Utilization of the direct grazing and plant detritus food chains by the striped mullet Mugil cephalus*

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ABSTRACT. Most foodchains in shallow estuaries are based upon macroplant detritus and benthic and epiphytic micro-algae rather than on phytoplankton. In such areas the zooplankton are relatively unimportant in energy transfer and are replaced as the critical herbivore link by benthic invertebrates and phytophagous fishes. This paper is an examination of the ability of one of these fish, *Mugil cephalus*, to successfully exploit the first trophic level and, in effect, "telescope the food chain".

INTRODUCTION

In the classical concept of aquatic food chains zooplankton are considered the first important link in secondary production. What is often ignored is that this concept, like so many other basic principles in marine biology, was derived from observations and research carried out either in the open ocean or at relatively high latitudes. To the ecologist whose work is oriented to estuarine areas, especially in the tropics and subtropics, it becomes apparent that zooplankton are not the most important herbivore link. Williams *et al.* (1968) have demonstrated that in the vicinity of Cape Hatteras, North Carolina, zooplankton become steadily less important with decreasing depth in areas shallower than 100 metres; in shallow inshore areas they were shown to be relatively unimportant in food chains since they grazed only two to nine per cent of available phytoplankton.

Moreover, in shallow estuaries the phytoplankton itself has been found to be of secondary importance (Schelske and E. P. Odum, 1961; Ragotzkie, 1959; Teal, 1962; Pomeroy, 1960); the most important primary producers in such systems are marsh grasses (*Spartina*, etc.), sea grasses (*Zostera*, *Thalassia*, etc.), attached macroalgae, mangroves (*Rhizophora*, etc.) and the benthic

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microflora (benthic diatoms, dinoflagellates, filamentous green and blue-green algae). In most cases food chains are based on detritus derived from marsh grasses, sea grasses, macro-algae and mangroves, or directly on the benthic and epiphytic microflora. Animals which are able to utilize such energy sources replace zooplankton as the critical herbivore link.

Two of the most important groups of these animals are: (*i*) the benthic invertebrates, whose role as detritus consumers was emphasized by Jensen and Petersen (1911) and many times since (summarized by Jørgensen, 1966); and (*ii*) a limited number of highly successful fishes which consume both benthic microplant material and macroplant detritus. Although this second group includes few species, their great abundance supports many fisheries. Important in this group are the milkfish, *Chanos chanos*, and the mullets, *Mugil* sp., plus their freshwater counterparts, the carps, *Cyprinus* sp. and the tilapia.

Telescoping of the food chain

The phenomenon of relatively large fishes feeding directly from the first trophic level has been referred to by Hiatt (1944) as "a telescoping of the food chain". A fishery based on a species with this ability to bypass steps in the food chain with their accompanying loss of energy will potentially produce far more than a fishery based on a third or fourth level carnivore. Since it is essential to have a basic understanding of how they are able to utilize such a food source, the first step in any management or culture operation should be the analysis of the trophic ecology of the individual species. In this paper I have made such an analysis for the striped mullet, *Mugil cephalus*. By attacking the problem in a number of different ways it is possible to obtain a picture of how *M. cephalus* exploits the first trophic level. Unfortunately, this type of approach often raises more questions than it resolves.

A widespread and successful fish

It would be futile to attempt to describe all the information which has accumulated concerning *Mugil cephalus*. Thompson, (1963, 1966) has published two complete synopses which summarize the literature.

To describe the distribution of the fish very briefly, it is probably the most widespread and successful inshore teleost species, with a range extending around the world between 40°N and 40°S in waters with salinities from near zero (Hellier, 1957) to 113 parts per thousand (Zenkevitch, 1963). It is found not only in neritic areas and estuaries, but also hundreds of miles up fresh-water rivers such as the Colorado (Dill, 1944). During spawning, mullet move offshore, at least in North America, and may be found beyond the continental shelf (Anderson, 1958) over depths as great as 1500 metres (Arnold and Thompson, 1958). In most areas of the world where *M. cephalus* occurs, its success is expressed by great abundance. Sizeable fisheries are supported in many regions, while in others the potential exists for a valuable industry. In Florida over twenty million kilograms are harvested annually even though low demand limits the fishery.

Feeding and feeding behaviour

Typically, *M. cephalus* feeds either by sucking up the surface layer of the mud or by grazing on submerged rock and plant surfaces. An extensive literature reviewed by Thompson (1954) has established that the major contents of the stomach may be categorized as: (*i*) micro-algae including epiphytic and benthic forms, (*ii*) decaying plant detritus, and (*iii*) inorganic sediment particles. The latter appear to function as a grinding paste in the degradation of plant cell walls in the highly modified gizzard-like pyloric stomach (Thompson, 1966). Juvenile mullet are primarily carnivorous until they reach a standard length of about 30 mm. During this period they feed on mosquito larvae, copepods and other zooplankton.

M. cephalus is uniquely equipped for its trophic feeding niche. Its highly modified stomach has been described by Al-Hussaini (1947) as consisting of two parts: (*i*) the cardiac portion, a thin walled, saccular, blind caecum used for storage, and (*ii*) the pyloric portion, a thick, muscular gizzard-like structure used for pulverizing the food. The intestine is extremely long and coiled, often being more than five times the length of the fish. Finally, there is a pharyngeal filtering device, described in detail by Ebeling (1957). This mechanism aids in selecting very fine particles from the coarser sediments which are expelled. This finer material has been shown to be much richer in adsorbed micro-organisms than the particles which are rejected (Wood, 1964; W. E. Odum, 1968).

More than one method of selecting food is used by *M. cephalus*. For sediment feeding the mullet inclines its body at an angle of 15 to 30 degrees to the surface of the sediment and extends the premaxillaries so that particles are picked up in one of two ways: either by taking up small mouthfuls at random, or by skimming along the bottom with the lips barely in contact with the sediments and sucking up the uppermost layer. The latter method often includes shaking of the head back and forth. By either method the result is a small quantity of sediment in the pharynx which is carefully strained by the pharyngeal filter. Any material found unsuitable (usually large particles) is expelled in a small cloud. The presence of mullet is often characterized by a trail of these clouds behind feeding fish.

A similar means of feeding is used when browsing on micro-algae attached to submerged surfaces. With the body at an angle to the substrate, with the premaxillaries extended and with a back and forth movement of the head, the attached algae are either nibbled or sucked off the surface. Finally, the food material is filtered in the pharynx, the suitable material ingested and the remainder expelled.

Under certain conditions *M. cephalus* will feed at the water surface. The location of the mouth in an almost terminal position allows it to be protracted and the surface film sucked in. This type of feeding is used when thick concentrations of micro-algae are present at the air-water interface.

TABLE 1. Important environmental parameters of the seven systems

	Georgia beach	*Spartina marsh pool*	*Spartina marsh stream*	*Florida mangrove swamp*	*Florida Thalassia bed*	*Florida brackish lake*	*Florida freshwater canal*
Normal salinity range (in %)	28-32	12-24	18-26	27-35	33-35	2-12	0
Yearly temperature range	12-30	10-32	12-30	16-36	18-34	14-30	15-30
Benthic substrate	siliceous sand	sandy mud	sandy mud	organic mud	calcium carbonate	organic mud	limestone rock
Organic content (% dry wt.) of sediment	0·5-1·1	3·6-4·8	1·1-3·1	—	—	5·1-7·2	—
Dominant main producer available to mullet	benthic microflora	benthic microflora	benthic microflora	benthic microflora	benthic microflora and epiphytic diatoms	green and blue-green algae	green and blue-green algae
main source of Macrophyte detritus	*Spartina*	*Spartina*	*Spartina*	mangrove	3 species of sea grasses	terrestrial plant material	terrestrial plant material

An "interface feeder"

In most types of feeding by this mullet there is a dependence on the presence of some type of physical surface. These include the top layer of the sediments, the surface film of the water, the surface of *Thalassia* leaves, the rock walls of canals and the exposed trunks and roots of trees along the water's edge. *Mugil cephalus* might be described as an "interface feeder", a role which differs markedly from filter feeders which utilize mucous nets or gill rakers to concentrate food particles.

FEEDING IN RELATION TO THE ENVIRONMENT

Despite the body of knowledge which has accumulated concerning *Mugil cephalus*, including many descriptions of the food materials which are ingested, there has not been a concerted attempt to analyse its feeding in relation to the food available in the environment and how this varies from one area to the next. For the present study seven very different environmental systems were chocen, and the mullet's diet analysed for each system. Four systems were located along the south-east coast of Florida (25°30′N), while the remaining three were six degrees of latitude to the north in the vicinity of Sapelo Island, Georgia.

The Florida systems were: (*i*) a red mangrove, *Rhizophora mangle*, swamp; (*ii*) a turtle grass, *Thalassia testudinum*, bed in Biscayne Bay; (*iii*) a limestone quarry pit filled with brackish water; and (*iv*) a small, freshwater, agricultural drainage ditch. One system at Sapelo Island, Georgia, consisted of an open siliceous beach, while the remaining two were associated with the extensive cord grass, *Spartina alterniflora*, marshes lying between Sapelo Island and the mainland. One of the latter was a small mud-bottom marsh creek and the other a high marsh tide pool which was connected with the sea only on high spring tides. Important ecological parameters that need to be considered in these systems are given in Table 1.

Methods of study

Samples of planktonic, epiphytic and benthic micro-organisms were collected from the environment in each system. Planktonic forms were removed from the water column at the surface and near the bottom with a Niskin Bottle and spun down in a continuous centrifuge (Kimball and Wood, 1964). Sediment samples came from the upper one-half centimetre of mud or sand and were collected with a glass vial. Epiphytes on *Thalassia* and algal growth on rocks were removed with a razor blade which was then washed in a vial of filtered sea water.

Mugil cephalus were collected with a nylon throw net of 4·5 metres diameter and 2 cm stretched mesh. Samples of food material were taken for both identification and quantitative counts from the cardiac stomach and selected sections of the intestine. They were measured volumetrically in a calibrated tube and then suspended in filtered seawater to make 25 ml of solution. Each sample was shaken thoroughly and a known volume pipetted onto a slide with an etched grid.

Identification of stomach contents was done with conventional light field microscopy. Diatoms were identified to species, but other unicellular algae, filamentous algae, Foraminifera and Protozoa were more broadly categorized. For quantitative comparison of various parts of the alimentary tract, fluorescence microscopy (Wood, 1955; Wood and Oppenheimer, 1962) was used in conjunction with acridine orange stain. The usefulness of this method rests in its ability to detect organisms even when they are adsorbed on or covered by clay or quartz particles.

Pillay (1952) has pointed out the difficulty of estimating the per cent composition of the stomach contents of mullet. For the present study Pillay's method (1953) of eye estimation with a graduated slide was utilized. In addition, an eyepiece micrometer was found invaluable to overcome bias on the observer's part. All materials were placed in three categories: (*i*) fresh plant material (live diatoms, blue-green algae, dinoflagellates, etc.). (*ii*) macroplant detritus, and (*iii*) inorganic particles (quartz, clay, calcium carbonate, etc.).

Obviously, some mistakes are inherent in a procedure which attempts three dimensional answers (volume) using two dimensional methods. Some difficulty was experienced with pennate diatoms and large pieces of detritus because of their asymmetrical shapes. In such cases rough estimates were made. Fortunately, most particles ingested by mullet are small and roughly spherical; thus, ratios from two dimensional measurements should closely approximate true volumes.

Determinations of the per cent of organic matter in sediments, stomach and intestinal contents were derived from loss on ignition at 550°C after 10 hours. Due to the large percentage of quartz, heavy metals and other inorganics, it was important to use small amounts which were burned for the full 10 hours to ensure complete ignition. This method was impractical for the majority of south Florida samples due to the high amount of calcium carbonate in the sediments.

The rate of oxygen consumption by the stomach and intestinal contents was measured with a potentiometer and variable resistor and was read with a linear scale recorder. Silver and platinum electrodes were used and the readings were standardized with the Winkler method.

Samples for plant pigment analysis were taken from the sediments and the cardiac stomach of the mullet. Half of each sample was dried to give the dry weight while the other half was extracted with 90% acetone. Extraction was aided by grinding for 10 minutes with a mortar and pestle. The resulting solution was filtered and analysed with a Beckman DU spectrophotometer. The amount of plant pigment was calculated using the formula of Richards with Thompson reported in Strickland and Parsons (1965). As Vallentyne (1955) has demonstrated, a portion of this value may be due to degradation products of plant pigments (phaeophytine, pheophorbides, etc.); however, for purely comparative purposes the origin of the total pigment value is unimportant.

Caloric analyses were made of mullet stomach contents using a Parr oxygen bomb calorimeter. The high ratio of inorganic to organic matter made it impossible to burn the samples directly; this was overcome by adding known quantity of benzoic acid to the sample and later subtracting the combustion value of the benzoic acid from the total combustion value. Even with this method it was impossible to burn sediment samples.

Utilization of two basic food sources

In the standard energy flow diagram there is a direct flow of energy from the first trophic level (the primary producers) to the second (the primary consumers) and then to the secondary and higher consumers. Classically, the bacteria and other decomposers have been considered as primary consumers along with the herbivores. Since there is a considerable time lag involved in decomposition, it is much more realistic to separate herbivores and decomposers. E. P. Odum (1962, 1963) has suggested a Y-shaped diagram emphasizing two principal pathways, which he refers to as the grazing food chain, in which living plants are the primary energy source for the consumer, and the detritus food chain, in which dead and decaying organic materials are the energy source.

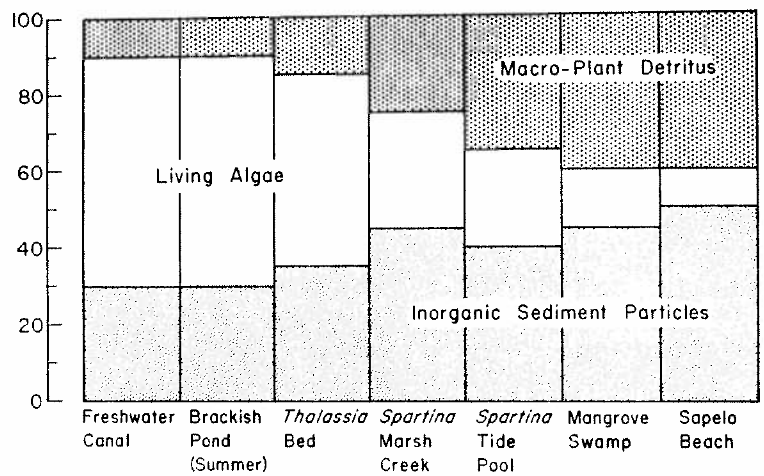

Fig. 1. Estimated percentages of the three important components occurring in the stomach contents of *M. cephalus* in the seven systems. The value for each system represents over 100 fish which were sampled over a period ranging from 3 to 12 months.

The estimated percentages of plant detritus, live plant material and inorganic sediments occurring in the stomach contents of mullet at the seven stations are shown in Fig. 1. It appears that *Mugil cephalus* occupies a position between the two food chains and is able to utilize whichever is the easiest to exploit in a given situation. Thus, mullet at the Sapelo beach station and in the Florida mangrove swamp depend to a great extent upon detritus and its associated micro-organisms, while those from the *Thalassia* bed in Biscayne Bay and from the freshwater canal subsist largely on live plant material. In the other systems investigated, feeding was a more equal combination of items from both food chains. Animal remains (harpacticoid copepods, nematodes, etc.) were found in less than 1% of the stomachs examined.

The preferred food chain

Hartley (1947) has suggested that, "it is . . . possible that the organization of the alimentary system of a particular species, as for example in the relative concentrations of its digestive enzymes, may be such as to obtain maximum advantage for only a limited part of the range of material which the animal is actually capable of ingesting." If this idea is true, *M. cephalus* should show a preference for either plant detritus or live plant material when both are present in abundance.

A situation exists in one of the systems where conditions are suitable to give an indication of which food source is preferred. In the Florida freshwater canal the bottom is covered with large quantities of fine terrestrial plant detritus which has been washed in from surrounding fields. Since the canal was dug through limestone rock the sides present an ideal substrate for the accumulation of a large mat of filamentous green and blue-green algae intertwined about diatoms and desmids. Faced with a choice between these two resources, *M. cephalus* feeds almost exclusively on live plant material (see Fig. 1). A similar situation exists at the *Thalassia* bed where mullet feed primarily on epiphytic diatoms in preference to copious quantities of plant detritus on the bottom. A small amount of detritus is ingested by mullet at both stations when sand grains are sucked from the bottom to triturate the ingested fresh micro-algae.

Parameters of the two diets

The question arises as to why *M. cephalus* would demonstrate a preference for live plant material over plant detritus. In Table 2 a comparison is made of stomach contents which represent three naturally occurring diets; (*i*) a

TABLE 2. Values of stomach contents taken from mullet feeding on three diets. Each value represents the mean for the stomach contents from 25 mullet

	Algal diet (Thalassia bed)	*Mixed algal and Detritus (Sapelo marsh)*	*Detritus diet (Sapelo beach)*
Plant pigment (mg/g dry wt.)	0·465	0·315	0·166
Per cent organic matter (dry wt.)	9·81%	6·22%	5·90%
Calorific value (kilocalories per ash-free gram)	5·226	4·552	3·957

predominantly macroplant detritus diet at the Sapelo beach, (*ii*) a mixed detritus and microalgae diet in the Sapelo marshes and (*iii*) a diet made up largely of fresh micro-algae at the Florida *Thalassia* bed. A rough indication of the relative amounts of living plant material in the three diets is given by the milligrams of plant pigment per gram of stomach contents. As a general rule stomach contents from fish feeding on live plant material had values three times as high as those from fish feeding on detritus.

Table 2 also shows that the percentage of organic matter in the stomach contents of mullet feeding on live plant material was almost twice as high as the percentage for those feeding on detritus. It should be remembered that the stomach contents always contain inorganic sediment particles; the weight of these particles is responsible for the low per cent organic matter values.

The most significant difference in the diets is in their caloric content. Clearly, the pure plant diet presents a much greater potential energy source than the plant detritus. According to Odum (1963), plant biomass averages about four kilogram calories per ash-free gram, and animal biomass five. The very high value of 5·226 kilogram calories for the contents of the mullet stomachs from the *Thalassia* bed is probably due to the preponderance of epiphytic diatoms in the diet. Diatoms have been shown to have a high caloric value due to the amounts of light oils which they store. Conover (1964) found a value of 5·342 kilogram calories for *Thalassia fluviatilis*, 5·225 for *Ditylum brightwelli*, and 5·270 for *Rhizosolenia setigera*.

The contribution of phytoplankton to the diet

Very little of the food ingested by mullet originates from the water column; the possible exception would be settled planktonic forms on the benthos. The most common planktonic diatoms occurring over the *Thalassia* bed were *Chaetoceros diversus*, *Ch. affinis*, *Ch. laciniosus*, *Ch. didymus*, *Rhizosolenia fragillissima*, *Nitzchia closterium* and *Skeletonema costatum*. Only the last two were ever noted in mullet stomachs and they are not strictly planktonic diatoms. In the Sapelo marsh the most common planktonic diatoms were *Chaetoceros affinis*, *Ch. curvisetum*, *Hemidiscus hardmanianus*, and *Rizosolenia setigera*. None of these appeared in mullet stomachs with any regularity.

Organic detritus, bacteria and Protozoa as food sources

Organic macroplant detritus was present in virtually all mullet stomachs which were examined (Fig. 1). In the Georgia salt marshes this consisted entirely of particles of decayed *Spartina alterniflora* leaves and stalks. In the Florida habitats it was derived from sea grass leaves, from mangrove leaves, root hairs and bark, and from terrestrial vegetation. Generally, the detritus particles which were ingested were smaller than 200 μ in diameter and often appeared to be organic aggregates of much smaller particles. Fluorescence microscopy with acridine orange stain revealed that these aggregates and particles were covered with large numbers of bacteria and Protozoa. Since the number of these organisms was greatly reduced during passage down the mullet's digestive tract, it is probable that they are utilized as an energy source.

Baier (1935) was one of the first to hypothesize that the nourishment from detritus particles comes from the bacteria involved in decomposition rather than the detritus itself. This idea has been more recently emphasized by Darnell (1967a, 1967b). Zobell and Felthan (1938) demonstrated that certain marine invertebrates could live almost indefinitely on an exclusive diet of bacteria. Zobell (1942) suggested that bacteria were useful as food in two ways: (*i*) they were important directly as nourishment, and (*ii*) they assisted the organism's digestion.

Although micro-organisms may not constitute an important fraction of the ingested food mass in a consumer's stomach, they may supply important nutrients (Burkholder and Burkholder, 1956; Burkholder and Burnside, 1957). Teshima and Kashiwada (1967) found that about half of the 198 strains of bacteria which were isolated from the intestinal canal of carp were capable of producing vitamin B_{12}. No vitamin B_{12} decomposing bacteria were found.

Fish (1955) while studying the feeding relationships of tilapia in East Africa concluded that the food of *Tilapia nilotica* and *T. leucosticta* was mainly bacteria and Protozoa adsorbed upon decomposing "debris". He suggested that the micro-organisms were making previously undigestible material available to the fish. Newell (1965) reached much the same conclusion concerning two marine deposit feeders, the prosobranch *Hydrobia ulvae* and the bivalve *Macoma baltica*. Neither organism is able to alter or utilize the basic carbon structure of ingested detritus particles, but both are capable of digesting micro-organisms adsorbed on the particles. These micro-organisms are capable of oxidizing the carbon of the detritus particles and indirectly convert the detritus carbon into mollusc carbon.

From these examples the following recurring cycle emerges. First, the adsorbed bacteria and fungi begin oxidation, hydrolysis and assimilation of the basic carbon structure of the detritus particle. During the process of microbial breakdown, these decomposers are continuously grazed by Protozoa. This creates a rich Protozoa-bacteria-detritus system with great potential food value. At intervals the entire complex may be ingested by a larger organism such as a snail or mullet and most of the bacteria, fungi, and Protozoa digested off the particle. In the case of organisms such as *Mugil cephalus* the detritus particle may be further fragmented by grinding or chewing. Once the particle (or fragments of the original particle) is released as faecal material into the environment, the entire process begins again.

Feeding periodicity

Under normal conditions mullet appear to feed almost continuously: however, the intensity of feeding is not always the same. Since ingested material is continuously transferred from the cardiac stomach to the pyloric stomach, the feeding intensity is reflected by the amount of material present in the cardiac stomach. If feeding is intensive the cardiac stomach will remain filled, but if feeding is sporadic the cardiac stomach will be only partially filled.

In areas which are influenced by tidal exchange there is a definite relationship between the rate at which food is ingested and the state of the tide. In

Fig. 2 the percentage of the cardiac stomach capacity which is occupied by ingested material is plotted against the stage of the tide. There is a marked increase in the amount of food ingested as the tide rises. This is not surprising as many of the optimal feeding areas become accessible to the mullet with the rising tide.

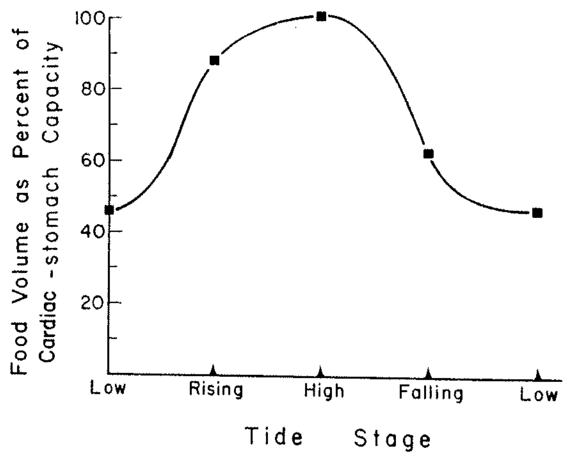

Fig. 2. The relationship between the feeding intensity (represented by the fullness of the cardiac stomach) and the stage of the tide. Each of the four data points represents the mean value for 50 mullet sampled at the Sapelo beach.

A prolonged cessation of feeding was noted only under unusual circumstances. Mullet with empty digestive tracts were found at the Georgia beach-station during extreme weather conditions when there was a great deal of turbidity and turbulence. In Biscayne Bay mullet ceased feeding immediately before and during the fall spawning migrations to offshore areas.

Food as a limiting factor

For a "broad spectrum" herbivore such as *Mugil cephalus* food does not appear to be a limiting factor. The ability to ingest and apparently utilize benthic and epiphytic diatoms, dinoflagellates, Protozoa, green and blue-green algae along with macroplant detritus and its associated micro-organisms ensures a constant energy source. In all the environmental systems examined at least two of these components were present in copious amounts. In the event of severe depletion or competition for any of these food materials, the mullet possesses the ability to switch to a different type of feeding.

Although adult mullet do not appear to be food limited, it has been noted by Suzuki (1965) and others that during the first several weeks of life (the Querimera stage) the young mullet feed chiefly on planktonic micro-crustaceans. It is possible that the survival of Querimera stage mullet may be controlled by the availability of micro-crustaceans in a density-dependent manner.

Selection-rejection rate

By comparing the amount of plant pigment in the contents of the cardiac stomach with the amount occurring in the sediments upon which the fish feed, it is possible to obtain a rough estimate of the amount of mud filtered by a mullet to obtain one gram of ingested material. Such a determination will be valid only if feeding is confined exclusively to the sediments.

In the Sapelo marshes all substances ingested by *M. cephalus* originate from the sediments. The upper one-half centimetre of these sediments was found to contain 2-4 micrograms of plant pigment per dry gram of sediment (range of values for 20 sediment samples). Mullet feeding upon these same sediments contained 350 micrograms of plant pigment per dry gram of stomach contents (mean value of stomach contents of 25 mullet). This indicates that a mullet must filter almost one hundred grams of sediment to obtain one gram of material in its digestive tract.

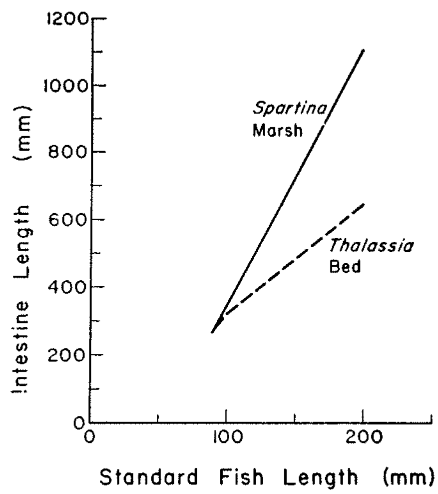

Fig. 3. The relationship between the standard fish length and the intestinal length for two populations of mullet; (1) a population from the *Spartina* marsh creek and (2) a population feeding in the vicinity of the Florida *Thalassia* bed. Each regression line was constructed from measurements made on 50 mullet.

Turnover effect on the sediments

A mullet of 200 mm standard length commonly contains about 3 grams (dry weight) of sediment material in its pyloric and cardiac stomachs and intestine. This would require filtration of 300 dry grams of sediment. Assuming more or less continuous feeding and a turnover rate of five times in 24 hours (discussed later in this paper), such a mullet would filter 1500 dry grams of sediment per day or over 450 kilograms (half a metric ton) a year. This means that a single mullet would be responsible for altering every year an area of sediment measuring 45 square metres and ½ centimetre deep. The effect of a large school of mullet on the environment is not difficult to imagine.

Morphological adjustment to the environment

The ratio of the length of a fish's intestinal tract to the total length of the fish is often a good indication of the type of food commonly ingested. Generally, this ratio is less than unity in carnivores, from one to three in omnivores and even greater in herbivores. Al-Hussaini (1949) has stated that this ratio is nearly constant for each individual species, but evidence suggests that this is only true for carnivores. Klust (1939) found that the length of the gut increased relative to the body length with age in the *Cyprinidae*. Kostomarov (1942) confirmed this for the carp, *Cyprinis*. However, in the tench, *Tinca*, which is normally a carnivore, the proportion of the gut length remained the same at all ages (Kostomarov and Pulankova, 1942).

Hiatt (1944) examined *M. cephalus* growing in Hawaiian fish ponds and found that the intestinal length and total fish length maintained a constant ratio of 3·2:1 in mullet of different sizes. On the other hand, milkfish, *Chanos chanos*, in the same ponds demonstrated heteronomous growth of the intestine by increasing the ratio of the intestinal length to total fish length from 3·5:1 for fish of 90 mm total length to 7·2:1 for fish of 115 mm. For larger fish the ratio tended to decrease slightly and finally reached 6·5:1 for fish of 272 mm. The great increase of intestinal growth for fish between 90 and 115 mm was correlated with a change in diet from unicellular algae to filamentous algae and plant fragments.

The length of intestine versus standard fish length of two populations of *M. cephalus* are plotted in Fig. 3; only fish between 75 and 200 mm were measured. The extremely steep slope for the Sapelo marsh population shows a much faster growth of the intestine—six or seven times greater than the increase of the standard fish length. As a result the ratio of the intestine to the standard length increased from 3·2:1 in 100 mm fish to 5·5:1 in those measuring 200 mm. In contrast, the data from the mullet feeding in the area of the Biscayne Bay *Thalassia* bed displays a slope of slightly greater than one or an almost constant ratio of 3·2:1, a result which is in close agreement with Hiatt's data.

The apparent discrepancy of these data can be explained by noting the most important components of the diet of these two groups of mullet and the population described by Hiatt in Hawaii. The Sapelo marsh mullet included a great deal of plant detritus in their diet while those in Biscayne Bay and the Hawaiian fish ponds fed predominantly on benthic and epiphytic diatoms, a food source which is much more easily broken down by the mullet's pyloric stomach and presumably easier to absorb. It seems that an intestine to fish ratio of about 3·2:1 is adequate to effectively assimilate a diatom diet, while a longer intestine is needed to extract nourishment from plant detritus.

Schuster (1949) has found a similar difference in intestinal length to fish length ratios for *Chanos chanos* feeding on different diets. In one pond where *Cyanophyceae* predominated the ratio was 7·9:1, while in another pond where

Chlorophyceae predominated the ratio was only 5·7:1. He concluded that the widespread utilization of *Chanos* as a pond fish could be partially explained by the ability of the species to adjust morphologically to the environment. The same could be said for *Mugil cephalus.*

Intestinal flagellate populations

Large numbers of very small (10-20 μ) colourless flagellates were usually present in the intestinal contents of *M. cephalus*. These flagellates, which could not be identified, probably function in the breakdown of organic particles, particularly the cellulose walls of plant detritus particles. They were characteristically observed clustered around the broken cell walls of pieces of mangrove and *Thalassia* detritus.

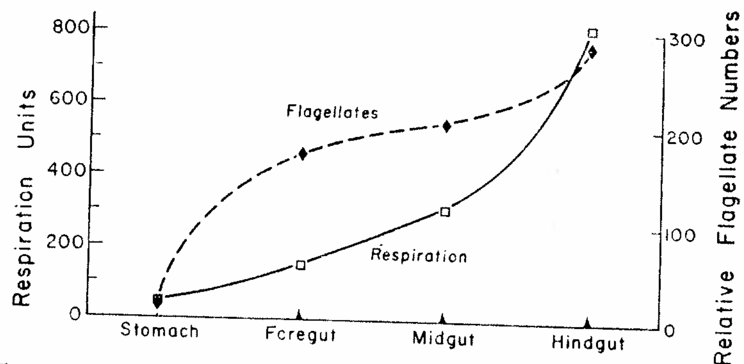

Fig. 4. Flagellate numbers and oxygen consumption rates for cardiac stomach contents and 3 portions of intestinal contents from a single Sapelo marsh mullet. The flagellate numbers were counted from 20 grids of a calibrated counting chamber using fluorescence microscopy. One respiration unit = $1{\cdot}70 \times 10^{-4}$ milligram atoms/O_2/hour.

Since most teleost intestinal fauna are facultative anaerobes (E. J. F. Wood, personal communication), it was possible to gain some idea of the activity of intestinal micro-organisms in general and the flagellates in particular by measuring the respiration rate of the intestinal contents at various points under aerobic conditions. To do this, small portions of intestinal contents from a freshly killed mullet were suspended in 25 ml of filtered and sterilized sea-water and measured in the dark with a respirometer. In Fig. 4 these respiration values for one mullet are plotted along with counts of flagellates made from the same samples using fluorescence microscopy and acridine orange stain. The lowest values for respiration and counts were in the cardiac stomach and were followed by a steady increase down the intestinal tract.

It is very likely that *M. cephalus* has the ability to digest these flagellates. Fish which have been starved for a day or two have nothing in the intestinal tract except quantities of mucopolysaccharide. Even under fluorescence microscopy with acridine orange no micro-organisms could be found.

Both Hunter (1920) and Wood (1940) have suggested that the intestinal tracts of many fish become sterile during periods when no food is ingested.

Wood found it difficult to obtain cultures from the guts of non-feeding, migrating *M. cephalus* in Australia; when organisms were found they were sporulating aerobes. He postulated a bactericidal or at least bacteriostatic influence in the intestinal tract, thus ruling out permanent intestinal flora and fauna.

Maximum power output

It is commonly accepted that the ideal natural system should approach maximum efficiency in converting food. In contrast to this supposition is the maximum power hypothesis of H. T. Odum and R. C. Pinkerton (1955) which is predicated upon the hypothesis that natural systems tend to operate at an efficiency which produces a maximum power output. Thus, a predator which may be feeding upon a scarce and potentially limiting food source will have a low rate of ingestion coupled with a high assimilation efficiency, while an omnivore feeding upon plentiful and easily obtained supplies of micro-algae and plant detritus will achieve the greatest power output from a high rate of ingestion and a relatively low assimilation efficiency.

The digestive tract of *M. cephalus* is efficient at breaking up diatoms; other particles such as plant detritus and blue-green algae are only partially destroyed. Mullet feeding upon a bloom of the dinoflagellate *Kryptoperidinium* have been found to pass from 20 to 30 per cent through the digestive system in a viable condition (W. E. Odum, 1968). The explanation for this lies in the ability of the dinoflagellate to encyst rapidly upon meeting adverse conditions.

It was of interest to see if the apparent low assimilation efficiency and high ingestion rate of *Mugil cephalus* were accompanied by a low retention time. To determine the retention time of food material, several groups of mullet ranging in length from 100 to 200 mm were fed a mud-detritus mixture containing fluorescent "Day-glo" (fireorange AG-14) particles (see Haven and Morales-Alamo, 1966). These particles, which have a mean diameter of 4·5 μ, were readily ingested and subsequently labelled the faecal matter very clearly.

A comparison of retention times in fish may be misleading due to the effects of temperature, the condition of the fish and the rate of feeding. For this reason several groups of fish were tested at three different temperatures: 20°C, 23°C, and 26°C. Retention time of the ingested material was highly variable, but could not be correlated with these temperature changes. Depending upon the intensity of feeding, the retention time ranged from two to six hours. The mean value was between four and five hours indicating a turnover rate of five times in 24 hours.

In summary, the maximum power output for *Mugil cephalus* results from a relatively large and continuous ingestion rate and short retention time coupled with an assimilation efficiency which is probably high for a few components of the diet such as epiphytic and benthic diatoms, but rather low when the entire bulk of ingested organic matter is considered.

SOME CONCLUSIONS AND HOW THEY RELATE TO POND CULTURE

Although *Mugil cephalus* is widely used as a pond culture species, in most cases it either is of secondary importance to other species such as eels (Nakamura, 1949; D'Ancona, 1955) and *Chanos chanos* (Acosta, 1953) or when it is the primary species, techniques have not been refined to the point where optimal yields are obtained. In reviewing the results of the present investigation several ideas emerge which might enhance the production of mullet in ponds.

First, it should be realized that mullet in a culture pond differ from those living in a natural ecosystem in that their growth may be easily limited by the availability of food. A culture pond is an artificial ecosystem with an artificially increased population size and, ideally, a lack of predators. To develop an unnaturally large population size and still retain optimal growth, it is necessary to increase the amount of food available to the mullet. Addition of commercial inorganic fertilizers can increase the production of mullet ponds somewhat, but this by itself may not be sufficient.

Earlier in this paper *M. cephalus* was characterized as an "interface feeder" dependent upon the availability of physical surfaces to concentrate food. If this is true, mullet in ponds are limited ultimately by the surface available for grazing. The way to increase production, then, is to increase the available surface area and at the same time supply adequate nutrients. There are two ways in which this might be done.

The first is to create an artificial grass bed in the pond. Natural sea grasses are difficult to transplant and in unnatural conditions are susceptible to sudden salinity changes and disease. Artificial grass beds, however, can be easily and inexpensively made from strips of polypropylene film. W. L. Rickards at the University of Miami has built such structures from long strips of this positively buoyant film attached at the bottom to panels of synthetic netting. The netting, which has a mesh size sufficiently large to allow fish to feed on the bottom, is weighted down every few square metres with concrete weights. The result is a luxuriant bed of the desired density and with the filaments stretching from the bottom to the surface. Within two weeks the surfaces of the filaments become encrusted with epiphytic micro-algae, increasing by at least 20 times the surface available for mullet grazing.

A second way to increase production in mullet ponds is to increase the surface area of the sediment particles. This can be accomplished by constructing the pond so that the bottom consists of clay-sized inorganic particles. In addition, large quantities of very finely chopped macroplant detritus can be periodically added to the bottom of the pond. The increased surface area of the fine inorganic and plant detritus particles presents an ideal substrate for growth of micro-algae, bacteria, Protozoa and fungi. This in turn should increase mullet production. It is important that both the inorganic sediment particles and the artificially created detritus particles be very fine (less than 200 μ) since most of the particles ingested by mullet are of this size (see W. E. Odum, 1968).

SUMMARY

1. It is suggested that in shallow estuaries most food chains are based not on phytoplankton, but on macroplant detritus and benthic and epiphytic micro-algae. It is the animals capable of utilizing such energy sources which replace zooplankton as the critical herbivore link.

2. To obtain the maximum yield of fish from a shallow estuary it will be necessary to concentrate management and culture operations upon species such as *Mugil cephalus* which obtain their energy directly from the first trophic level.

3. From analyses of the diet in seven different environmental systems it appears that *M. cephalus* is able to utilize either the direct grazing or plant detritus food chains as an energy source depending upon which is the easiest to exploit. When both food sources are present in abundance, the mullet exhibits a preference for living micro-algae. Such an algal diet has a higher caloric content than a macroplant detritus diet.

4. Fine particles of decaying plant detritus (mangrove, *Spartina*, *Thalassia*) were present in virtually all mullet stomachs which were examined. Bacteria and Protozoa adsorbed to these particles may be important in the diet of the striped mullet, either as a source of essential nutrients or by providing assistance in the breakdown of plant material. Unidentified colourless flagellates, often present in the intestinal contents, seem to function in the destruction of cellulose cell walls. Starved fish have a digestive tract which is practically sterile.

5. Although feeding is almost continuous, a marked increase in the rate of ingestion was found during rising and high tides. Feeding ceases during adverse weather and at the time of offshore spawning migrations.

6. For a "broad spectrum" herbivore such as *M. cephalus* food does not seem to be a limiting factor. The ability to ingest and apparently utilize benthic and epiphytic diatoms, dinoflagellates, Protozoa, green and blue-green algae along with macroplant detritus ensures a constant energy source.

7. By comparing the amount of plant pigment in the contents of the cardiac stomach with the amount in the sediments upon which the fish feed, it was found that *M. cephalus* filters almost 100 dry grams of sediment to obtain one dry gram of material in its digestive tract. Assuming more or less continuous feeding and a turnover rate of five times in 24 hours, a 200 mm S.L. mullet would filter 1500 dry grams of sediment per day or over 450 dry kilograms (half a metric ton) a year.

8. Mullet populations adjust morphologically to the type of food available in the environment by lengthening the intestine for coarser diets. An intestine length to fish length ratio of 3·2:1 is adequate to effectively assimilate a diatom diet, while a longer intestine is needed to extract nourishment from plant detritus and blue-green algae.

9. The maximum power output for *Mugil cephalus* results from a large, continuous ingestion rate and short retention time coupled with an assimilation efficiency which is probably high for diatoms, but low when the entire bulk of ingested organic material is considered.

10. To obtain the maximum yield of mullet from a culture pond it is necessary to increase the available surface area for growth of microfauna and microflora which are subsequently grazed by *M. cephalus*. This can be accomplished by creating artificial grass beds and constructing the bottom of the pond so that it is composed of very fine inorganic and plant detritus particles.

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