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The food and feeding ecology of Mugilidae in the St. Lucia lake system

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The diet and feeding interrelationships of ten species of Mugilidae were studied over a two-year period in the St. Lucia lake system of South Africa. Qualitative stomach analyses were performed on over 1000 fish of more than 5 cm (standard length). All are soft bottom substrate feeders ingesting inorganic particles mixed with food items. The food of most species is the same and consists of *Assiminea bifasciata*, foraminifera, the large centric diatom *Aptinoptychus splendens*, small centric and pennate diatoms, and filamentous algae. Individual species of mullet however, differ, in the size of inorganic particles ingested and exhibit marked sand grain size preferences. The consumption of the various food items may depend upon their occurrence on substrates of the preferred particle size. There is no apparent change in diet and particle size preference according to age in any of the species and no seasonal variation was recorded in the diet. It is suggested that interspecific competition for food is reduced by substrate particle size selection and perhaps by differences in feeding periodicity. Where there is an apparent overlap in diet, as in the case of *Assiminea bifasciata*, on substrates of the same size then there is a superabundance of the food organism which serves to minimize competitive interactions.

CONTENTS

INTRODUCTION

The grey mullets (Mugilidae) are a widespread and successful coastal and estuarine teleost family consisting of a relatively large number of closely related species. Although the diet of the most widely occurring species, *Mugil cephalus* L., has been extensively studied (Odum, 1970; Thomson, 1966) little information is available on food and feeding interactions among sympatric

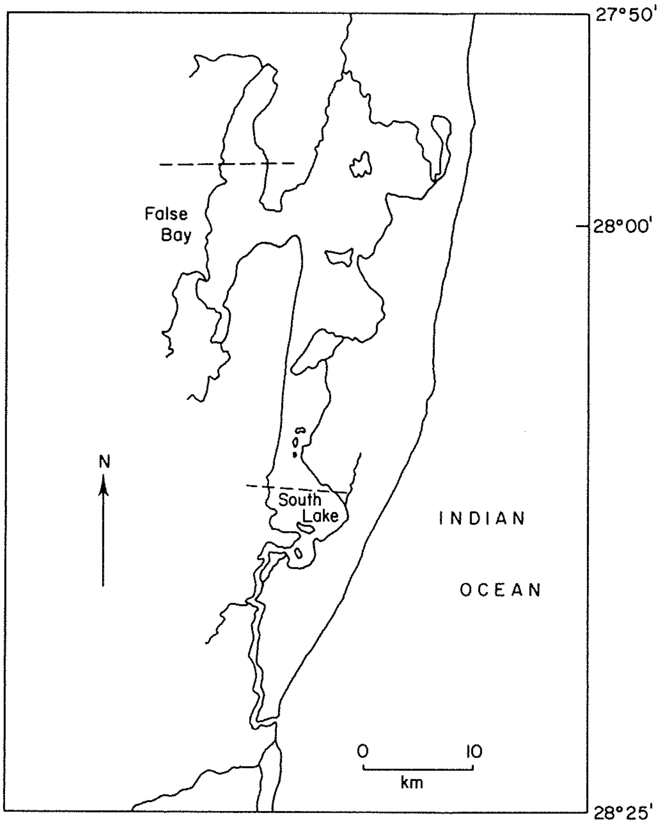

Figure 1. The St. Lucia lake system showing sampling areas and substrate analyses transects (– – – –).

mullet species. Twelve species of Mugilidae occur along the Natal coast of south east Africa (Table 1) and ten of these are found in the St. Lucia lake system of Zululand (Fig. 1). In a coastal lagoon system such as St. Lucia, where a relatively large number of mullet species coexist, complex competitive interactions may occur in relation to diet. This paper presents the results of a two-year study into the food and feeding ecology of grey mullet in St. Lucia, special attention having been given to the diets of each species and how the food resources are partitioned among the ten species. Fish of less than 5 cm (standard length) were studied separately and form the basis of a subsequent report.

MATERIALS AND METHODS

Study area

Fish were collected from False Bay and South Lake (Fig. 1) on a monthly basis using gill, seine and cast nets. It should be noted that St. Lucia nowhere exceeds about 2.5 m in depth. Stomachs were removed from captured fish and immediately preserved in 10% formalin for analyses in the laboratory. Fish lengths were recorded to the nearest mm as standard length. In addition the

Table 1. Species of Mugilidae occurring in the two regions of St. Lucia investigated during 1974 and 1975

Species*	Common name*	South Lake	False Bay
Mugil cephalus L.	Flathead mullet	†	†
Liza alata (Steindachner)	Diamond mullet	†	‡
L. dumerili (Steindachner)	Groovy mullet	†	†
L. macrolepis (Smith)	Large scale mullet	†	†
L. tricuspidens (Smith)	Striped mullet	†	‡
Myxus capensis (Val.)	Freshwater mullet	†	‡
Valamugil buchanani (Bleeker)	Bluetail mullet	†	‡
V. cunnesius (Val.)	Longarm mullet	†	‡
V. robustus (Günther)	Robust mullet	†	‡
V. seheli (Forsskal)	Bluespot mullet	†	‡

* Scientific and common names taken from Smith (1975).
† Present.
‡ Absent or recorded only once.

total gut length of *M. cephalus* was measured in the field in order to obtain a gut length to body length ratio for comparison with the results of other workers.

Stomach analyses

Food material was removed from both the cardiac and pyloric regions of the stomach by washing into a Petri-dish. Food items were divided into the categories shown in Table 2 and analysed numerically by frequency of occurrence. Measurements of substrate particle sizes from stomach contents were performed with an eyepiece micrometer.

Feeding periodicity

The feeding periodicities of *M. cephalus, Liza macrolepis* (Smith) and *Liza dumerili* (Steindachner), the three most abundant mullet species in St. Lucia (Wallace, 1975), were determined by sampling over two 24-hour periods in July 1974 and July 1975. Not less than ten fish of each species were captured every four hours by seining. Whole fish were preserved in 10% formalin. The stomach contents were removed in the laboratory and both the food and fish were dried to constant weight at 60° C. The quantity of food in the stomach was expressed as g of food per g of body weight.

Substrate analyses

The particle size composition of the various surface substrates in South Lake and False Bay were determined by collecting a known volume of the substrate to a depth of about 2 cm and passing it through a set of standard sieves (Endecott's test sieves Ltd., London).

Table 2. Percentage frequency of food items of Mugilidae longer than 5 cm (standard length) from St. Lucia. (*n*, Number of fish analysed, fish with empty stomachs or stomachs containing gill raker filaments excluded)

Species	*Mugil cephalus*	*Liza macrolepis*	*L. dumerili*	*L. alata*	*L. tricuspidens*	*Valamugil seheli*	*V. cunnesius*	*V. robustus*	*V. buchanani*	*Myxus capensis*
n	249	332	174	60	4	20	61	25	35	1
Food items										
Aptinoptychus splendens	46	24	34	2	—	65	62	96	80	—
Coscinodiscus granii	7	2	2	—	—	—	8	—	—	—
Small centrales	7	14	28	—	25	80	18	88	60	—
Pennales	9	24	7	5	—	40	13	32	60	100
Assiminea bifasciata	34	12	46	43	—	5	3	—	—	—
Foraminifera	37	9	40	—	—	15	33	—	20	—
Harpacticoid copepods	3	—	—	2	—	—	—	—	—	—
Cyclopoid copepods	4	1	1	—	—	—	2	—	3	—
Ostracoda	4	2	3	—	—	—	—	—	—	—
Flagellates	17	18	—	—	25	5	—	—	—	—
Cyanophyta	—	6	5	—	—	30	7	20	—	—
Filamentous algae	11	30	10	93	100	25	2	32	6	—
Ruppia spp.	11	12	4	—	25	—	—	—	40	—
Terrestrial plant debris	—	—	2	75	—	—	—	16	—	—
Particulate organic matter	3	4	10	—	—	—	8	8	—	100
Mean particle diameter (μm)	225	250	300	500	450	200	150	180	200	—
Standard error	4	5	9	20	—	17	10	8	4	—
Observed size range (μm)	50-400	50-400	100-600	400-600	—	100-250	100-250	150-250	100-200	—

RESULTS

Table 2 shows the percentage frequency of the various food items in the stomach of about 1000 Mugilidae from St. Lucia. The data for fish from False Bay and South Lake have been combined as there was no difference in diet among the individual species which occur in the two areas. Fish containing gill raker filaments in the stomach were excluded from the analyses since the presence of the filaments in the stomach is an artefact caused by capture and indicates that food may have been regurgitated (Blaber, 1975).

M. cephalus feeds mainly on the gastropod *Assiminea bifasciata* (Nevill), foraminifera of the genera *Quinqueloculina* and *Rotalia*, and the large centric diatom *Aptinoptychus splendens* (Ehbg). The latter usually exceeds 150 μm in diameter. Of the two other numerically dominant species in St. Lucia *L. dumerili* has a diet similar to that of *M. cephalus* whereas *L. macrolepis* consumes fewer foraminifera and *Assiminea*, and more small diatoms and filamentous algae. *Liza alata* (Steindachner) is more specific in its feeding and exhibits a preference for filamentous algae, terrestrial plant debris and *Assiminea*. The diets of *Valamugil buchanani* (Bleeker), *V. seheli* (Forsskal) and *V. robustus* (Günther) are similar and consist of *A. splendens* and small centric diatoms, pennate diatoms and filamentous algae or macrophytes. Relatively small quantities of animal material are consumed by these three species. *V. cunnesius* (Valenciennes) also consumes mainly diatoms and filamentous algae in addition to significant numbers of foraminifera. Examination of the hindguts of those species which feed on filamentous algae or macrophytes revealed that the filaments were broken up and the plant cell walls smashed. Ostracods, harpacticoid copepods and cyclopoid copepods appear infrequently in the stomach contents of mullet from St. Lucia although they are abundant in the benthos (Boltt, 1975). Insufficient numbers of *Myxus capensis* (Valenciennes) and *Liza tricuspidens* (Smith) (Table 2) were captured to permit accurate analyses of their diet.

There was no difference in diet according to length within a species. Little seasonal variation in diet was recorded with the exception of Cyanophyta and green flagellates. During the first five months of 1975 both blue-green algae of the genera *Chroococcus* and *Xenococcus*, and unidentified green flagellates appeared in the stomach contents of mullet. *M. cephalus*, *L. macrolepis* and *V. seheli* ingested significant quantities of flagellates, while cyanophytes were eaten by *L. macrolepis*, *L. dumerili*, *V. seheli* and *V. cunnesius*.

Measurements of the total gut length of *M. cephalus* of between 100 mm and 700 mm indicate that the ratio of gut length to body length increases with age. There was a very significant correlation for the linear regression of body length on body length to gut ratio ($r = 0.554$, $n = 39$). The ratio of total gut length to standard length ranged from 2.0 : 1 for fish of 120 mm to 6.5 : 1 for fish of 500 mm.

The results of the feeding periodicity experiments are shown in Fig. 2. *L. macrolepis* and *L. dumerili* feed predominantly during daylight hours while the peak feeding time for *M. cephalus* is around 18.00 hrs. *L. macrolepis* apparently ceases feeding at night whereas *L. dumerili* and *M. cephalus* continue feeding but at a lower intensity. It is notable that a few individuals of *M. cephalus* and *L. dumerili* were captured in 1974 and 1975 at 02.00 hrs with full stomachs.

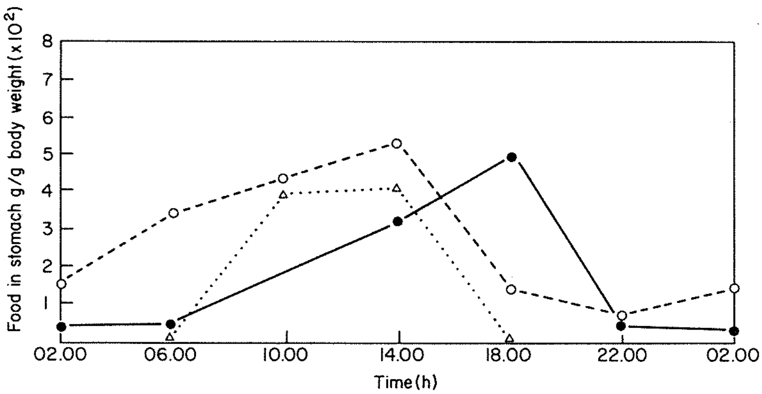

Figure 2. Feeding periodicity of *Mugil cephalus* L (•), *Liza macrolepis* (Smith) (△) and *L. dumerili* (Steindachner) (○).

The mean diameters of the sand particles found in the stomachs of each species are shown in Table 2. The four species of *Valamugil* contained sand particles between 100 and 200 μm mean diameter while the three most abundant species: *M. cephalus, L. macrolepis* and *L. dumerili* ingested particles of between 200 and 300 μm mean diameter. *L. alata* always contained coarser particles with a mean diameter of 500 μm. The actual observed size ranges of particles found in each species are shown in Table 2. Although considerable overlap occurs between the species the standard errors of the means indicate how uniform the particle size is for each species. All species were remarkably constant in the size of particles in their stomachs and the wide range of observed values shown in Table 2 can be attributed in each case to a very few fish which differed from the mean values.

Table 3 shows the differences in mean particle size between five species seine netted from the same locality on the eastern shores of South Lake in a single 24-hour period. Clearly *L. alata* and *V. buchanani* were ingesting particles of a

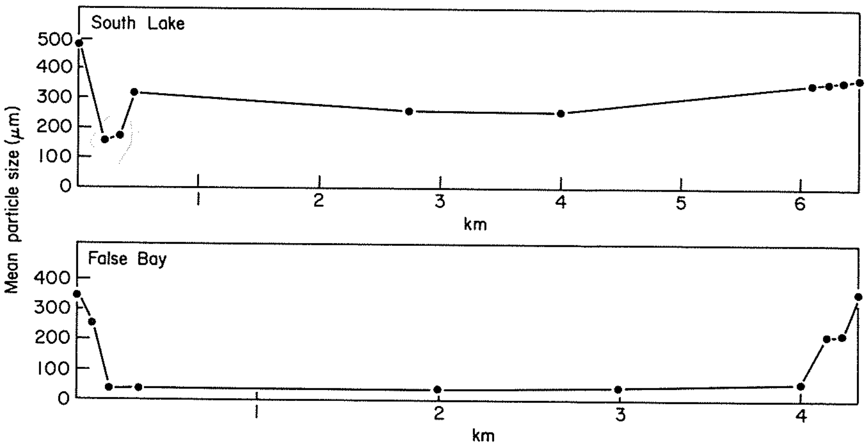

Figure 3. Substrate analyses transects of South Lake and False Bay, St. Lucia. Location of transects shown in Fig. 1.

Table 3. Food and sand particle sizes in 5 species of mullet netted from the same localities in South Lake, St. Lucia, over a single 24-hour period in February 1975

Species	Number captured	Mean particle size (μm)	Range (μm)	Food items
Mugil cephalus	28	250	Nil	*Assiminea, A. splendens,* flagellates, *Ruppia* sp. foraminifera
Liza macrolepis	49	270	250-400	*Assiminea,* flagellates, filamentous green algae
L. dumerili	24	300	250-400	*Assiminea,* small centrales, filamentous green algae, flagellates
L. alata	15	600	Nil	*Assiminea,* filamentous green algae, terrestrial plant debris
Valamugil buchanani	17	200	Nil	*A. splendens,* small centrales

different size and differed from *M. cephalus, L. macrolepis* and *L. dumerili* which overlapped in particle size preference. Also shown in Table 3 are the food items found in the five species; these are similar for nearly all species.

The substrate analyses of False Bay (Fig. 3) show that the surface of most of the region consists of particles with a diameter of less than 45 μm with the exception of the margins where particle sizes may exceed 350 μm. In contrast the South Lake substrate analyses (Fig. 3) show that the most commonly occurring particle size over the whole area is between 125 and 350 μm with diameters of greater than 350 μm being common in eastern marginal areas.

DISCUSSION

Mullet feed by sucking up the surface layer of the substrate or by grazing on submerged rock and plant surfaces (Odum, 1970). All the species investigated at St. Lucia were found to ingest large quantities of inorganic particles together with food items. It has been suggested that the function of these particles is to act as a grinding paste in the degradation of plant cell walls in the pyloric portion of the stomach (Thomson, 1966). The examination of the hindguts of these species at St. Lucia which ingest plant material showed that this was the case and it is probable that the fish are only able to digest plant material due to the breaking up of the plant cells by the grinding action of the sand grains. It is possible that many of the small centric and pennate diatoms found in the stomachs of Mugilidae are epiphytes which have been either chemically or physically removed from ingested filamentous algae or macrophytes. It is unlikely however that the filamentous algae or macrophytes are consumed only for their epiphytes as in *Rhabdosargus holubi* (Steindachner) (Blaber, 1974) since the mullet are able to break up and digest all the plant material.

The predominance of relatively large food organisms with a mean diameter greater than 100 μm in the diet of *M. cephalus* from St. Lucia is significant when compared with results obtained from studies on *M. cephalus* elsewhere in the world. Odum (1968) states that the diet of *M. cephalus* is comprised of epiphytic and benthic diatoms, dinoflagellates, blue-green algae and decaying plant detritus, and that micro-algae are the primary source of nutrition; Thomson (1959) working at Lake Macquarie in Australia found that *M.*

cephalus feeds mainly on diatoms, filamentous algae and blue-green algae; Luther (1962) reported that the main food items of *M. cephalus* in eastern India are decayed organic matter, algae and foraminifera; and Hiatt (1944) states that in Hawaii this species subsists primarily on littoral diatoms and blue-green algae. According to Odum (1970) when both living micro-algae and macroplant detritus are available, *M. cephalus* exhibits a preference for living micro-algae. In St. Lucia where very high densities of *Assiminea* and foraminifera occur (Boltt, 1975) *M. cephalus* appears to prefer feeding on these animals rather than on plant material.

Various authors have used the ratio between gut length and body length as an indication of the diet of *M. cephalus.* Hiatt (1944) found that Hawaiian *M. cephalus* have an intestine to fish length ratio of 3.2:1 which Odum (1970) suggests is adequate to assimilate a diatom diet. Odum (1970) however showed that in some Florida populations of *M. cephalus* the ratio between gut and body length increases with age. This he attributes to a change in diet from one of predominantly diatoms to one of plant detritus. The gut length of *M. cephalus* of between 100 and 700 mm in St. Lucia increases relative to body length with age but the diet remains the same. Hickling (1970) has suggested that the longer gut of larger grey mullet may be an adaptation to food which contains a high proportion of indigestible matter.

The absence of a significant seasonal variation in the diet of any of the mullet and lack of change in diet with length at St. Lucia corresponds with the situation reported for *M. cephalus* in Hawaii (Hiatt, 1944) and *M. cephalus* and *L. macrolepis* in India (Luther, 1962). The St. Lucia lake system, which nowhere exceeds 2.5 m in depth, undergoes cyclical changes in salinity due to the effects of rainfall and evaporation (Day *et al.*, 1954; Millard & Broekhuysen, 1970) and during 1972 experienced salinities above 70‰ (Boltt, 1975). This present study was made during a period when salinities were between 25‰ and 10‰ and life had returned to the system after a period of high salinities. Only *M. cephalus* remains common in St. Lucia under high salinity conditions (Wallace, 1975) and it is probable that during such periods its diet is different from that reported in this investigation. *M. cephalus* has been found in abundance at St. Lucia at 70‰ (Wallace, 1975) while one of its main food items, *Assiminea,* is not tolerant of salinities in excess of about 55‰.

Although there is considerable overlap in the diets of mullet species at St. Lucia the substrate particle size ingested by each species may be different (Table 2). The results of this study suggest that individual species of mullet exhibit a marked preference for particles of a certain diameter and furthermore that the occurrence of a particular food item in the diet may depend upon whether it occurs on substrates of the preferred particle size. However, the absence of significant numbers of very abundant animals such as ostracods and harpacticoid copepods and the high numbers of *Assiminea* and *Aptinoptychus* in the diets of mullet at St. Lucia suggest that the fish are capable of selecting particular food items or at least substrates rich in these organisms. Odum (1968) working in North America and Wood (1964) in Australia found that *M. cephalus* prefers very fine particles of less than about 10 μm in diameter, these being richer in adsorbed organic material. This investigation shows that *M.*

cephalus from St. Lucia are markedly different in this respect since their mean preferred particle diameter is 225 μm despite finer grained substrates being available, covering most of False Bay (Fig. 3). These fine substrates may perhaps not be utilised by *M. cephalus* because, according to Boltt (1975), they support relatively few *Assiminea.*

The mechanisms whereby each species selects a particular particle size is not known, nor is it clear whether the particle sizes present in the stomach are a result of a selective filter mechanism involving rejection of unwanted particles or whether the fish feed in areas where the surface substrate is of the preferred size. According to Thomson (1966) and Odum (1968) *M. cephalus* selects fine sediment particles by means of a pharyngeal filter apparatus. Pillay (1953) reported that in *Mugil tade* (Forskaal) both a pharyngeal filter and gill rakers were used in the sorting of food. The results from St. Lucia are not conclusive in this respect but it appears that since there is a relationship between the distribution of mullet species and of particle sizes that the size of particles present in the stomach may be the result of a combination of the choice of a suitable substrate and a filter mechanism. The distribution of mullet in St. Lucia may be related to their particle size preferences. Only the three most common species are found in False Bay while all ten species occur in South Lake. It is evident from Fig. 3 that the surface substrate over most of False Bay is composed of particles with a mean diameter of less than 45 μm. This is below the mean preferred particle size of any of the mullet species (Table 2) and therefore probably only the marginal areas of False Bay, where particle sizes are greater, are utilized for feeding. In marked contrast South Lake substrates are made up from particles within the preferred size ranges of all ten mullet species (Fig. 3, Table 2). It is unlikely that distribution of mullet is directly related to diet; for example Boltt (1975) showed that densities of *Assiminea* were very high around the margins of South Lake and data from stomach analyses during this present investigation and from Boltt (1975) indicate that similar densities occur around the edges of False Bay. Stomach analyses data also show that the amounts of centric diatoms and filamentous algae in the margins of the two areas are similar. It is possible therefore that the absence of most species from False Bay may be due to the composition of the marginal substrates. These substrates are perhaps either too coarse or too fine for all species other than *M. cephalus, L. macrolepis* and *L. dumerili.*

Results from the feeding periodicity experiments are interesting because, although there is extensive overlap of feeding times, the peak feeding hours of the three common species are different. This together with the fact that *L. macrolepis* does not feed at night might serve to reduce competition between the three numerically dominant species.

The diet of a relatively large number of sympatric mullet species has not previously been investigated and therefore the results of this study are of considerable interest with regard to interspecific competition and the partitioning of food resources. In St. Lucia there is considerable overlap in the diet of mullet but interspecific competition may be reduced by the particle size preference of each species. *L. alata* only feeds in areas where the sand grains are about 500 μm in diameter (South Lake, Fig. 3) and thus does not compete with other mullet species with the possible exception of *L. tricuspidens.* The geographical range of *L. alata* and *L. tricuspidens* barely overlaps, the former does not extend much further south than Pondoland while the latter is rare at St. Lucia which is at the northern limit of its distribution (Smith, 1965). *Myxus capensis* is also rare at St. Lucia although common further north in the Sodwana estuary (Bruton & Appleton, 1975) and to the south (Smith, 1965). The virtual absence of this species at St. Lucia is puzzling but it is perhaps excluded by interspecific competition.

Although interspecific competition is reduced among the ten species of mullet in St. Lucia by particle size preferences and perhaps by feeding periodicity, competition for food may occur between *M. cephalus, L. macrolepis,* and *L. dumerili* and between the four species of *Valamugil* since the members of each of these two groupings coexist in the same areas and share food resources. Luther (1962) showed that the diets of *M. cephalus* and *L. macrolepis* from Pullamadam lagoon, India (09° 17′N, 79° 06′E) were the same. Fryer (1959) similarly showed that certain herbivorous fish in Lake Malawi were able to coexist on the same food resource due to its superabundance. This sharing and coexistence in St. Lucia may also be possible due to a superabundance of certain foods (for example *Assiminea*) and thus not be at variance with the Gaussian niche hypothesis (Gause, 1934).

At St. Lucia competitive interactions between mullet are perhaps reduced by behaviour patterns, and if as suggested, food is present in excess, will be of very limited duration. As Weatherley (1972) stated: "Probably in the majority of cases competition between fish will be discontinuous, restricted to more or less acute convergence of requirements for a resource for limited periods". Further research in south-east African estuaries might reveal whether the ecological interrelationships of mullet species in St. Lucia are unique or whether potential competitive interactions are a general phenomenon among members of this family.

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