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THE RELATIONSHIP BETWEEN FEEDING HABITS AND DIGESTIVE PROTEASES OF SOME FRESHWATER FISHES

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Ya-Li Hsu and Jen-Leih Wu (1979) The relationship between feeding habits and digestive proteases of some freshwater fishes. *Bull. Inst. Zool., Academia Sinica* **18**(1): 45-53. The freshwater cultured fishes, such as *Anguilla japonica*, *Channa maculatus* and *Clarias fuscus* belong to carnivores; *Ctenopharyngodon idellus* belongs to herbivores; *Carassius auratus* and *Hypothalmichthys molitrix* belong to microphages; and *Cyprinus carpio* and *Tilapia mossambica* belong to omnivores. From the comparison of total pepsin activity in stomach, it reveals that the carnivorous fishes have highest pepsin level in their stomachs, the omnivorous fishes with stomachs have lower pepsin, while the stomachless fishes only show negligible pepsin activity in their alimentary tract. Whereas the comparison of total intestinal chymotrypsin activity, it shows that the microphageous fishes had highest chymotrypsin level, followed by omnivores, herbivores and carnivores. As in the case of intestinal trypsin, the omnivorous *T. mossambica* had highest trypsin level, followed by carnivores, herbivores and microphages. The relationship among feeding habits, relative length of the gut and intestinal chymotrypsin or stomachal pepsin level are correlated well. The carnivores with shortest gut have highest pepsin level and lowest chymotrypsin level, while the microphages with longest gut have highest chymotrypsin level and no pepsin activity. The herbivores have intermediate chymotrypsin level with intermediate gut length, but with no pepsin activity.

Fishes can be classified as carnivores, omnivores, herbivores and microphages, according to their natural feeding habits[1,2,10]. The digestive enzymes are inducible so that the higher carbohydrase activity should be found in the digestive tract of herbivores, and higher protease activity should be found in those of carnivores. The amylase level in the hepatopancreas of common carp was found to be much higher than that of blue gill sunfish or largemouth bass[10]. Kitamikado and Tachino[11] found that the digestive amylase level in common carp was higher than that in rainbow trout. Morishita *et al.*[16] also found a lower amylase activity in the digestive tract of salmon, eel and yellowtail jack than that of common carp and ayu. However, Kawai and Ikeda[7,9] found that the diet composition is not always a dominant factor to affect the quantity of the amylase.

As far as the protease activity is concerned, the difference among different feeding habits are far less significant. The data obtained has shown that the digestive protease activity of fishes always correlated with sex[10], age[22], spawning[10], diet composition[7,8], feeding intensity[10,17], feeding frequency[22], season[3], and salinity[12]. The ambiguity is due to the protease assay is not specific enough to distinguish the various proteases. Therefore, the relationship between fish pepsin, trypsin and chymotrypsin activity and their feeding habits remains to be established.

In this study, eight cultured fishes with

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typical different feeding habits in Taiwan were examined by pepsin-, trypsin- and chymotrypsin-specific enzyme assay methods. The result shows that carnivorous fishes have highest stomachal pepsin levels but have lowest intestinal chymotrypsin levels. The microphageous fishes have highest intestinal chymotrypin levels but have lowest intestinal trypsin level and no pepsin activity. The correlation among feeding habits, relative length of the gut and digestive proteases were discussed.

MATERIALS AND METHODS

Fishes

The following cultured freshwater fishes were bought for this study.

Anguilla japonica (Japanese eel), carnivores, weight 400–650 g.

Channa maculatus (Formosan snakehead), carnivores, weight 150–250 g.

Clarias fuscus (Formosan freshwater catfish), carnivores, weight 100–150 g.

Cyprinus carpio (common carp), omnivores, weight 450–750 g

Tilapia mossambica (tilapia), hybrid, omnivores, weight 180–300 g.

Ctenopharyngodon idellus (grass carp), herbivores, weight 800–900 g.

Carassius auratus (golden crucian carp), microphages, weight 350–550 g.

Hypophthalmichthys molitrix (silver carp), microphages, weight 1000–1200 g.

Enzyme preparation

Fishes had been fasted for at least 18 hours before sacrifice. Diffferent parts of the alimentary tract and other organs such as oesophagus, stomach, pyloric caeca, intestine, hepatopancreas and spleen were kept in an ice box. The tissue was divested of fat and connective tissue and blotted on filter paper, weighed, cut into small pieces, and homogenized with a Poltler-Elvehjem homogenizer in 4 vol (v/w) of chilled 0.05 M Tris-HCl, pH 7.0. The homogenated tissue was centrifuged at 1,400×g for 30 min at 0°C and the resulting supernatant was used for the following enzyme assay.

Enzyme assay

Chymotrypsin: Chymotrypsin activity was assayed by the difference in absorption between the undissociated carboxyl group of L–tyrosine ethyl ester and dissociated L–tyrosine[20]. The reaction can be monitored by adding 10 μl of properly diluted tissue homogenate to 0.99 ml substrate solution containing 0.002 M L–tyrosine ethyl ester, 0.05 M Tris-HCl, pH 7.0, and 0.45 M $CaCl_2$. The optical density was measured at 234 nm against 0.001 M L–tyrosine. The total activity of chymotrypsin was expressed in μ moles substrate hydrolyzed/10 min/100 g B. W..

Trypsin: Trypsin activity was assayed by direct spectrophotometric measurement of the carboxyl group liberated from benzoyl–L–arginine methyl ester (BAME)[20]. With the total volume of 1.0 ml, the reaction was monitored by adding 20 μl of properly diluted tissue homogenate to 0.98 ml substrate solution containing 0.001 M BAME, 0.05 M Tris-HCl, pH 8.0, and 0.45 M $CaCl_2$. The substrate solution and tissue homogenate were prewarmed to 27°C in a water bath. The optical density was measured at 254 nm. The total activity of trypsin was expressed in μ moles substrate hydrolyzed/min/100 g B. W..

Pepsin: Pepsin activity was assayed by spectrophotometric measurement of the tyrosine and tryptophan liberated from casein substrate[21]. The reaction was proceeded by adding 0.5 ml of properly diluted enzyme solution to 2.5 ml of substrate solution containing 2% casein, and 0.06 N HCl, pH 1.8, at 35.5°C. After 10 min incubation, the enzyme reaction was stopped by adding 5.0 ml of 5% trichloroacetic acid. Then the solution was centrifuged and the supernatant was measured at 280 nm. The total activity was expressed as the optical density units increased/min/100 g. B. W..

RESULTS

Relative length of the gut (R. L. G) and feeding habits

The different feeding habit and adaptation to diet composition of fish can be reflected by the different length of digestive tract. The

TABLE 1
Feeding habits and relative length of the gut (R. L. G.) of cultured fishes

Species	Common name	Feediug habit	R. L. G.[a] (Mean ± S. E.)
Anguilla japonica	Japanese eel	Carnivorous[(5,23)b]	0.4560±0.0499
Channa maculatus	Formosan snakehead	Carnivorous[(5)]	0.5772±0.0901
Clarias fuscus	Formosan freshwater catfish	Carnivorous[(5)]	0.6823±0.1141
Cyprinus capio	common carp	Omnivorous[(5,13,14,23)]	2.0400±0.3450
Tilapia mossambica	tilapia	Omnivorous[(5,13,19)]	6.2927±0.1909
Ctenopharyngodon idellus	grass carp	Herbivorous[(4,13,22,24)]	2.1560±0.4133
Carassius auratus	golden crucian carp	Microphageous[(5,13,23,24)]	5.1480±0.9452
Hypophthalmichthys molitris	silver carp	Microphageous[(13)]	5.2835±0.2920

a. $\text{R. L. G.} = \frac{\text{Digestive tract length (DL)}}{\text{Body length (BL)}}$

b. Reference numbers.

relative length of the gut (R. L. G.) is expressed as the length ratio of digestive tract to body. The relationship between R. L. G. and artificial reared fish with typical different feeding habit was shown in Table 1. The carnivorous fishes such as *Anguilla japonica*, *Channa maculatus* and *Clarias fuscus* had smallest R. L. G. value which were ranged from 0.46 to 0.68. The omnivorous *Tilapia mossambica* and microphageous fishes such as *Carassius auratus* and *Hypothalmichthys molitrix* had an R. L. G. value over 5.0. The omnivorous *Cyprinus carpio* and herbivorous *Ctenopharyngodon idellus* had an R. L. G. value of about 2, which were ranged between carnivores and microphages. From these results, the R. L. G. values were correlated well to their feeding habits of these cultured fishes. In general, the digestive tract lengths of carnivores, herbivores and microphages are half, two and five times of their body-length, while the omnivores are varied from two to six times.

Pepsin, trypsin and chymotrypsin in digestive tract

Proteases such as pepsin, trypsin and chymotrypsin are the three most important protein hydrolysis enzymes in digestive tract. Then the resulting oligopolypeptides can be further digested to utilizable amino acids by various endo- and exo-peptidases. Since the relative length of gut is varied with different feeding habit, one can speculate that the distribution and existance of proteases will be differred from fishes. However, the relationship between pepsin, trypsin and and chymotrypsin with fish feeding habit remains to be explored.

The carnivorous and one omnivorous fishes such as *C. maculatus*, *A. japonica*, *C. fuscus*, and *T. mossambica* are the only four test fishes which have stomach (Table 2). Usually, the stomach is the major pepsin-secretion and site of action organ. Among these stomachal fishes, *C. maculatus* had strongest pepsin activity and *T. mossambica* had lowest activity. Tilapian intestine contained considerable pepsin activity and its origin is still obscure. The herbivorous and microphageous fishes had negligible pepsin activity in the organ tested. It is obvious that the carnivorous fishes can secret a lot of pepsinogen to stomach to digest the ingested diet proteins. The pepsin activity in stomach was clearly related with relative length of gut and feeding habit (Fig. I). The R. L. G. of *T. mossambica* was 10 times longer than *C. maculatus*, but its pepsin activity was only 3.7% of the latter. Similar tendency was observed when *T. mossambica* was compared with *A. japonica* and *C. fuscus*. Although the carnivores have shortest alimentary tract, however, they secrete strongest pepsin for protein digestion.

Trypsin and chymotrypsin are the two major digestion enzymes in intestine. As

TABLE 2
Pepsin activity in different organs of fishes

Species \ Organs (Total activity[a])	Oesophagus	Stomach	Pyloric caeca	Intestine	Hepato-pancreas	Spleen
Anguilla japonica	0.5325	10.1454	b	0.2892	c	0.0170
Channa maculatus	b	26.2448	0.1780	0.3161	0.6796	0.1451
Clarias fuscus	b	8.3916	b	1.2112	0.0000	0.0000
Cyprinus carpio	b	b	b	0.7990	0.1527	0.0369
Tilapia mossambica	b	0.9656	b	10.9898	1.7613	1.1127
Ctenopharyngodon idellus	0.1562	b	b	0.5044	0.1601	0.0392
Carassius auratus	b	b	b	1.1482	c	0.0159
Hypophthalmichthys molitrix	b	b	b	0.0726	0.4631	0.0512

a. Total activity=O. D. increase/min/100 g. B. W..
b. No such organ existed.
c. No test was performed.

shown in Table 3, chymotrypsin activity of these eight cultured fishes was found in each of the existed digestive organs, especially in intestine, hepatopancreas and pyloric caeca. The microphageous *H. molitrix*, *C. auratus* had highest chymotrypsin level in intestine. The omnivorous *T. mossambica* had almost same chymotrypsin activity as microphages. However, the *C. carpio* chymotrypsin activity was only one-third of *T. mossambica*. Carnivorous *A. japonica*, *C. maculatus* and *C. fuscus* had low chymotrypsin activities in intestine which were 7%, 36% and 60% of *H. molitrix* respectively. The herbivorous *C. idellus* chymotrypsin activity was only 29% of *H. molitrix*. The hepatopancreases of these test fishes contained considerable amount of chymotrypsin activity (Table 3). It indicated that hepatopancreas might be the chymotrypsinogen-secreting organ. Fig. 2 shows the relationship between chymotrypsin activity in intestine and the R. L. G. values. The fish with R. L. G. value over 5 had stronger chymotrypsin activity in intestine than R. L. G. value lower than 2. Therefore, the microphageous *H. molitrix* and *C. auratus* and omnivorous *T. mossambica* had one to thirteen times higher chymotrypsin activity than carnivorous and herbivorous fishes.

As shown in Table 4, trypsin activity of

TABLE 3
Chymotrypsin activity in different organs of fishes

Species \ Organs (Total activity[a])	Oesophagus	Stomach	Pyloric caeca	Intestine	Hepato-pancreas	Spleen
Anguilla japonica	0.0966	0.1610	b	0.3362	0.7011	0.4397
Channa maculatus	b	0.4708	0.4112	1.6645	0.0055	0.0250
Clarias fuscus	b	0.4539	b	2.7632	3.5506	0.1124
Cyprinus carpio	b	b	b	1.3088	0.8062	0.2872
Tilapia mossambica	b	1.5341	b	4.1834	5.6481	0.2844
Ctenopharyngodon idellus	0.1207	b	b	1.3410	8.6178	0.1557
Carassius auratus	b	b	b	4.1240	2.6164	0.1084
Hypophthalmichthys molitrix	b	b	b	4.5912	0.7949	0.3816

a. Total activity=*m* moles substrate hydrolyzed/10 min/100 g. B. W..
b. Means no such organ existed.

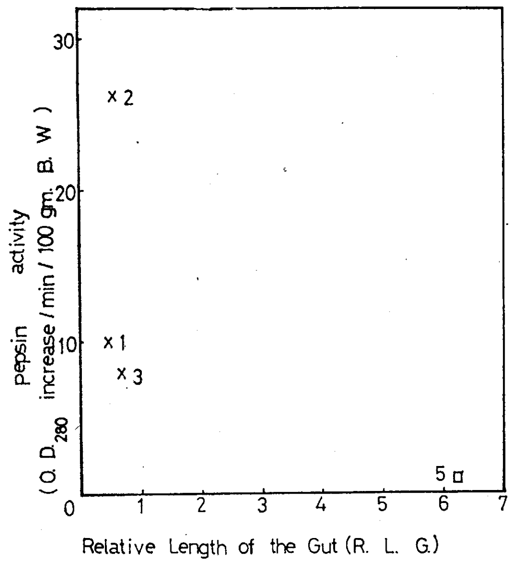

Fig. 1. The relationship between relative length of the gut and pepsin activity in stomach.
×: Carnivores. □: Omnivores.
1. *Anguilla japonica*
2. *Channa maculatus*
3. *Clarias fuscus*
4. *Tilapia mossambica*

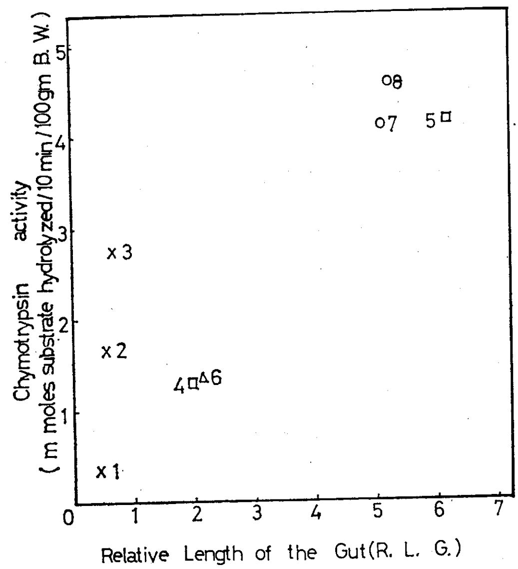

Fig. 2. The relationship between relative length of the gut and chymotrypsin activity in intestine.
×: Carnivores. □: Omnivores.
△: Herbivores. ○: Microphages.
1. *Anguilla japonica*
2. *Channa maculatus*
3. *Clarias fuscus*
4. *Cyprinus carpio*
5. *Tilapia mossambica*
6. *Ctenopharyngodon idellus*
7. *Carassius auratus*
8. *Hypophthalmichthys molitrix*

TABLE 4

Trypsin activity in different organs of fishes

Total activity[a] / Organs / Species	Oesophagus	Stomach	Pyloric caeca	Intestine	Hepato-pancreas	Spleen
Anguilla japonica	0.1130	5.6510	b	47.0026	20.3800	3.0877
Channa maculatus	b	2.2023	27.0394	46.0995	33.8975	2.6333
Clarias fuscus	b	5.1123	b	12.6075	14.0145	0.6580
Cyprinus carpio	b	b	b	3.2604	5.8950	0.5593
Tilapia mossambica	b	15.4823	b	189.4911	198.2300	8.7380
Ctenopharyngodon idellus	0.0494	b	b	4.5919	11.9446	0.3830
Carassius auratus	b	b	b	1.8530	3.3146	0.5179
Hypophthalmichthys molitrix	b	b	b	4.7564	3.6285	2.4553

a. Total activity=μ moles substrate hydrolyzed/min/100 g B. W..
b. Means no such organ existed.

these cultured fishes were found in each of the existed digestive organs, especially in intestine, hepatopancreas and pyloric caeca. The intestine of *T. mossambica* had strongest trypsin activity and other fishes were descreased in the following order: *A. japonica, C. maculatus, C. fuscus, H. molitrix, C. idellus, C. carpio* and *C. auratus.* The trypsin activity in the hepatopancreas of these test fishes had similar order as in the intestine. Generally, the omnivorous *T. mossambica* had exceeding strong trypsin activity in both intestine and pancreas. The carnivorous fishes had second strongest trypsin activity, however, these activities in intestines were only 7 to 25% of *T. mossambica.* The herbivorous and microphageous fishes had very weak trypsin activity in intestine in comparing with *T. mossambica.* As shown in Fig. 3, only the fishes with an R. L. G. values over 6 or lower than 0.7 had strong trypsin activity. The fishes with an R. L. G. value in the between had rather low trypsin activity.

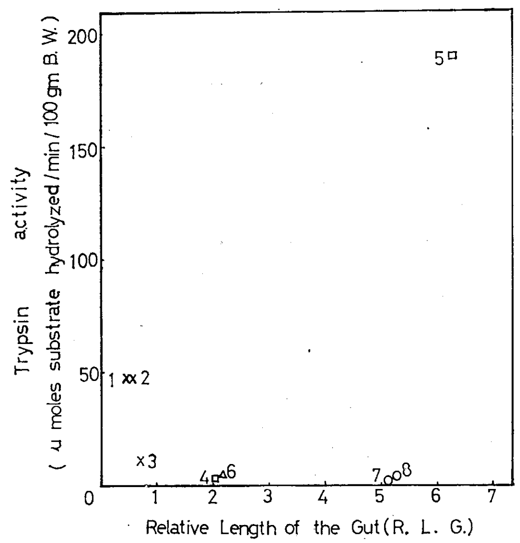

Fig. 3. The relationship between relative length of the gut and trypsin activity in intestine.
×: Carnivores. □: Omnivores.
△: Herbivores. ○: Microphages.
1. *Anguilla japonica*
2. *Channa maculatus*
3. *Clarias fuscus*
4. *Cyprinus carpio*
5. *Tilapia mossambica*
6. *Ctenopharyngodon idellus*
7. *Carassius auratus*
8. *Hypophthalmichthys molitrix*

DISCUSSION

Al-Hussaini[1], Barrington[2] and Kapoor *et al.*[10] pointed out that the R. L. G. was clearly connected with the different feeding habits of fishes, paticularly related to the quantity of indigestible material. The longest intestine occurs in microphageous (algae-eating) and some herbivorous fishes; the shortest in carnivores. The variety of intestinal length in omnivorous fish depends upon the proportion of the indigestible to digestible materials in the diet[1,10]. Therefore, considerable variation of intestinal length is expected to occur in omnivores. From the present finding, the R. L. G. of carnivorous fishes range from 0.46 to 0.68, which is within the range reported by Kapoor *et al.*[10], and Al-Hussaini[1]. The R. L. G. of *A. japonica* is 0.46, which is close to 0.5[24].

The R. L. G. of microphageous *C. auratus* and *H. molitrix* range from 5.14 to 5.28 which fit the level between 3.7 and 6.0 defined by Al-Hussaini[1]. The R. L. G. of *C. auratus* is 5.15 which is higher than 2.1 to 3.2[13], and 3.0[24], but much lower than 11 recorded by Suyehiro[23]. The R. L. G. of *H. molitrix* is 5.28 which is in the range of 5.1 to 7.5[13], but much lower than 13[11]. The R. L. G. of *C. idellus* is 2.16 which is close to 2.3[4], 2.4[13], and 2.5[24].

The R. L. G. of omnivores ranged from 2.04 to 6.29 which is larger than that of Kapoor's[10] and Al-Hussaini's[1] reports. The R. L. G of *T. mossambica* is 6.29 which is within the range of 5 to 7[13]. The R. L. G. of *C. carpio* is 2.04 which is close to 1.8[13] and lower than 2.5[24] and 4[23]. The difference of the R. L. G. in these species may be due to variations in habitat, salinity, season, age, and sex[3,10,12,14,22].

Vonk[26] indicated that the pepsin activity of gastric extracts with an optimal proteolytic activity at pH 2, was found in all stomach-containing fish. Therefore, the relationship between feeding habit and pepsin activity can be compared in the stomach of these fishes. It had been reported that the stomach of *A. japonica* had higher pepsin level than *T. mossambica* and *Plecoglossus altivelis*[16]. The carnivores have high digestion efficiency of ingested high-protein diet, although they have shortest alimentary tract. In order to adapt their feeding habit, the stomach of carnivores can secrete very strong pepsin to digest proteins (Table 2). On the other hand, the omnivorous *T. mossambica* develops very long alimentary tract and secretes very strong trypsin and chymotrypsin activities (Fig. I, Tables 3–4). These intestinal proteases can compensate the low pepsin activity in stomach (Table 2). In conclusion, the fish has shorter alimentary tract can secrete stronger pepsin and *vice versa*.

Kawai and Ikeda[6] reported that the pancreatic tissue was found in the spleen of *C. carpio*. Moriarty[15] also stated that the pancreas of *T. nilotica* is a diffused form which spreads around the alimentary tract. Trypsinogen and chymotrypsinogen have been found in the pyloric caeca of *Onchorhyncus keta*[25]. Trypsin activity has been detected in the esophagus of young *C. carpio*[6] and in the pyloric caeca of mackerel[18].

In the screening of the existence of trypsin and chymotrypsin, most of them are found in intestine and hepatopancreas (Tables 3-4). Some minor activities are still existed in pyloric caeca, spleen, oesophagus and stomach. This indicated that pancreatic tissue may also exist in these organs.

The microphages have no stomachal pepsin to digest protein, however, they can induce very strong chymotrypsin activity in intestine (Table 3). Usually the microphages ingest algae as their food source which contain large portion of indigestible materials. Also, they don't have stomach to perform digestion. Therefore, they need long digestive tract and strong intestinal proteases to digest their ingested food. However, the carnivores have strongest stomachal pepsin activity and lowest intestinal chymotrypsin activity (Tables 2–3). The relationship among feeding habits, relative length of the gut and intestinal chymotrypsin level are correlated well. The carnivores have highest pepsin level with shortest gut and lowest chymotrypsin level, while the microphages have highest chymotrypsin level with longest gut and no pepsin activity. The herbivores have intermediate chymotrypsin level with intermediate gut length.

The contribution of trypsin to protein digestion in fish intestines is rather insignificant when compared with chymotrypsin. As shown in Tables 3 and 4, the chymotrypsin activity was *m* moles level, while the trypsin activity was μ moles level. Only omnivorous *T. mossambica* develop significant level of trypsin in its intestine.

Trypsin is only specific for the hydrolysis of the peptide linkages in which the carbomyl function is contributed by lysine and arginine[20]. Chymotrypsin is not only specific for the hydrolysis of the peptide linkage in which the carbomyl function is contributed by aromatic amino acid residues, such as tyrosine, tryptophan and phenylalanine; but also hydrolyze the amides and esters of these aromatic amino acides[20]. In other words, chymotrypsin has broad spectrum of protein digestion than trypsin. The result is that fish need to induce more chymotrypsin secretion for complete digestion of proteins and peptides.

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淡水魚類消化蛋白酵素和食性的關係

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臺灣淡水養殖魚類如鰻、鱧魚和塘虱魚屬肉食性；草魚屬草食性；鯽魚、鰱魚屬藻食性；鯉魚、吳郭魚爲雜食性。從魚胃之胃蛋白酶總活性比較顯示：肉食性魚之胃蛋白酶活性很高；雜食性有胃的魚其活性低；而無胃的魚，其消化道內幾無胃蛋白酶活性。比較不同食性的魚腸之胰凝乳蛋白酶，以藻食性魚活性最高：次爲雜食性、草食性、和肉食性。而魚腸之胰蛋白酶則是雜食性吳郭魚最高，次爲肉食性、草食性和藻食性。魚類食性和腸長比及腸胰凝乳蛋白酶及胃蛋白酶之活性三者有很好的關連。綜合言之，肉食性魚腸最短，胃蛋白酶活性最高，而腸胰凝乳蛋白酶活性最低。藻食性魚腸最長，腸之胰凝乳蛋白酶活性最高，但無胃蛋白酶之活性。草食性魚，是魚腸之長度與腸之胰凝乳蛋白酶活性都居間。