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Occurrence of cellulase activity in the stomachs of fishes

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The stomachs of 148 elasmobranch and teleost fishes representing 35 families and 62 species were examined by viscometry for cellulase activity. Sixteen species of Georgia estuarine fish and the freshwater fish, *Ictalurus punctatus* (Rafinesque) showed some cellulase activity. Elasmobranchs and teleosts captured in Florida Bay, Florida, and over the continental shelf off Georgia lacked cellulase activity. Cellulase activity in fishes is probably produced by microflora of the alimentary tract.

I. INTRODUCTION

Sucrase, maltase, lactase, amylase and invertase have been demonstrated among the carbohydrate digesting enzymes present in various species of fishes (Phillips, 1969). Yokoe & Yasumasu (1964) using techniques developed by Yokoe (1960) which assured the removal of bacteria from stomachs before analyses, concluded that the presence of cellulase correlates closely with phylogeny. Most invertebrate phyla include members which demonstrate cellulase production, whereas vertebrates seemed to lack the capability of producing this enzyme (Yokoe & Yasumasu, 1964). Crosby & Reid (1971) in a study of bivalve molluscs, concluded that cellulase activity in these animals was a function of cellulose abundance in the food and not necessarily phylogenetically related. The studies outlined in this paper were designed to determine the incidence of occurrence of cellulase activity in the stomachs of common species of southeastern United States marine and estuarine teleost and elasmobranch fishes, and to determine if the presence or absence of cellulase activity could be related to general food habits of the fish examined.

II. MATERIALS AND METHODS

A total of 148 individual elasmobranch and teleost fishes were examined for cellulase activity. Thirty-five families represented by 62 species including one freshwater fish, *Ictalurus punctatus* (Rafinesque), were included. The estuarine and offshore species were collected from coastal Georgia with the exceptions of *Priacanthus arenatus* Cuvier *Caranx crysos* (Mitchill) *Lutjanus synagris* (L.) *Haemulon plumieri* (Lacépéde) and *Archosargus probatocephalus* (Walbaum) which were obtained from Florida Bay. Methods for collection included otter trawling, beach seining and gill netting. Small fish were frozen whole, while the stomachs were frozen after removal from fish weighing in excess of about 200 g. Fish were frozen at time of capture when a freezer was available on board ship or the fish were maintained alive until return to the laboratory when small boats were used. Stomachs were frozen upon their removal and analyses were run within 72 h in most cases. Methods of determining cellulase activity include radiographic techniques (Koningsor *et al.*, 1972); turbidometric, colorimetric and histochemical techniques (Crosby & Reid, 1971); and zone

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TABLE I. Cellulase activity in fish stomachs

Scientific name		Common name	Number individuals examined	Cellulase activity
Carcharinidae				
Carcharinus obscurus (Lesueur)	(O)	Dusky shark	2	−
Galeocerdo cuvieri (Peron and Lesueur)	(O)	Tiger shark	1	−
Sphyrnidae				
Sphyrna tiburo (L.)	(O)	Bonnethead	1	−
Dasyatidae				
Dasyatis sabina (Lesueur)	(O)	Atlantic stingray	3	−
Gymnura micrura (Bloch and Schneider)	(O)	Smooth butterfly ray	1	−
Clupeidae				
Brevoortia tyrannus (Latrobe)	(E)	Atlantic menhaden	3	+ +
Opisthonema oglinum Berry and Barrett	(E)	Atlantic thread herring	3	−
Engraulidae				
Anchoa hepsetus (L.)	(E)	Striped anchovy	1	+ +
Anchoa mitchilli (Valenciennes)	(E)	Bay Anchovy	3	+ +
Synodontidae				
Synodus foetens (L.)	(E)	Inshore lizardfish	3	−
Ictaluridae				
Ictalurus punctatus (Rafinesque)		Channel catfish	3	+
Ariidae				
Arius felis (L.)	(E)	Sea catfish	3	+ +
Bagre marinus (Mitchilli)	(E)	Gafftopsail catfish	1	+
Batrachoididae				
Opsanus tau (L.)	(E)	Oyster toadfish	3	−
Gadidae				
Urophycis floridanus (Bean and Dresel)	(O)	Southern hake	3	−
Cyprinodontidae				
Fundulus majalis (Walbaum)	(E)	Striped killifish	3	+
Atherinidae				
Menidia beryllina (Cope)	(E)	Tidewater silverside	3	+ +
Syngnathidae				
[illegible] Günther	(E)	Chain pipefish	1	+

Priacanthidae				
Priacanthus arenatus Cuvier	(F)	Bigeye	2	–
Pomatomidae				
Pomatomus saltatrix (L.)	(E)	Bluefish	3	–
Rachycentridae				
Rachycentron canadum (L.)	(O)	Cobia	1	–
Carangidae				
Caranx crysos (Mitchill)	(F)	Blue runner	2	–
Chloroscombrus chrysurus (L.)	(E)	Atlantic bumper	3	–
Selene vomer (L.)	(E)	Lookdown	3	+
Trachinotus carolinus (L.)	(E)	Florida pompano	3	–
Coryphaenidae				
Coryphaena hippurus (L.)	(O)	Dolphin	3	–
Lutjanidae				
Lutjanis synagris (L.)	(F)	Lane snapper	2	–
Pomadasyidae				
Haemulon plumieri (Lacépéde)	(F)	White grunt	3	–
Sparidae				
Archosargus probatocephalus (Walbaum)	(F)	Sheepshead	2	–
Lagodon rhomboides (L.)	(E)	Pinfish	3	–
Sciaenidae				
Bairdiella chrysura (Lacépéde)	(E)	Silver perch	4	+ +
Cynoscion nebulosus (Cuvier)	(E)	Spotted seatrout	1	–
Cynoscion nothus (Holbrook)	(E)	Silver seatrout	1	–
Cynoscion regalis (Bloch and Schneider)	(E)	Weakfish	3	–
Larimus fasciatus Holbrook	(E)	Banded drum	3	–
Leiostomus xanthurus Lacépéde	(E)	Spot	3	–
Menticirrhus americanus (L.)	(E)	Southern kingfish	3	–
Menticirrhus saxatilis (Bloch and Schneider)	(E)	Northern kingfish	3	–
Micropogon undulatus (L.)	(E)	Atlantic croaker	3	–
Stellifer lanceolatus (Holbrook)	(E)	Star drum	3	+ +
Ephippidae				
Chaetodipterus faber (Broussonet)	(E)	Atlantic spadefish	3	+
Labridae				
Hemipteronotus novacula (L.)	(O)	Pearly razorfish	3	–
Mugilidae				
Mugil cephalus (L.)	(E)	Striped mullet	3	+

TABLE 1.—*continued*

Scientific name		Common name	Number individuals examined	Cellulase activity
Sphyraenidae				
Sphyraena barracuda (Walbaum)	(O)	Great barracuda	1	–
Trichiuridae				
Trichiurus lepturus L.	(E)	Atlantic cutlassfish	3	–
Scombridae				
Sarda sarda (Bloch)	(O)	Atlantic bonito	2	–
Scomberomorus cavalla (Cuvier)	(O)	King mackeral	3	–
Scomberomorus maculatus (Mitchill)	(E)	Spanish mackeral	3	–
Stromateidae				
Peprilus alepidotus (L.)	(E)	Harvestfish	3	–
Triglidae				
Prionotus carolinus (L.)	(E)	Northern searobin	1	+
Bothidae				
Ancylopsetta quadrocellata Gill	(E)	Ocellated flounder	2	–
Citharichthys spilopterus Günther	(E)	Bay whiff	1	+
Etropus crossotus Jordan and Gilbert	(E)	Fringed flounder	3	–
Paralichthys dentatus (L.)	(E)	Summer flounder	3	–
Syacium papillosum (L.)	(O)	Dusky flounder	1	–
Soleidae				
Trinectes maculatus (Bloch and Schneider)	(E)	Hogchoker	3	–
Cynoglossidae				
Symphurus plagiusa (L.)	(E)	Blackcheek tonguefish	3	+
Tetraodontidae				
Sphoeroides maculatus (Bloch and Schneider)	(E)	Northern puffer	3	–
Sphoeroides nephalus (Goode and Bean)	(E)	Southern puffer	1	–

electrophoresis (Miller & Blum, 1956). The majority of workers used changes in viscosity of cellulose solutions exposed to enzyme extracts to determine the presence of cellulase activity. The methods described have been adapted from techniques described by Yokoe & Yasumasu (1964), Lewis & Whitney (1968), Soedigdo *et al.* (1970), Crosby & Reid (1971) and Halcrow (1971). Viscometry has been discussed by Joos *et al.* (1969), and a means by which data obtained from viscometry determinations may be quantified in terms of standard international units has been proposed by Hulme (1971). Stomachs were analyzed in fishes having well developed stomachs. Fishes of the families Atherinidae, Cyprinodontidae, Labridae, Mugilidae and Syngnathidae, among others, lack morphological stomachs (Chao, 1973), so upper alimentary tract tissue was removed from fishes in these families. Following thawing whole digestive organs or portions weighing less than 2·0 g were rinsed with 0·1 M phosphate buffer solution at pH 6·8. Any food present in the tracts was removed during washing and discarded. The tissue was then ground in a glass tissue homogenizer with a small volume of

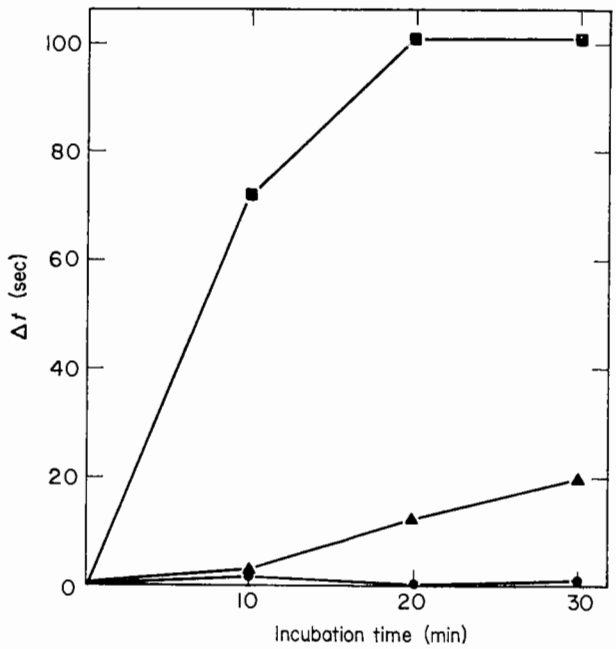

FIG. 1. Change in flow rate (Δt) versus incubation time for representative fish showing high, low and zero of cellulase activity. ●, *Chlorscombrus chrysurus*; ▲, *Ictalurus punctatus*; ■, *Menidia beryllina*.

the phosphate buffer solution. Following grinding the homogenate was diluted to 10 ml with the phosphate buffer and centrifuged at 2200 rpm for 15 min. A 0·2% sodium carboxymethylcellulose (Na–CMC) solution was prepared using the phosphate buffer solution described above as the solvent. Five ml of the Na–CMC solution were added to each of four Ostwald viscometers and the flow time of the contents of each viscometer was recorded in a water bath at 30° C. A 0·5 ml aliquot of the enzyme extract (supernatant solution from the centrifuged tissue sample) was added to three of the Ostwald viscometers and 0·5 ml of phosphate buffer was added to the fourth Ostwald viscometer to serve as a blank. The viscometers were retained in the water bath at 30° C and flow rates were determined in the series of viscometers at 10 min intervals for 30 min. Cellulase activity was indicated by a reduction in flow time when compared with the blank. All glassware was washed between uses in concentrated nitric acid, rinsed twice in double distilled water and dried for 1 h at 140° C.

TABLE II. Relationships between cellulase activity and the food habits of selected teleosts

Species	Food habits	References
Fish with low cellulase activity		
Ictalurus punctatus	Algae, vascular plants, amphipods, foraminifera, decapods, detritus, insects	Menzel (1943), Darnell (1958), Perry (1969)
Bagre marinus	Decapods, cephalopods, insects, fish	Miles (1949), Darnell (1958), Odum & Heald (1972)
Fundulus majalis	Molluscs, crustaceans, insects, fish	Bigelow & Schroeder (1953)
Syngnathus louisianae	Amphipods, copepods, schizopods, fish eggs, algae (incidental). (Data based on closely related species)	Hildebrand & Schroeder (1928), Bigelow & Schroeder (1953)
Selene vomer	No information on juveniles. Adults eat small crustaceans and fish	Hildebrand & Schroeder (1928)
Chaetodipterus faber	Small crustaceans, annelids, detritus, ctenophores	Smith (1907), Hildebrand & Schroeder (1928), Breder (1948)
Mugil cephalus	Algae, detritus, vascular plants, crustaceans	Darnell (1958), Odum (1968), Odum & Heald (1972)
Prionotus carolinus	Decapods, amphipods, cephalopods, molluscs, annelids, fish, algae and mysids	Hildebrand & Schroeder (1928), Bigelow & Schroeder (1953)
Citharichthys spilopterus	Mysids, decapods, fish and stomatopods	Stickney *et al.* (1974)
Symphurus plagiusa	Polychaetes, molluscs, cumaceans, mysids, amphipods, isopods, decapods, copepods, ostracods, echinoderms	Stickney (unpublished data)
Fish with high cellulase activity		
Brevoortia tyrannus	Algae, planktonic crustacea	Bigelow & Schroeder (1953), June & Carlson (1971)
Anchoa hepsetus	Copepods, mysids, isopods, molluscs, fish	Hildebrand & Schroeder (1928), Springer & Woodburn (1960)

Anchoa mitchilli	Rotifers, copepods, decapods, fish, schizopods, molluscs, amphipods, mysids, ostracods, detritus	Hildebrand & Schroeder (1928), Reid (1954), McLane (1955), Darnell (1958), Springer & Woodburn (1960), Odum (1971), Odum & Heald (1972)
Arius felis	Amphipods, decapods, insects, hydroids, molluscs, copepods, schizopods, isopods	Darnell (1958), Odum & Heald (1972)
Menidia beryllina	Isopods, amphipods, copepods, mysids, detritus, algae, insects, veliger larvae	Hildebrand & Schroeder (1928), Reid (1954), McLane (1955), Darnell (1958), Springer & Woodburn (1960), Odum & Heald (1972), Carr & Adams (1973)
Bairdiella chrysura	Schizopods, decapods, fish, detritus, copepods, mysids, amphipods, polychaetes, ectoprocts	Linton (1905), Hildebrand & Schroeder (1928), Hildebrand & Cable (1930), Reid *et al.* (1956), Darnell (1958), Odum & Heald (1972), Carr & Adams (1973), Stickney (unpublished data)
Stellifer lanceolatus	Amphipods, isopods, copepods, cumaceans, mysids, stomatopods, decapods, acanthocephalans, fish	Stickney (unpublished data)
Fish without cellulase activity		
Opisthonema oglinum	Veliger larvae, copepods, mysids, decapods, molluscs, algae, cirripeds, fishes, polychaetes	Springer & Woodburn (1960), Randall (1967), Fuss, Kelly & Prest (1968), Carr & Adams (1973)
Synodus foetens	Fish	Linton (1905), Hildebrand & Schroeder (1928), Reid (1954), Reid (1955), Springer & Woodburn (1960), Carr & Adams (1973)
Urophycis floridanus	Detritus, amphipods, crustacea	Sikora *et al.* (1972)

TABLE II.—*continued*

Species	Food habits	References
Haemulon plumieri	Polychaetes, molluscs, decapods, echinoderms	Beebe & Tee-Van (1928), Longley & Hildebrand (1941), Reid (1954), Carr & Adams (1973)
Lagodon rhomboides	Fish, crustaceans, vascular plants, algae, detritus, copepods, mysids, molluscs	Linton (1905), Smith, (1907) Hildebrand & Schroeder (1928), McLane (1955), Hanson (1969), Odum & Heald (1972), Carr & Adams (1973)
Cynoscion nebulosus	Copepods, decapods, fish, mysids, carideans	Moody (1950), Darnell (1958), Springer & Woodburn (1960), Odum & Heald (1972)
Cynoscion regalis	Polychaetes, copepods, amphipods, mysids, stomatopods, decapods, fishes	Stickney (unpublished data)
Leiostomus xanthurus	Polychaetes, copepods, isopods, amphipods, mysids, cumacea	Stickney (unpublished data)
Micropogon undulatus	Polychaetes, molluscs, amphipods, isopods, copepods, decapods, stomatopods, mysids, cumacea, ascidians, fish	Stickney (unpublished data)
Ancylopsetta quadrocellata	Mysids, copepods, polychaetes, decapods, stomatopods, fish	Stickney *et al.* (1974)
Etropus crossotus	Polychaetes, molluscs, copepods, isopods	Stickney *et al.* (1974)
Trinectes maculatus	Annelids, algae, amphipods, detritus, foraminifera, plant seeds, copepods, insect larvae, molluscs, cumaceans	Hildebrand & Schroeder (1928), Reid (1954), McLane (1955), Darnell (1958), Odum & Heald (1972), Stickney (unpublished data)
Sphoeroides nephalus	Decapods, molluscs, detritus	Reid (1954), Carr & Adams (1973)

III. RESULTS AND DISCUSSION

Of the 62 species of elasmobranchs and teleosts examined (Table I), 17 showed cellulase activity. One species of freshwater catfish, *Ictalurus punctatus*, which demonstrated cellulase activity, was obtained from an indoor intensive culture system. The catfish examined had not been exposed to natural food for at least a year prior to examination, but had been fed an artificial diet. In an attempt to determine the source of the cellulase activity in *I. punctatus*, additional experiments were performed with this species. The artificial pelleted diet was tested and demonstrated no cellulase activity. The presence of cellulase activity in fingerling *I. punctatus* was confirmed using fish averaging approximately 15 g (the previously described results having been obtained on fish in excess of 500 g). Thereafter, two groups of *I. punctatus* fingerlings were starved for five days, after which cellulase activity was determined on the first group and the second group was exposed to a 200 mg/l solution of streptomycin for 24 h prior to determination of cellulase activity. The starved fish which had not been exposed to the antibiotic continued to demonstrate cellulase activity, while those which had been exposed to the streptomycin showed no cellulase activity. From these results, it is apparent that cellulase activity, at least in *I. punctatus*, results from alimentary tract microflora rather than from cellulase secreting cells within the fish.

An example of change in flow rate (Δt) versus incubation time shown by fish with no cellulase activity is provided by *Chloroscombrus chrysurus* (L.) and presented in Fig. 1. Fishes which demonstrated low cellulase activity such as *Ictalurus punctatus* (Fig. 1) included *Bagre marinus* (Mitchill), *Fundulus majalis* (Walbaum), *Syngnathus louisianae* Günther, *Selene vomer* (L.), *Chaetodipterus faber* (Broussonet), *Mugil cephalus* L., *Prionotus carolinus* (L.), *Citharichthys spilopterus* Günther, and *Symphurus plagiusa* (L.). High cellulase activity [as demonstrated by *Menidia beryllina* (Cope) in Fig. 1] was recorded in *Brevoortia tyrannus* (Latrobe), *Anchoa hepsetus* (L.), *Anchoa mitchilli* (Valenciennes), *Arius felis* (L.), *Bairdiella chrysura* (Lacépéde) and *Stellifer lanceolatus* (Holbrook).

The food habits of selected fish showing low cellulase activity, high cellulase activity and no cellulase activity are presented in Table II. No correlation was found between food habits as reported in the literature and the presence of high or low cellulase activity in those fish which demonstrated activity. Replicate sampling for cellulase activity virtually always gave the same information. Three replicates were examined in all cases possible; due to lack of occurrence in catches, fewer than three individuals were examined in some cases (Table I). The procedure for washing the stomachs was identical with all fish, and the high correlation of results among replicates within species indicate that there was little or no bias contributed by the washing techniques. There was also no apparent pattern in the presence or absence of cellulase activity found when activity was compared with phylogeny. Cellulase activity was demonstrated in fish with and without morphological stomachs and throughout much of the phylogenetic tree. Comparison of several species within families showed that one or more might demonstrate cellulase activity while others did not, even though the food habits of the fishes were nearly identical. This lack of correlation can readily be seen among the Sciaenidae and Bothidae, for example (Tables I and II). No species of offshore fish demonstrated the presence of cellulase activity. This may result from the relatively lower levels of cellulose in the offshore marine environment which is based on a phytoplankton food web. Georgia estuarine food webs are based, in part, on plant detritus, especially that formed from the

degradation of *Spartina alterniflora* (Odum & de la Cruz, 1963, 1967). In addition, large quantities of allochthonous plant detritus high in cellulose are often present in estuaries.

Little evidence has been seen of detritus in samples taken even a few miles offshore. The offshore fishes collected from Georgia waters were taken a minimum of 20 km offshore and no detrital material of land origin was apparent as confirmed by bottom samples taken in these and other areas along the coast. The Florida Bay samples were obtained from an area which was also relatively detritus free. It is not clear from these studies why fishes with the same feeding habits, and living within the same habitat vary so widely in terms of cellulase activity. On the basis of the data presented herein, food habits of the fishes involved cannot be positively related to cellulase activity although patterns of this nature have been proposed for invertebrates (Crosby & Reid, 1971). The idea that cellulase activity is phylogenetically related cannot be applied to fish either, especially in relation to our results with *I. punctatus*, although there is evidence to indicate that such a relationship may hold in invertebrates (Yokoe & Yasumasu, 1964). Fish are presumed to lack the ability to form cellulase and must obtain cellulase activity from their food or by means of the establishment of a cellulase producing bacterial flora within the alimentary tract.

In conclusion, this study provides evidence for the presence of cellulase activity in the digestive tracts of several species of estuarine fishes along the coast of the southeastern United States and freshwater fish reared in aquaculture. This paper raises questions as to the source of the cellulase activity and its relationship to the food contained within the stomachs of the fishes at the time of capture. The fact that replicate examinations yielded the same results within species, although not necessarily between species exhibiting similar food habits and the presence of cellulase activity in starved but not in antibiotically treated catfish indicates that cellulase activity is more closely related to alimentary tract microflora than to the presence of cellulase within the food consumed.

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