

QUANTITATIVE BENTHIC SAMPLES FROM THE DEEP GULF OF MEXICO WITH SOME COMMENTS ON THE MEASUREMENT OF DEEP-SEA BIOMASS¹

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ABSTRACT

Anchor dredge samples and a photographic survey indicate that the benthic fauna of the deep Gulf of Mexico is depauperate compared to other basins. Infaunal biomass (expressed in terms of wet weight, dry weight, animal numbers, and organic carbon) decreased logarithmically with depth (i.e., $\log_{10} \text{mg C/m}^2 = 2 - 0.000522 [\text{depth}]$) suggesting considerable energy loss in the passage of food along a complex food "ladder" in the water column.

INTRODUCTION

Interest in the flow of energy through oceanic ecosystems led to investigations of the distribution of organic carbon at various latitudes and under various extremes of surface productivity (Menzel, 1967). To date, studies have dealt with the distribution of carbon in the water column and sediment, but have ignored the macrobenthos. The Gulf of Mexico was recently included because of its unique features as a semitropical mediterranean sea with generally low surface productivity (Bogdanov, Sokolov & Khromov, 1968; and Corwin, 1969). The following benthic analyses and interpretations are presented because no quantitative data have been published on the sea-floor animals in the deep gulf. Sampling locations (Table 1) have been mapped in Figure 1.

METHODS

An anchor dredge was used for estimation of the abundance of small infaunal species (Sanders, Hessler & Hampson, 1965). After sieving the samples through 0.42-mm screen aboard ship, the benthonts were separated into major taxa, counted, weighed wet (10 per cent formalin),² and dried in the laboratory. In addition, they were analyzed for organic carbon using a Perkin-Elmer No. 240 Elemental Analyzer.³ This latter approach, never used to our knowledge on deep-sea benthic samples, allows a direct comparison of the standing crop of organic carbon and nitrogen on the sea

¹ Contribution No. 2401 from the Woods Hole Oceanographic Institution. This investigation was supported in part by Contract AT(30-1)-3862 with the U. S. Atomic Energy Commission (Reference NYO-3862-22) and National Science Foundation grants GZ 259 and GA 1298.

² Two minutes drying on absorbent paper allowed before each wet weighing.

³ CaCO_3 skeletons were first treated with dilute phosphoric acid. A similar treatment and analysis was used to estimate organic carbon in sediment.

floor with that in the water column and in the sediments. A photographic survey was conducted in a manner similar to that of Rowe & Menzies (1969) for discovering populations of large invertebrates which may be rare relative to the small infauna, but which could comprise a substantial portion of the biomass.

RESULTS

Camera Survey.—In a survey in the western North Atlantic basin, dominant epibenthos occurred frequently enough in photographs and trawl samples that populations could be mapped quantitatively from photographs (Rowe & Menzies, *op. cit.*). In the gulf this was not possible, due evidently to an extreme paucity of the fauna. Only 16 epibenthos (ophiroids, asteroids, and galatheid decapods) were seen in the 19 stations covering ca. 1000 square meters of the deep-sea floor. The abundance of large species therefore appeared to be far below that of equivalent depths in the North Atlantic.

The photographs were compass-oriented in order to determine direction of possible deep bottom currents. Ripples in the sediment were seen in the eastern Gulf on the lower Mississippi Cone, but there was no evidence (such as bent, stalked animals) that currents strong enough to cause rippling were actually present at that time. That ripple orientation (Fig. 1) suggested that these may have resulted from sporadic turbidity flows emanating from the shallow Mississippi Cone. On the other hand, orientation of tubes and faint sediment streamers on the bottom indicated that long-term drift on the east gulf floor was to the east. In the west basin, all indications of current, past or present, vanished, and the sediment, a foraminiferal lutite, was highly mottled. In contrast, the Atlantic deep-sea floor off the eastern United States appears to be strongly influenced by the Atlantic Western Boundary Undercurrent, which extends from depths of approximately 1000 to 5000 m (Rowe & Menzies, 1968). There is no comparable deep current, to our knowledge, in the gulf.

Comparison of Measures of Biomass.—A comparison of four different measurements of biomass from the Gulf of Mexico (Fig. 2) suggests that in general all provided essentially the same ecological information. The slopes of the four semilogarithmic plots of biomass and density (animal numbers) versus depth appear to be virtually identical. The wet weight of the animals ranged from ca. 5 to 10 times the dry weight, and the latter was ca. 5 to 15 times the weight of organic carbon.

Product-moment correlation coefficients calculated for pairs of the different measurements indicate there was high correlation between wet weight and carbon (0.96), numbers and carbon (0.86), and wet weight and dry weight (0.85); moderate correlation between numbers and wet weight

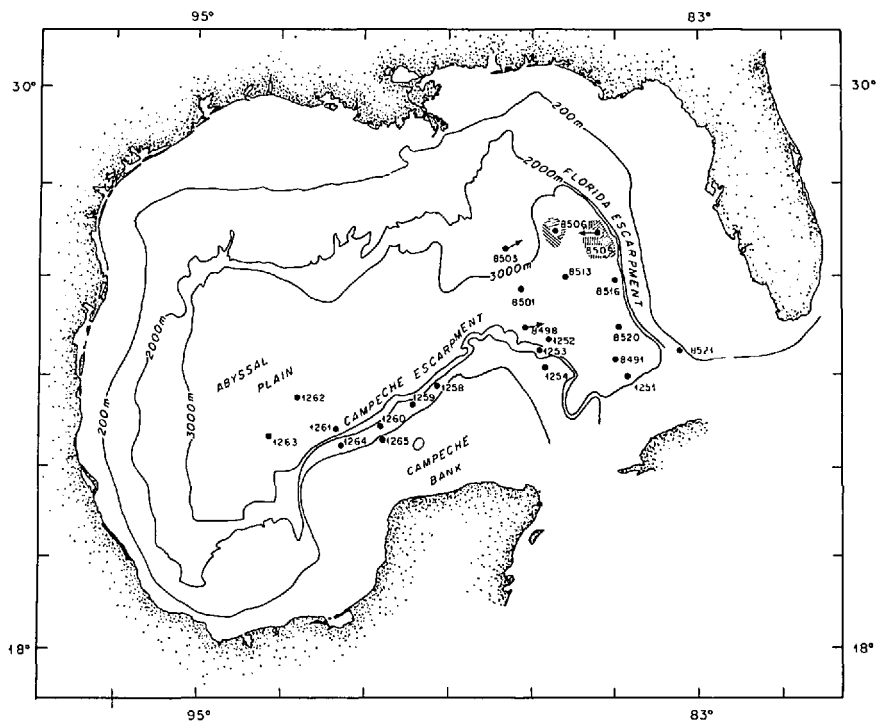


FIGURE 1. Gulf of Mexico stations. Parallel lines indicate sediment ripples; arrows indicate directions of currents as deduced from orientation of animals and faint streamers of sediment seen in photographs.

(0.75), and dry weight and carbon (0.73); but considerably less between numbers and dry weight (0.36).

Least squares regressions (Fig. 2) of the four measurements against depth (converting to semilogarithm, base 10) also indicate that the above observations are valid. Each fits a linear regression with high confidence ($P < 0.01$ that the slopes = 0). Although the slopes of the regressions of the weight measurements are statistically equivalent, there is a strong suggestion that the rate of decrease of density (animal numbers) is slightly less than the decrease of biomass ($P = 0.13$ that the slope of \log_{10} of density vs. depth = slope of \log_{10} carbon vs. depth). This suggests animals on the average are smaller in deep water or that the inclusion of a few large individuals, which dominated the biomass at several of the shallow stations, biased the results.

Spatial variations in the biomass of the macrofauna should reflect differences in available food (assuming turnover remains the same). Since

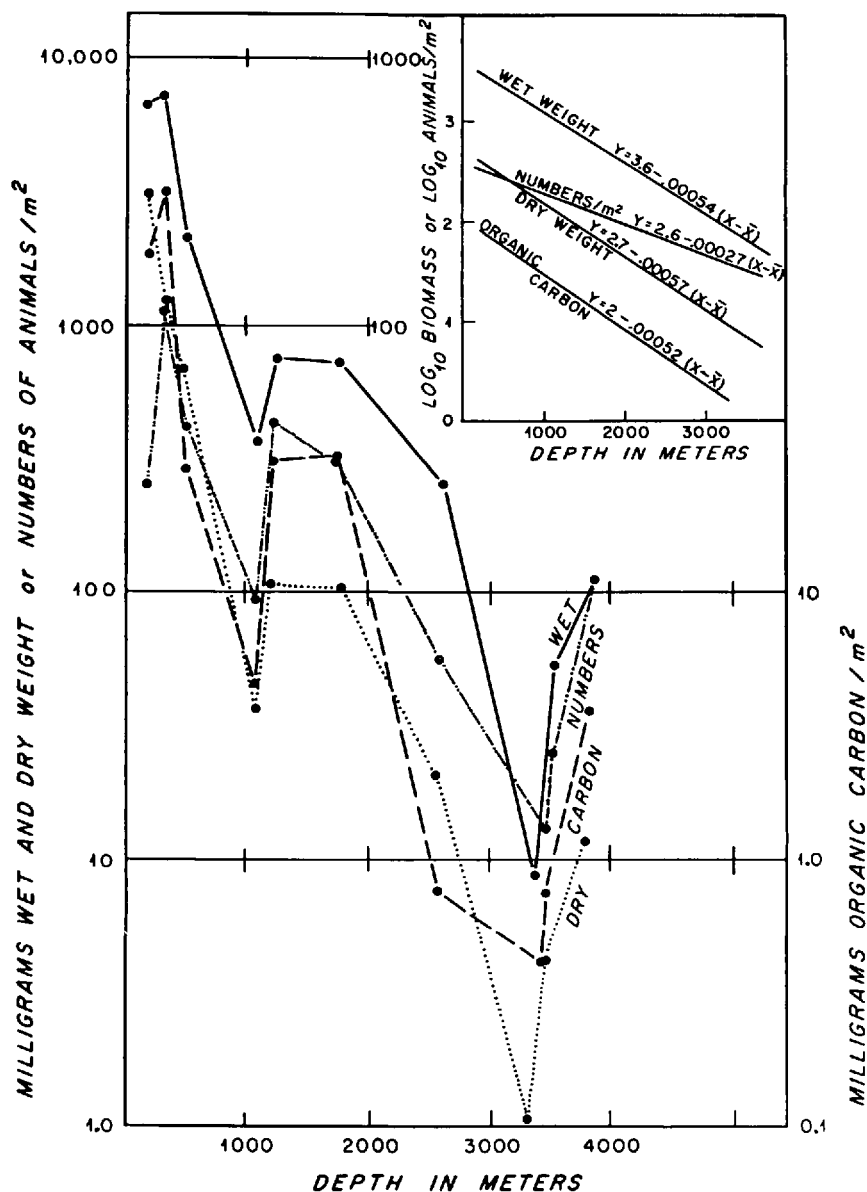


FIGURE 2. Infaunal biomass data from anchor dredge samples (Table 2). Ordinate is biomass and abscissa is depth. (Insert: least squares regressions of biomass measurements [\log_{10}] versus depth. Slopes significantly different from zero at $P = 0.01$ level.)

TABLE 1
SAMPLES FROM THE GULF OF MEXICO

Station number	Position	Depth (m)	Type sample*
EASTWARD			
8491	24°23'N, 85°00'W	3400	Ca, H, Co
8498	24°59'N, 87°11'W	3350	Ca, H, Co
8501	25°40'N, 87°14'W	3250	Ca, H, Co
8503	26°27'N, 87°38'W	2875	Ca, H, Co
8506	27°01'N, 86°27'W	3125	Ca, H, Co
8509	26°59'N, 85°30'W	3250	Ca, H, Co
8513	26°00'N, 86°15'W	3200	Ca, H, Co
8516	25°58'N, 85°00'W	3270	Ca, H, Co
8520	25°01'N, 84°58'W	3370	Ca, H, Co
8521	24°33'N, 83°26'W	390	Ca, H, Co
ATLANTIS II			
1251	24°00'N, 84°48'W	3440	H, AD, Co, BT, Ca
1252	24°34'N, 86°30'W	3375	Co, H, AD
1253	24°29'N, 86°42'W	2050	Co, Ca
1254	24°00'N, 86°48'W	1100	Co, H, BT, AD, Ca
1258	23°49'N, 89°11'W	2150	Co, AD
1259	23°29'N, 89°41'W	510	Co, AD, H, Ca
1260	22°57'N, 90°39'W	960	Co, AD, H, Ca
1261	22°47'N, 92°06'W	3730	Co, AD, Ca
1262	23°56'N, 92°21'W	3780	Co, AD, H, Ca
1263	22°42'N, 93°12'W	3715	Co, H, BT, AD, Ca
1264	22°24'N, 91°36'W	255	Co, AD, BT
1265	22°35'N, 90°34'W	200	Co, AD
1266	22°45'N, 91°00'W	2600	AD

* Ca, camera; H, bottom hydrographic cast; Co, sediment core; AD, anchor dredge; BT, Blake trawl.

estimates of changes in biomass were approximately equivalent using all the above methods, conclusions concerned with the ecology of the benthos should be equally reliable no matter which method is employed. This close relationship, although not necessary for interpreting our data, does allow comparisons with other reports. The previously untested assumption (Sanders *et al.*, 1965) that animal density is a more or less creditable measure of biomass, however, must be used cautiously because of slight disparity between the rates at which animal numbers and weights decrease with depth. Throughout the remainder of this paper, biomass will be synonymous with organic carbon.

Decrease of Infaunal Biomass with Depth.—The anchor-dredge data (Tables 1 and 2) indicate that biomass decreased logarithmically with depth (Fig. 2). Maxima of 180.5 mg C/m² and 312 mg C/m² occurred

TABLE 2
BIOMASS AND ORGANIC CARBON AT STATIONS IN THE GULF OF MEXICO

Station	Depth (m)	Wet wt. (mg/m ²)	Dry wt. (mg/m ²)	Organic carbon (mg/m ²)	No. per m ²	Carbon in sed. (%)	Large detrital aggregates	
							Amount (mg/m ²)	Type
1251	3445	53.2	4.1	0.8	25.5	0.305	73.4	Cellulose fibers, <i>Thalassia</i> root
1252	3440	8.8	1.1	0.4	13.2	0.839	47.8	Cellulose fibers
1253	—	—	—	—	—	0.293	no dredge sample	
1254	1190	768.0	106.2	30.7	437	0.193	1.7	Cellulose fibers
1258	1650-1745	722.2	103.6	32.8	313	0.401	negligible	
1259	500	2145.0	68.4	28.5	417	0.359	negligible	
1260	1040	371.0	35.7	4.5	95	0.555	negligible	
1261	3740	98.5	14.4	6.3	61.5	0.661	373.0	Cellulose fibers
1262	3770	155.5	12.9	2.8	113	1.213	2.6	Cellulose fibers, <i>Sargassum</i> fragments
1263	3740	82.5	10.6	2.2	161	0.583	4.8	Cellulose fibers
1264	270-295	7320.0	1235.0	312.0	1095	0.720	57.8	Cellulose fibers
1265	185	6800.0	3100.0	180.5	265	1.060	7.5	Cellulose fibers
1266	2400	25.8	2.1	0.8	58.5	no core sample	13.3	Cellulose fibers, <i>Sargassum</i> fragments

at stations on the upper slope (180 and 275 m), and minima of 0.4 and 0.8 mg C/m² were found on the abyssal plain (3440 m) of the eastern gulf.

The biomass on the abyssal (3740-3770 m) plain of the western gulf had an average of 3.8 mg C/m² (based on 3 samples) compared to an average of 0.6 mg C/m² for the two eastern stations (3440 m), indicating a six-fold increase in the west, even though the depth was some 300 m greater in the west. At intermediate depths, on the slope (1000-2000 m), values fell between the shallow and deep extremes, with overlap only between the 1040-m station (4.5 mg C/m²) and the station adjacent to the Campeche Escarpment (6.3 mg C/m²) at 3740 m.

Large perturbations in concentration with depth are evident. This variance may have ecological significance and reflect valid differences resulting from patchiness on a local level (e.g., between individual samples within essentially similar habitats), or may be due to sampling error. To estimate the latter, we have calculated least squares regressions of biomass versus depth in the hope of more precisely defining the relationship (Fig. 2).

East-West Differences.—The exception to the generalization relating the log₁₀ of biomass to depth, of course, was the difference in the east and west abyssal plain ($P < 0.01$ that the biomass is the same). This led to attempts to correlate biomass with various measurable carbon sources, but these met with little success. For example, primary productivity measurements ranged from 0.09 to 0.36 g C/m² per day, with an average of 0.20 g C/m² per day. There was no discernible difference, however, between the east and west. Particulate organic carbon ranged from 20-40 µg/l in the surface water, and from 3-5 µg/l in the deep samples 100-500 m above the bottom on the abyssal plain, and there were no longitudinal gradients in these data.

Carbon in the Sediments.—Another possible source of energy is the organic carbon in the sediment (Table 2). For the core samples, the range was from 0.193 to 1.213 per cent by weight in the top one centimeter of mud, with averages of 0.574 per cent and 0.819 per cent, respectively, on the east and west of the abyssal plain; 0.890 per cent on the upper, relatively level slope; but only 0.361 per cent at intermediate depths on the steep slope. Differences in these means, however, are not statistically significant.

In the anchor-dredge samples, there were aggregates of organic material, apparently cellulose fibers from terrestrial and shallow-water plant detritus, and this had a somewhat different quantitative distribution. The average for all the Sigsbee Deep floor was 100.2 mg C/m², while the average for the upper slope (Stas. 1264 to 1266) was 32.7 mg C/m². On the lower, steep slope the average was the lowest, 2.9 mg C/m². For the abyssal floor, the average was somewhat skewed because of the single sample with 373.0 mg C/m², but there appeared to be great disparity between east and west

averages (60.1 mg C/m² in the east and 7.4 mg C/m², again omitting Sta. 1261, in the west). This distribution is the inverse of animal biomass, which was greater in the west. The carbon in the aggregates amounted to only a small fraction of the total in the top centimeter of sediment (ca. 30,000-80,000 mg C/m²).

DISCUSSION

Samples taken on a transect south of New England down to a depth of ca. 4000 m by methods comparable to those used here (Sanders *et al.*, 1965) yielded numbers of animals 10 to 100 times higher than these from the Gulf of Mexico. On the Hatteras Abyssal Plain (ca. 5000 m), the Atlantic density approximated that from the shallower abyssal plain of the gulf. Farther south on the Bermuda Rise and up the Bermuda Pedestal, density continued to be about the same as at equivalent depths in the gulf. This suggests that energy available to gulf benthos is of a magnitude similar to that below the nonproductive Sargasso Sea, rather than to the productive, near-shore environment adjacent to the Continental Slope off New England. Alternatively, the low biomass of the gulf may be attributable to a faster cycling of carbon (high turnover rate) due to the higher temperatures (ca. 4.3°C) in deep water relative to equivalent depths and latitudes in the Atlantic (2.1°C).

The invertebrates in the gulf were distributed among the same major taxa in about the same proportions as described for comparable investigations in the deep Atlantic (Rowe & Menzies, 1969; and Sanders *et al.*, 1965), even though their abundance was greatly reduced. In general, there was also good agreement in the percentage distributions among the different measures of biomass previously discussed. Some exceptions, however, that deserve comment were on the shallow slope where numerically rare (1 per cent and 2 per cent at Stas. 1264 and 1265) decapod crustaceans amounted to 50 per cent and 68 per cent of the organic carbon at those locales. We conclude that where the fauna is sparse (i.e., in deep, depauperate basins), the biomass must be parcelled into small packages of equivalent size, but as the influx of energy increases, the community is able to cycle carbon efficiently through larger organisms.

In the sea, the initial source of organic energy is primary production at the surface, but the routes and rates of energy flow to the deep-sea bottom are unknown. Suggestions usually have been based on conjecture and follow one or two lines of thought. One was a rain of detrital particles sinking at some unknown rate, but this seems unlikely since there is little measurable change in particulate organic carbon with depth below about 300 m (Menzel, 1967). This constancy with depth remains at all the different locations where analyses have been made. A second possibility is that energy is transferred vertically through a complex food web involving

numerous trophic steps among diurnal migrators and mesopelagic plankters (Vinogradov, 1962). Turbidity flows and slumps, fragments of near-shore and terrestrial plants (generally functions of distance from land), and dead animals (whales and fish) have also been suggested as sources of energy.

On the basis of our data, inferences can be made about the above possibilities. The decline of macrofaunal organic carbon with depth followed a linear regression of $\log_{10} \text{ mg C/m}^2 = 2 - 0.000522 (X - \bar{X})$ (for which $P < .01$ that $0.000522 = 0$). The semilogarithmic nature of the data indicates that available energy disappears rapidly with increase in depth, in a fashion that supports Vinogradov's (1962) food web. At the same series of stations, particulate organic carbon did not vary in the water column with depth ($> 300 \text{ m}$), and if this were a food source whose availability and potential were not degraded with sinking, the benthic biomass would hypothetically remain relatively constant, contrary to its displayed behavior. As indicated, the logarithm (base 10) of biomass (any measure) decreases by approximately 0.5 of a logarithmic unit for every increase of 1000 m in depth, which is equivalent to saying the biomass decreases by a factor of 10 every 2000 meters. If an efficiency of 10 per cent is assumed for each trophic step in the water column, one might estimate, using the benthic biomass as an indicator, that the energy transfer from one level of the food chain to the next occurs every 2000 meters.

Turbidity flows and slumps emanating from the Mississippi Cone could be a source of organic material from shallow water, but this was difficult to assess. Movement directly down the Campeche Scarp might be suggested by the data from Sta. 1261, located adjacent to the scarp. It had the greatest biomass of all samples from the abyssal plain, and cellulose fibers from detrital aggregates of shallow-water grass were more abundant than at any other station.

It is interesting that Sokolova (1968), evidently dealing with considerably more samples than we have, correlated rates of sedimentation with dominant feeding types. Implicit in her analysis is the assumption that near-shore sediments contain greater available organic carbon than those offshore. Sanders *et al.* (1965), on the other hand, concluded more or less as we have, that the small, statistically unreliable variations in measurable carbon in the sediment could not account for logarithmic decreases in density and biomass of benthic animals. Measurable organic carbon, whether in the sediment or the water column, probably plays an insignificant role in the carbon cycle in the deep sea.

CONCLUSIONS

Based on anchor dredge and photographic surveys, it can be concluded that the deep-sea benthos of the Gulf of Mexico is depauperate in numbers

and biomass relative to other basins. This paucity of living organic carbon appears to have resulted from low productivity at the surface, a general feature of the offshore water of the gulf and Caribbean (Bogdanov *et al.*, 1968).

The deep-sea biomass of benthic organisms was measured in terms of organic carbon, as well as animal numbers, wet weight, and dry weight. All four appeared to be satisfactory indices for estimating biomass, though close correlations between these various measures may hold only in seas, such as the gulf, where production and standing crops are relatively low.

Significant differences in biomass between the east and west floors of the gulf appeared to be a product of down-slope slumping of detrital material and perhaps an absence of a deep current. The semilogarithmic relationship between biomass and depth suggests that considerable organic energy is expended in a complex food web in the water column, in agreement with Vinogradov's (1962) proposed "food ladder."

ACKNOWLEDGMENTS

The samples considered were taken on Duke University's R/V EASTWARD, supported by the U. S. National Science Foundation (ship-time to Florida State University, M. G. Goodell, Chief Scientist), and on the ATLANTIS II of the Woods Hole Oceanographic Institution. Organic analyses of the sediment and animals were done in D. W. Menzel's laboratory by John Clarner. Howard Sanders and Robert Hessler helped the authors formulate an approach to the problem. Willis E. Pequegnat and his students Robert Carney and Bela James are to be thanked for discussing with G. T. Rowe their deep benthic work in the Gulf of Mexico.

SUMARIO

MUESTRAS BÉNTICAS CUANTITATIVAS DE LAS PROFUNDIDADES DEL GOLFO DE MÉXICO CON ALGUNOS COMENTARIOS SOBRE MEDIDA DE LA BIOMASA DEL MAR PROFUNDO

Muestras obtenidas con rastra de ancla y fotografías del fondo tomadas en cruceros del B/I EASTWARD y B/I ATLANTIS II sugieren que el bentos de las aguas profundas del Golfo de México está depauperado en número de animales y biomasa en relación con otras hoyas y ésto parece ser el resultado de la relativamente baja productividad de las aguas superficiales frente a la costa. La biomasa fue medida en términos de carbón orgánico, así como en número de animales, peso húmedo y peso seco. Una regresión de los cuadrados menores del logaritmo (base 10) de la biomasa (carbón orgánico) a profundidad sugiere considerable pérdida de energía orgánica en la columna de agua.

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