimal do conteúdo do trato digestivo do curimbatá, *Prochilodus scrofa*, em tanque experimental de cultivo com adubação orgânica. *In*: REUNIÃO ANUAL DA SOCIEDADE BRASILEIRA PARA O PROGRESSO DA CIÊNCIA, 38., São Paulo, 1986. **Resumos**. São Paulo : SBPC, 1986. p.1009.

25- LEITE, R.G.; VERANI, J.R.; CESTAROLLI, M.A.; GODINHO, H.M.; FENERICH-VERANI, N.; BASILE-MARTINS, M.A. Estudos biométricos do curimbatá, *Prochilodus scrofa*, em experimento de cultivo com suplementação alimentar. (II) Crescimento. *In*: SIMPÓSIO BRASILEIRO DE AQÜICULTURA, 3., São Carlos, 1983. **Anais**. São Carlos, SP, 1984. p.345-65.

26- LESSI, E. **Aspectos químicos - bromatológicos do curimbatá, *Prochilodus scrofa* Steindachner, 1881**. Araraquara, 1965. 44p. Tese (Doutorado) – Faculdade de Farmácia e Odontologia de Araraquara.

27- MAGNUSON, J.J. Digestion and food consumption by skipjack tuna *Katsuwonus pelamis*. **Transactions of the American Fishery Society**, v.98, n.1, p.379-92, 1969.

28- MALIYENKO, A.V. Rate of passage of food through the alimentary canal in juveniles of some fish species from the Kremenchug Reservoir. **Hydrobiological Journal**, v.11, n.2, p.65-8, 1975.

29- MOLNÁR, G.; TAMASSI, E.; TÖLG, I. The gastric digestion of living predatory fish. *In*: GERKING, S.D. (Ed.) **The biological basis of freshwater fish production**. Oxford, Edinburgh. Blackwell Scientific, 1967. p.135-49.

30- NACHI, A.M. **Absorção de macromoléculas e atividade fagocitária no epitélio intestinal de *Prochilodus scrofa***. São Paulo, 1993. 81p. Tese (Doutorado) – Instituto de Ciências Biomédicas, Universidade de São Paulo.

31- NACHI, A.M. **Intestino de *Prochilodus scrofa* (Curimbatá)**: estudo histológico, histoquímico de glicoconjugados e da absorção de lipídios utilizando diferentes métodos de inclusão. São Paulo, 1988. 126p. Dissertação (Mestrado) – Instituto de Ciências Biomédicas, Universidade de São Paulo.

32- OPUSZYNSKI, K.; SHIREMAN, J.V. Food passage time and daily ration of bighead carp, *Arestichthys nobilis*, kept in cages. **Environmental Biology of Fishes**, v.30, n.1, p.387-93, 1991.

33- PANDIAN, T.J. Intake, digestion, absorption and convertion of food in fishes *Megalops cyprinoides* and *Ophiocephalus striatus*. **Marine Biology**, v.1, p.16-32, 1967a.

34- PANDIAN, T.J. Transformation of food in fish *Megalops cyprinoides* I. Influence of quality of food. **Marine Biology**, v.1, p.60-4, 1967b.

35- PETERS, D.S.; HOSS, D.E. A radio isotopic method of measuring food evacuation time in fish. **Transactions of the American Fishery Society**, v.102, p.759-63, 1974.

36- RICKER, W.E. Production and utilization of fish populations. **Ecological Monographs**, v.16, p.373-91, 1946.

37- ROZIN, P.N.; MAYER, J. Some factors influencing short-term food intake of the goldfish. **American Journal of Physiology**, v.206, n.4, p.1430-6, 1964.

38- SANTOS, E. **Peixes de água doce: vida e costumes dos peixes do Brasil**. Rio de Janeiro : F. Briguiet, 1954. 270p.

39- STOREBAKEN, T.; AUSTRENG, E.; STEINBERG, K. A method for determination of feed intake in salmonids using radioactive isotopes. **Aquaculture**, v.24, n.1, p.133-42, 1981.

40- STRANGE, C.D.; KENNEDY, G.J.A. Stomach flushing of salmonids: a simple and effective technique for the removal of stomach contents. **Fisheries Management**, v.12, n.1, p.9-15, 1981.

41- TALBOT, C.; HIGGINS, P.J.; SHANKS, A.M. Effects of pre-and post-prandial starvation on meal size and evacuation rate of juvenile Atlantic salmon, *Salmo salar* L. **Journal of Fish Biology**, v.25, n.2, p.551-60, 1984.

42- TYLER, A.V. Rates of gastric emptying in young cod. **Journal of the Fisheries Research Board of Canada**, v.27, n.11, p.1177-89, 1970.

43- WINDELL, J.T. Rates of digestion in fishes. *In*: GERKING, S.D. (Ed.) **The biological basis of freshwater production**. Oxford : Blackwell Scientific, 1967. p.151-73.

Received: 29/04/1996
Accepted: 30/07/1997