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LIVING AND ANCIENT POPULATIONS OF THE CLAM *Gemma gemma* IN A MAINE COAST TIDAL FLAT

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ABSTRACT

Sagadahoc Bay is about 2 miles long and half a mile wide; its southern end is open to the Gulf of Maine. At low tide, about a mile of flat is exposed; the seaward two-thirds of this is made up of fine sand and the other third is muddy. *Gemma gemma* lives in great abundance in the sandy sediment but is scarce in the muddy sediment.

Gemma is ovoviviparous, produces young through much of the summer, has a life expectancy of about 2.2 years, and a maximum life span of about 4 years. Shells range in length from about 0.02 to 0.2 inch (0.6 mm. to nearly 5 mm.). In subdued light, *Gemma* feeds with only the siphons exposed above the sediment surface. It feeds most actively in the dark, when it raises the colored posterior half of the shell above the sediment surface and moves about somewhat as the much larger clam *Spisula* does. An average population of 25 gemmas per square inch draws food from about 16 percent of the bottom layer of water.

Gemmas are most numerous in the sandy midsection of the flat where the tidal currents close to the bottom are maximum (0.3 to 0.4 foot per second). Gemmas are distributed in a bunched pattern. In a statistical sense, they have a log normal distribution. *Gemma* and *Mya* have occupied the flat jointly for more than 1,000 years; *Mya* being numerically dominant in the muddy areas, *Gemma* in the sandy areas. The two clams tend to be incompatible either because they compete for food or for some other reason.

The total *Gemma* population of the bay in 1954 was about 11.5×10^9. In 1950, it was about twice as great, and in 1956 it was about 54 percent less than that of 1954.

Ancient *Gemma* shells are distributed irregularly from the surface down to as much as 4 feet below the surface. The average population over the past 400 years was about half, or less than half, of what it was in the interval 1950–55.

Research is needed to determine the food temperature tolerances and the toxicity of metabolic wastes of both *Gemma gemma* and *Mya arenaria*. The hypothesis is advanced, without supporting data, that *Gemma* is favored by the recent warming of the climate and that *Mya* is adversely affected. The *Gemma* population, by 1956, decreased to less than 25 percent of what it was in 1950. If *Gemma* is a competitor of *Mya* and the *Gemma* population continues small or declines further, this should permit *Mya* to reestablish itself in the sandy part of the flat.

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LIVING AND ANCIENT POPULATIONS OF THE CLAM *GEMMA GEMMA* IN A MAINE COAST TIDAL FLAT

By W. H. Bradley and Peter Cooke, *United States Geological Survey*

During a study of the late geologic history and present-day processes of sedimentation and erosion in Sagadahoc Bay (Maine) the senior author noted the great abundance of living gemmas in the sandy parts of the extensive intertidal flat and the lesser, but still comparable, abundance of their dead shells to depths of 3 or 4 feet below the present surface. Large areas of the sandy part of the flat contain 25 or more living gemmas per square inch, and as many as 190 per square inch have been counted. Although these tiny clams rarely, if ever, reach 0.2 inch (5 mm.) in length, their present abundance suggests that they may play a more significant role in the economy of the tidal flat today than in the past. Some of the observations we made suggest that *Gemma* is a competitor of minute *Mya* larvae and that the recent marked decline of the population of *Mya*, the well-known soft-shell clam of commerce, in the sandy part of the Sagadahoc Bay tidal flat may have been caused partly by this competition.

Two facts make it possible to consider the *Gemma* population in this bay as an isolated community. One is that the physical environment of the tidal flat and its recent geologic history have limited the *Gemma* population to essentially the same area for at least the past thousand years; the other is that gemmas, unlike other clams in these waters, reproduce ovoviviparously, and therefore their young are not transported, except in very small numbers by rare events, to other *Gemma* communities in neighboring bays, or vice versa. We have attempted to identify and evaluate some of the factors operating within the community, particularly within the past 400 years, that may have affected the changing size and other characteristics of the population.

Note.—Approved for publication July 12, 1957. Fishery Bulletin 137.

Our study of the present and past *Gemma* populations is a byproduct of the geologic study of the Sagadahoc Bay tidal flat undertaken in 1949 in response to a suggestion made jointly by Joseph M. Trefethen, then State Geologist of Maine, and Robert L. Dow and Dana Wallace of the Maine Department of Sea and Shore Fisheries. The purpose of the study was to see whether changes could be found in the regimen of sedimentation and erosion that might help to account for the observed progressive decline in the population of the soft-shelled clam *Mya arenaria*. Many of the results of these investigations have been published in another paper (Bradley 1957). Nothing was found in the regimen of sedimentation and erosion that could account for the decline of the *Mya* population.

Biologists of the U. S. Fish and Wildlife Service and of the Maine Department of Sea and Shore Fisheries have for some years been engaged in comprehensive studies of *Mya arenaria*, its changing populations, growth rates, food supplies, and larval abundance and distribution in Sagadahoc and other bays along the Atlantic coast. They have also been carrying on comparable studies of the life history and habits of *Mya* predators. It is a pleasure to acknowledge the generous help of scientists of the U. S. Fish and Wildlife Service, especially John Glude and Walter Welch, and the Maine Department of Sea and Shore Fisheries, and from the former State Geologist of Maine. We wish also to thank Joel Hedgpeth of the Scripps Institution of Oceanography for his helpful criticisms of the manuscript. The manuscript was also read critically by my colleagues John T. Hack, Harry S. Ladd, and Wendell P. Woodring of the U. S. Geological Survey and we are grateful for their suggestions. Other Survey colleagues participated in the investigation and are mentioned at appropriate places in the text.

Most of the field work on which this paper is based was done in the summers of 1954 and 1955, but during the summers of 1950, 1956, and 1957 the senior author sampled the living *Gemma* population over parts of the flat and in 1950 had an opportunity to observe the distribution of *Gemma* shells in the sidewalls of many pits that were dug in the flat in order to determine the stratigraphy of the sediments. The senior author also visited the flat briefly in February 1956.

ECOLOGY

Physical environment

Sagadahoc Bay is at the southern end of Georgetown Island, roughly 10 miles south by east from the city of Bath (fig. 1). The bay is about 2¼ miles long, north to south, and approximately half a mile wide, though it widens into the fair-sized Bedroom Cove on its western side. At its southern end, Sagadahoc Bay is open to the ocean. Low bedrock hills that have a thin gravelly soil surround the bay except at the north end where there is a long salt marsh. Another much smaller salt marsh fills a small cove in the bedrock terrain on the eastern side of the bay. At the northern end of the bay and around much of Bedroom Cove, are sandy beaches. The rest of Sagadahoc Bay is bordered either by steep rocky shores or gently sloping shores of sandy mud overgrown with cordgrass (*Spartina alterniflora* and *Spartina patens*). In the northern part of the bay two elongate masses of bedrock rise above the surface of the flat. These are known locally as the Black Rocks Islands.

No fresh-water streams of consequence enter Sagadahoc Bay. Small springs bring to the bay its only fresh water except in times of heavy rains and melting snow when the salt marsh at the head of the bay collects a considerable quantity of fresh water, which drains off into the bay. Lesser amounts of fresh water drain into the bay during heavy rains from small gulches and hill wash. During the winter and spring, when the ground is frozen, appreciably larger volumes of fresh water enter from these gulches and hill wash. Intense rains flood the tidal flat temporarily with a sheet of water one-half to 2 or 3 inches deep, making the flat look almost as though the tide had not gone out.

At average low tides, the upper mile of the bay is exposed as a muddy and sandy tidal flat. Extreme low tides expose about one-fifth of a mile more.

Virtually all the tidal flat proper lies below mean sea level. From the average low-tide line, the surface of the flat rises only about 4½ feet in its length of nearly a mile. Water drains off this flat continuously while it is exposed between tides. The sandy mud, which makes up most of the flat, is sufficiently porous that it slowly yields its contained water at a nearly uniform rate from all parts of the flat that slope. Parts of abandoned channels and extremely shallow depressions remain ponded between tides though they continue to drain very slowly. A few small, slightly higher areas that consist of relatively clean, fine sand drain out nearly dry between tides.

Two kinds of sediment make up the great bulk of the flat; one, medium- to fine-grained, well-sorted sand that contains little very fine sand and silt and a few tenths of one percent of organic matter; the other, similar fine sand, which is made soft and muddy by a somewhat greater content of very fine sand, silt, and clay and about 2 percent of organic matter. Figure 2 shows the size distribution and the degree of sorting of representative samples of these two kinds of sediment. Figure 3 shows the distribution on the flat of these two dominant kinds of sediment. Almost everywhere the boundaries between these two kinds of sediment are characterized by a subtle gradation from one into the other. Gemmas live in both kinds of sediment but are far more abundant in the sandy sediment.

The soft muddy sediment represents a relatively quiet environment where the finest particles settle to the bottom and accumulate. The sandy sediment represents an environment where the bottom is frequently (nearly every tide) stirred up by waves and tidal currents so that most of the silt and clay-sized particles and much of the organic matter are winnowed out and transported elsewhere.

In the muddy sediment it is obvious that most of the organic matter is fecal, for the form of the feces is quite evident. Presumably most of the fecal matter that retains its form comes from small worms, which are abundant in the mud. Although the sandy sediment contains only about one-tenth as much organic matter, it is still adequate to darken the sand and give it a drab or olive cast, especially just below the surface. Probably most

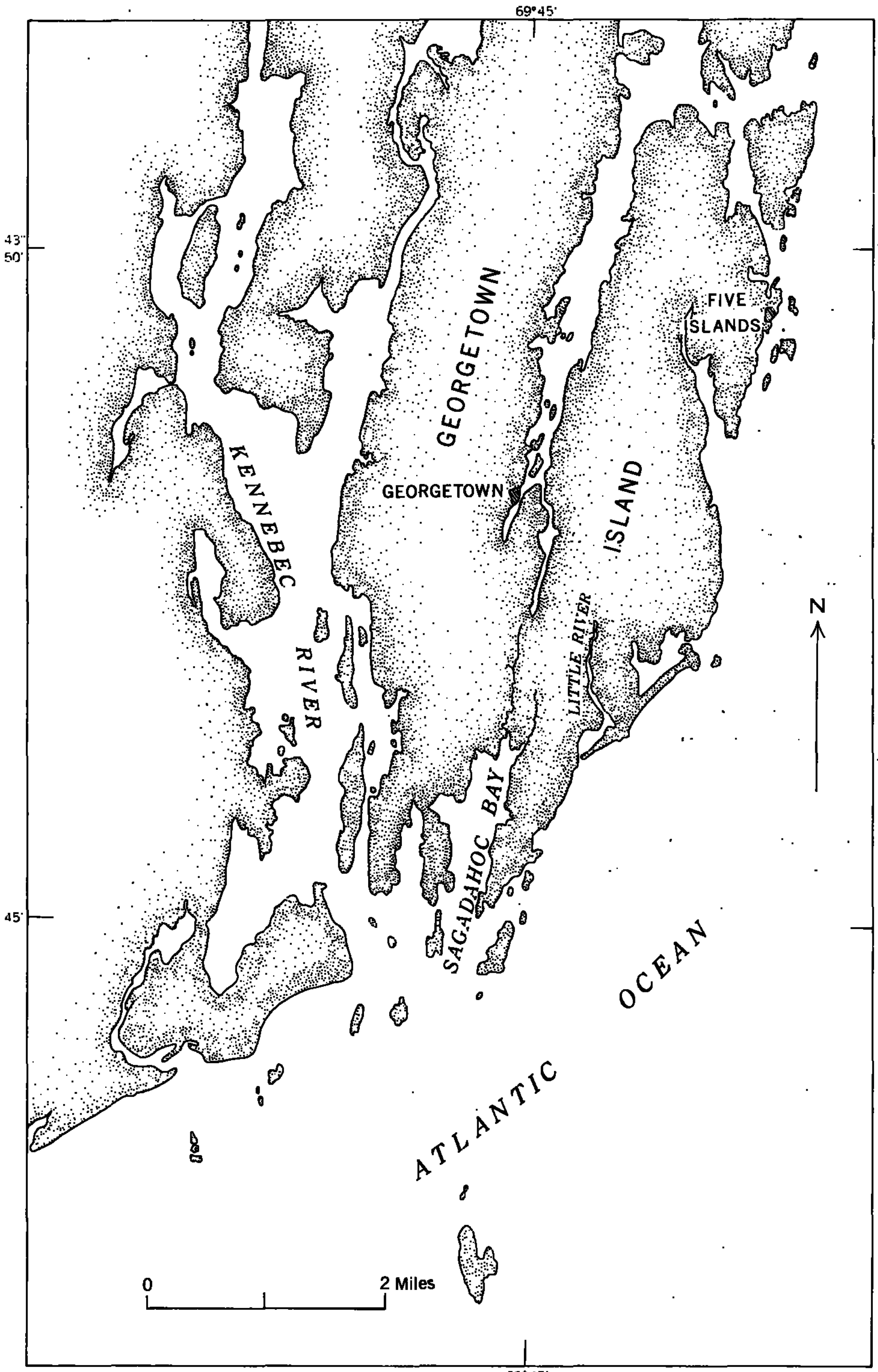

Figure 1.—Location of Sagadahoc Bay, Maine, the mouth of the Kennebec River, and Little River.

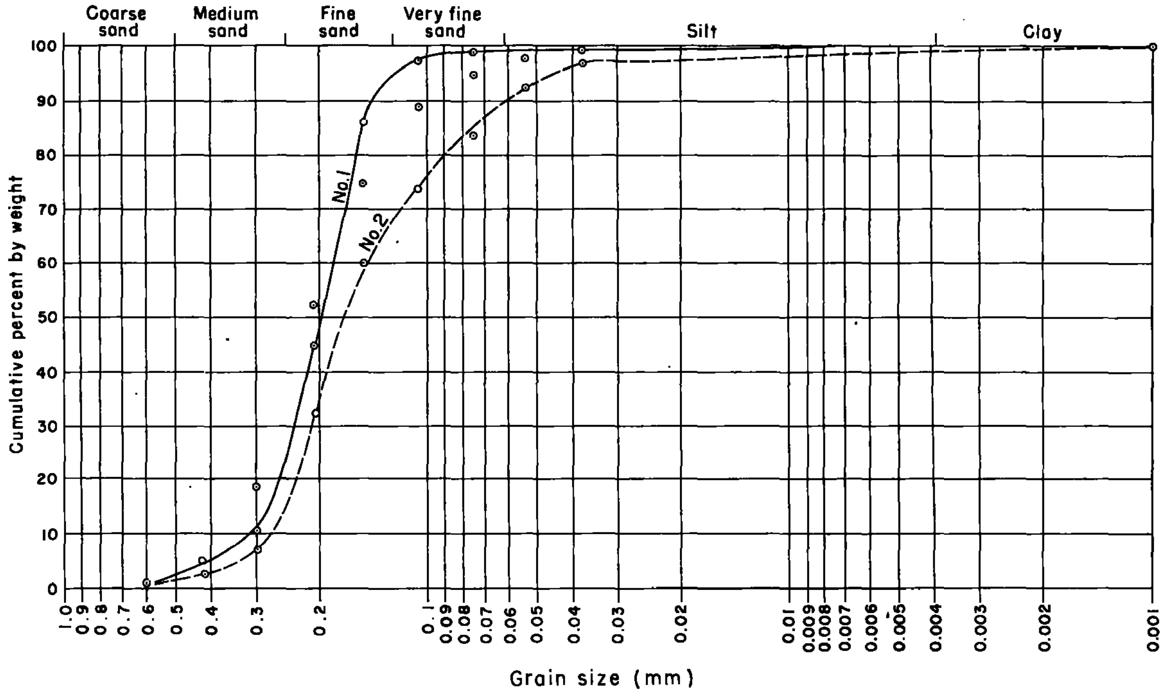

Figure 2.—Cumulative curves show size distribution and degree of sorting of grains that form the two dominant kinds of sediment in Sagadahoc Bay: (1) Sandy sediment that characterizes midsection and outer parts of the flat; (2) Muddy sediment that characterizes the quieter coves and the area at the head of the Bay.

of the organic matter in the sand is also fecal though recognizable feces are rare. Particulate organic detritus is locally common, though mostly near the low-tide zone. In winter this particulate organic detritus, presumably derived mostly from *Spartina*, is more abundant and is distributed more generally over the flat.

Both the muddy and sandy sediment have rather well-defined surficial zones in which the decomposing organic matter is being oxidized. This layer is thin in the muddy sediment, a small fraction of an inch, and is hardly perceptible in the very soft deep muds, which contain the most organic matter. In the sandy sediment the oxidizing zone ranges in depth from a small fraction of an inch to two or more inches and averages about an inch. The depth of the oxidizing zone is a function of permeability of the sediment and the depth to which the sediment is stirred by the waves during each tide.

Below the oxidizing zone the sediments, both muddy and sandy, are gray to almost black and are reducing environments containing hydrogen sulphide. Little difference was found in either the pH or redox potential (Eh) of the two kinds of sediment near the surface. The pH at or slightly below the surface of the sediments ranged from 7.02 to 7.45 and the Eh from +304 to +394. At a depth of 2.4 inches the pH ranged from 7.13 to 7.43 and the Eh from −124 to −194. The water close to the bottom had a pH range of 8.11 to 8.48 and was oxidizing (Eh +275 to +320) but no more so than the surface layers of the mud and sand. At depths of 2 to 3 feet below the surface of the sediment the pH and Eh values are only slightly lower than at a depth of 2.4 inches below the surface.

The uppermost half inch of sediment, both mud and sand when exposed at low tide, ranges in temperature from below the freezing point of salt water in the winter to at least 84° F. in the summer. In sunny weather, heat is absorbed by the dark sediment so that its temperature sometimes rises 20° F. higher than the air temperature. Few winter-temperature measurements were made, but in February 1956, on a clear sunny but windy day, the air temperature near noon was 27.5° F., whereas the temperature of the fine sand one-fourth inch below the surface was 41° F.

Most gemmas dig in about one-fourth inch

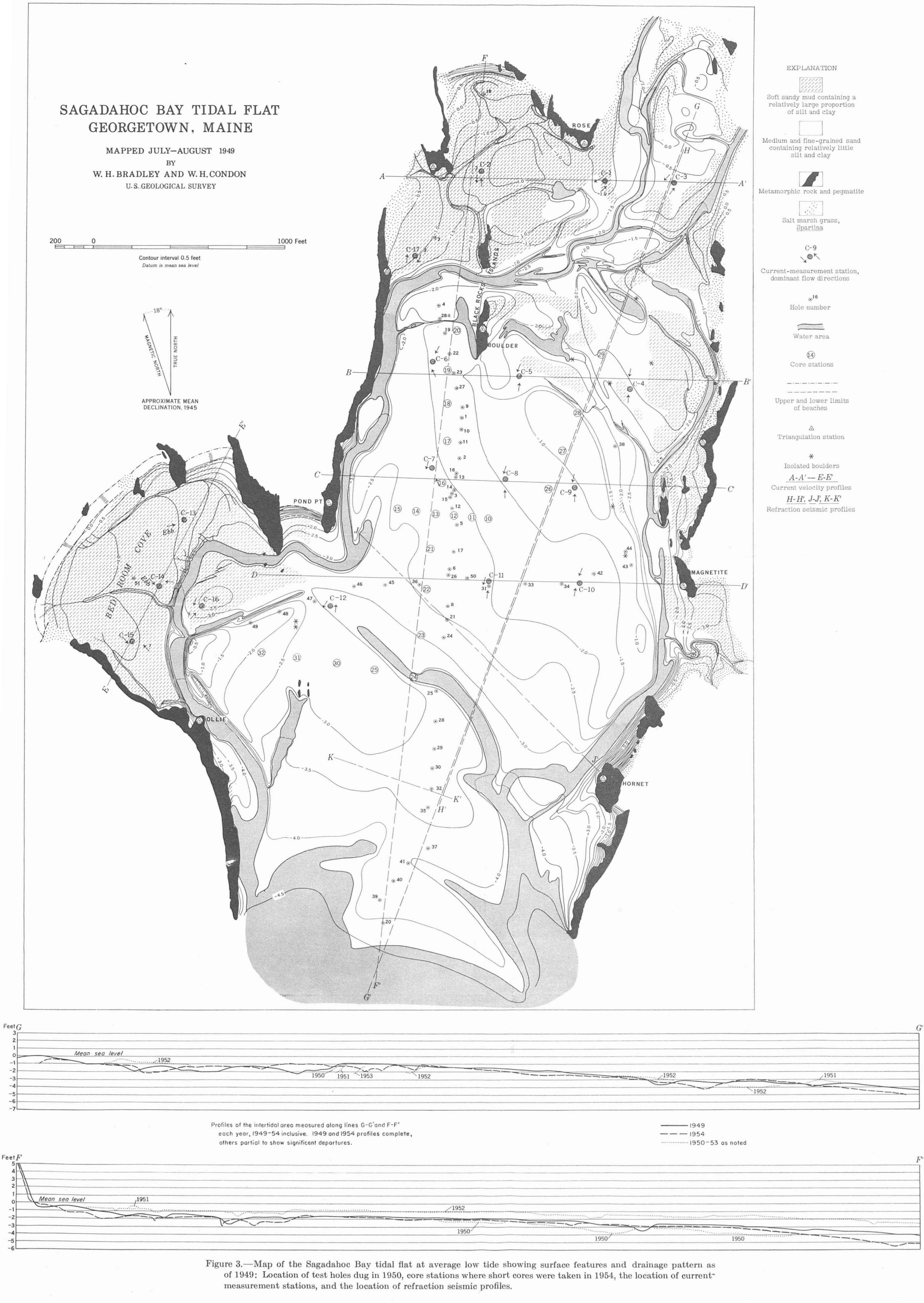

Figure 3.—Map of the Sagadahoc Bay tidal flat at average low tide showing surface features and drainage pattern as of 1949: Location of test holes dug in 1950, core stations where short cores were taken in 1954, the location of current-measurement stations, and the location of refraction seismic profiles.

below the surface but a few go deeper, even to three-fourths inch. At one place near the midsection of the flat, we measured the depths shown in table 1 to which they had dug and from many casual observations, we believe this is fairly typical, though just after a heavy downpour of rain that literally flooded the flat we found that they had dug in at least one-half inch below the surface.

In the summer of 1956, J. R. Balsley of the U. S. Geological Survey and the senior author measured the thermal conductivity of the sandy sediment in the midsection of the flat and the muddy sediment near the head of the bay. The sandy sediment has a thermal conductivity of about 4.4×10^{-3} cal per cm sec °C and the muddy sediment slightly more, 4.6×10^{-3} cal per cm sec °C. The moisture content of the sandy sediment is 20.1 percent of wet sample and the muddy sediment 21.2 percent. The specific heat of these sediments is about 0.24 ± 5 percent cal per gm °C and the thermal diffusivity is about 0.009 ± 10 percent cm^2 per sec. The thermal conductivities were measured with a probe designed by Arthur H. Lachenbruch of the U. S. Geological Survey and he made all the computations given above.

During the winter (observations made on 1 day only Feb. 21, 1956) the gemmas were found to be distributed rather unevenly through a much greater range of depths than in the summer (table 1). As they were inactive it was not surprising to find them oriented predominantly on their sides, as are most dead shells found either at the surface or at any depths below the surface where we have observed them. It seems possible that the hibernating gemmas reach these depths by settling through the fine sand when storm waves stir it up. Some doubt is cast on this inference, however, by the fact that the heavy mineral sand grains, garnet, magnetite, hornblende, and others, have not similarly concentrated to depths of several inches. On the contrary, they are randomly distributed as though there had never been any opportunity for them to settle selectively.

We were surprised to see, during the summer, that gemmas, when they dig in, do not remain oriented with their posterior ends up, but are rather erratically positioned: four of the 40 had their anterior ends up.

TABLE 1.—*Summer and winter depth distribution of living gemmas*

Depths (inches)	Numbers of gemmas		Depths (inches)	Numbers of gemmas	
	Summer	Winter		Summer	Winter
1/8	3		1		27
1/4	28	19	2		39
3/8	7		3		22
1/2	1		5		1
3/4	1				

During large storms, gemmas get buried to considerable but unknown depths. Because gemmas are strong, active animals, we were curious to know how deeply they could be buried and still rise to the surface and survive. Accordingly, we made the following simple tests in a small aquarium. Live gemmas of about equal size were sieved from the flat and transferred to a large, deep receptacle filled with sand from the flat. This sand was wet-sieved to remove all other gemmas. The aquarium was divided by a vertical septum; on one side 10 living gemmas (the controls) were set on the surface; on the other side of the septum 10 living gemmas were buried beneath 2 inches of sand. For the next two days or so the aquarium was filled with fresh sea water and then drained at roughly tidal intervals to simulate the tides. This same experiment was repeated twice more, but the depths of burial were 4 and 8 inches, respectively. Each experiment was started with freshly collected gemmas. The results (table 2) suggest that gemmas can extricate themselves from remarkably deep burial.

TABLE 2.—*Survival of* Gemma gemma *at selected depths*

At depth of—	Date planted	Date recovered	Number planted	Number recovered [1]
2 inches:				
test clams	Aug. 30	Sept. 1	10	10
control clams	Aug. 30	Sept. 1	10	[2] 10
4 inches:				
test clams	Sept. 1	Sept. 3	10	7
control clams	Sept. 1	Sept. 3	10	10
8 inches:				
test clams	Sept. 3	Sept. 5	10	5
control clams	Sept. 3	Sept. 5	10	10

[1] Feeding.
[2] At the surface, half emerged.

These tests were made on uncrowded animals in prime condition. Older or much younger animals might have been less successful, particularly if they had been much crowded.

The tide in Sagadahoc Bay averages about 9.6 feet, and ranges from a little more than 5 to nearly 13 feet. The velocities of the tidal currents in the bay play a significant role in the economy of the shellfish living there because their food is brought to them in suspension in the water that passes over them. Of particular value is a knowledge of the velocities close to the bottom where they are not usually measured. Accordingly, special equipment was designed and made for us by Arthur H. Frazier, Chief of the U. S. Geological Survey's Water Resources Development Laboratory at Columbus, Ohio (fig. 4).

During the summer of 1953, Charles E. Knox, hydraulic engineer from the Boston office of the Geological Survey, measured the current velocities at 17 stations in the intertidal part of Sagadahoc Bay. The stations, selected in consultation with John Glude of the U. S. Fish and Wildlife Service, were located where the velocities are most nearly representative of flow over the flat and are least affected by the faster-flowing water in the major drainage channels. The velocities observed at these stations were related by time to the corresponding water-surface elevations shown by an automatic stage recorder, which was installed near the low-tide line. Current velocities were measured continuously at 0.1 foot, and 1.0 foot, and 3.0 feet above the bottom, but only the velocities at 0.1 foot above the bottom were fully worked out.

On the basis of data obtained during July and August 1953, bottom velocities measured at the 17 stations gave similar patterns. The velocities at the start of incoming tide were the highest recorded during the tidal cycle and ranged from 0.35 fps. to 0.82 fps. The velocities decreased rapidly and then leveled off, reaching a minimum around the change of tide. Minimum velocities ranged from zero to 0.15 fps. Measurable velocities were recorded at all but one station in Bedroom Cove. The velocities increased after the turn of the tide and reached another peak as the water drained off the flat. These peak velocities as the water drained off ranged from 0.20 fps. to 0.58 fps. The velocities at the start of a tidal cycle averaged about 25 percent higher than those near the end.

The velocities varied rather uniformly throughout the bay. In Bedroom Cove they were about half those in other parts of the bay. The velocities in the upper end of the main part of the bay were about 35 percent lower than those farther out in the bay.

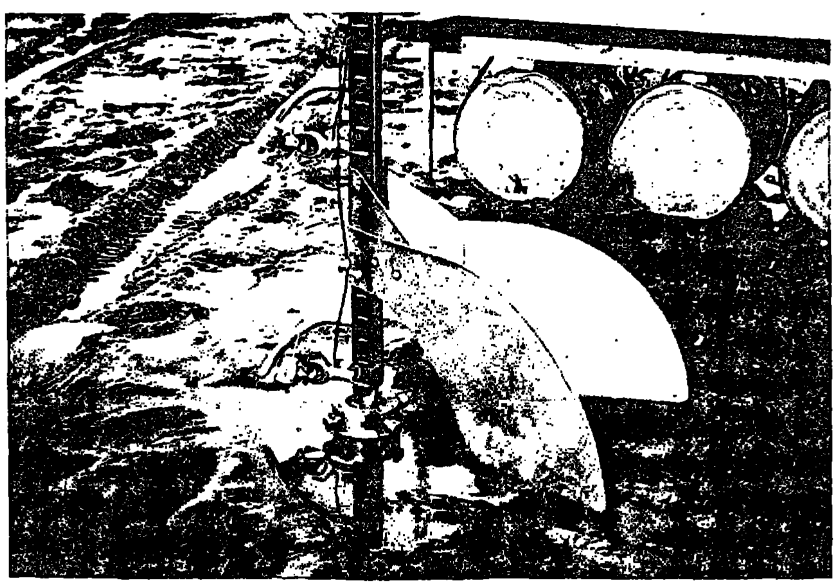

FIGURE 4.—Pygmy Price current meters mounted near the bottom of a tube which surrounds a stainless steel rod. The tube hangs from a pivot at the top of the rod so it is free to rotate as the rudders dictate. The steel rod is set in the cone-shaped bottom of an iron pipe driven 3 feet into the mud. Centering collar at top of the pipe provides for plumbing the rod. The corks resting against the current-meter rotors prevent rotation in the wind but rise when the tide comes in to let the rotors turn only when fully submerged. Impulses from the three current meters were recorded on paper tape moving through a battery-driven, clock-controlled recording device, which was supported on a float.

The average velocities varied directly with the range of the tide and for the tide of August 18, 1953 (7.7 ft.), were 30 percent lower than those for the tide of August 25–26, 1953 (11.2 ft.). Flow into and from the bay varied at a fairly uniform rate. However, there were times, especially when a pronounced swell was running, when the water moved in surges, that is, seiches were established. These surges, which have a period of something less than 10 minutes, may be edge waves described by Munk, Snodgrass, and Carrier (1956, pp. 127–129). At these times, the current moved alternately in and out for intervals of several minutes, especially near the turn of the tide. The same seiches have been observed at the low-tide line. The recorded velocity was the resultant of the two velocities.

The detailed observations and graphs may be consulted in an open-file report (Knox and Bradley, 1954) on deposit at the library of the U. S. Geological Survey.

Surface water velocities (ca. 30 inches below the surface) were measured from stick-buoy surveys on August 8, 1952 and averaged nearly 0.3 fps. on the flood tide and 0.59 fps. on the ebb tide. These are averages over nearly the full length of the intertidal zone on a tide whose range was greater than average.

The waters of Sagadahoc Bay have somewhat less than ocean salinity owing to the freshening of a large area off the entrance to the bay by the Kennebec River, whose mouth is adjacent to Sagadahoc Bay on the west. For several miles out to sea beyond the mouth of the Kennebec River, the surface water has salinities of 25.1 to 25.4 parts per thousand. In Sagadahoc Bay, during the summer, the salinities range from about 26 parts per thousand at the entrance to 29.8 near the landward end. More saline water comes into Sagadahoc Bay from the east through the narrow passage between Indian Point and Salters Island and accounts for the greater salinities within the bay. Summer evaporation from the much warmer water near the head of the bay tends to increase the salinities at the head of the bay. Generally, these shallow waters are turbulent enough so that all the water in any vertical column is effectively mixed.

The long rocky ribs that form the east and west sides of Sagadahoc Bay refract the ocean waves, regardless of their orientation at sea, and direct them up the bay with their crests essentially normal to the long axis of the bay. During storms, two zones of breakers form, one seaward from the average low-tide line and the other farther up the bay. The positions of these zones of breakers, of course, shift with the stage of the tide and the size of the waves.

During quieter times, the waves that come in over the intertidal area of the bay generally have steep flanks and wide flat troughs. These are only the crests of ocean waves whose bottoms have been sheared off by the shoaling bottom in the outer half of the bay. As each of these waves passes over the bottom, it creates beneath it, and in back of it, a family of horizontal parallel vortices (fig. 5). The hydrodynamics of these vortices (Russell 1952, pp. 114–116) is such that they have at first small orbits and high orbital velocity, but immediately the axis of the vortex begins to rise, the orbit grows larger, and the orbital velocity decreases. Such wave-generated vortices are effective erosive agents, which not only move detritus and fine sand grains but doubtless also small gemmas and myas. This is the process that throws the surface of the sandy part of the flat into its characteristic, ever-present ripples.

Gemma life cycle

Gemma gemma is ovoviviparous and according to Sullivan (1948, p. 2) "the larvae pass their entire veliger stage in the adult and on liberation settle in a cluster around the parent." Sullivan notes further (p. 31) that "*Gemma* eggs are large, and so are the earliest shelled larvae. The smallest larva measured was 272x295 microns. When liberated, they are generally around 340x410 microns." Apparently they are liberated through the summer nearly up to freezing weather for we have found minute forms all through July and August and some in February. These must have been born very late in summer as they showed very little growth beyond the larval shell. On the Sagadahoc flat, gemmas grow to a maximum length of almost 0.2 inch (5 mm.) but the bulk of the mature population averages nearer 0.16 inch (4 mm.) in length.

According to our observations, the gemmas living in Sagadahoc Bay today live at most 4 years but the great bulk of them live only 2 years. These age determinations are based on growth increments

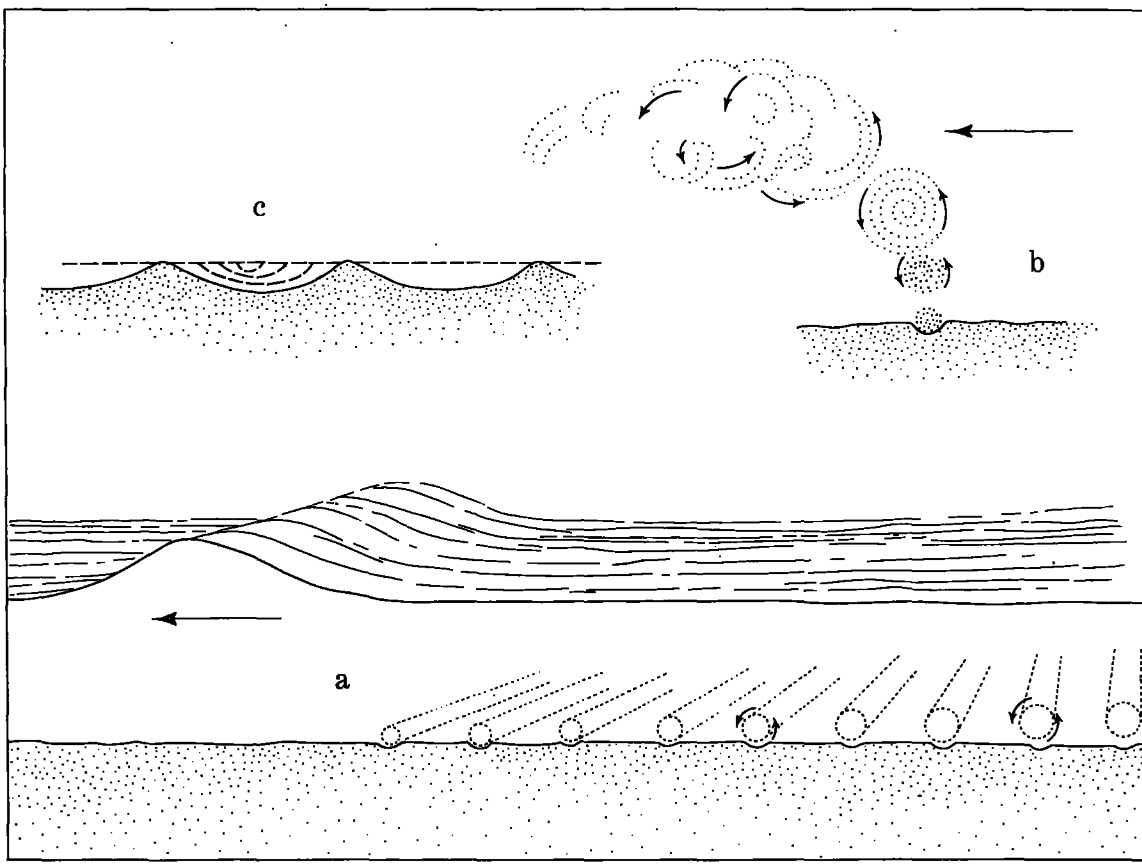

FIGURE 5.—Family of horizontal vortices (a) that form below waves traveling up the tidal flat have at first small orbits and high orbital velocity; each vortex (b) erodes a trough, rises, enlarges its orbit, decreases its orbital velocity, becomes turbulent and dissipates; ripple marks (c) formed by scour of successive families of wave-generated horizontal vortices.

of the shells of living gemmas. On most shells the larval stage is sharply defined and, except on those less than 1 year old, is deeply corroded, white, and chalky (fig. 6). On shells less than a year old the larval shell is recognizable by its rugose surface and by a fine bounding groove. Shell grown after expulsion from the parent is glassy smooth (fig. 6). The first year's growth is plainly set off from the second year's growth by a groove. In the 2-, 3-, and 4-year olds the first year's growth has many chalky blotches and the second year's growth of shell is sparsely marked with white chalky blotches. Chalky spots more than a year old are pitted. Also, the second year's shell, especially on the posterior end, is a deeper violet. Both this color difference and the groove representing the winter cessation of growth are more conspicuous from the posterior end (fig. 6).

In all the following age determinations (both living and dead shells) the animal was considered to be 2 years old if it lived into the second year, even though it may have died early in that year. In the same way, those that lived into the third and fourth years were counted as 3- and 4-year olds.

Gemmas that lived in Sagadahoc Bay many years ago lived longer and apparently grew somewhat more slowly than those that live there today. Some grew for 6 years, and possibly longer, but after the fifth year the growth zones are too narrow and obscure to be very reliable indicators. The ages of 202 gemma shells were determined from an extensive shell-pavement layer that underlies much of the sandy part of the flat at depths ranging from 20 to 24 inches below the present surface. The age distributions of the living, modern dead, and ancient gemmas are shown in table 3. The modern dead gemmas were collected in February 1956 from the surface of the flat near the southern end of Black Rocks Islands.

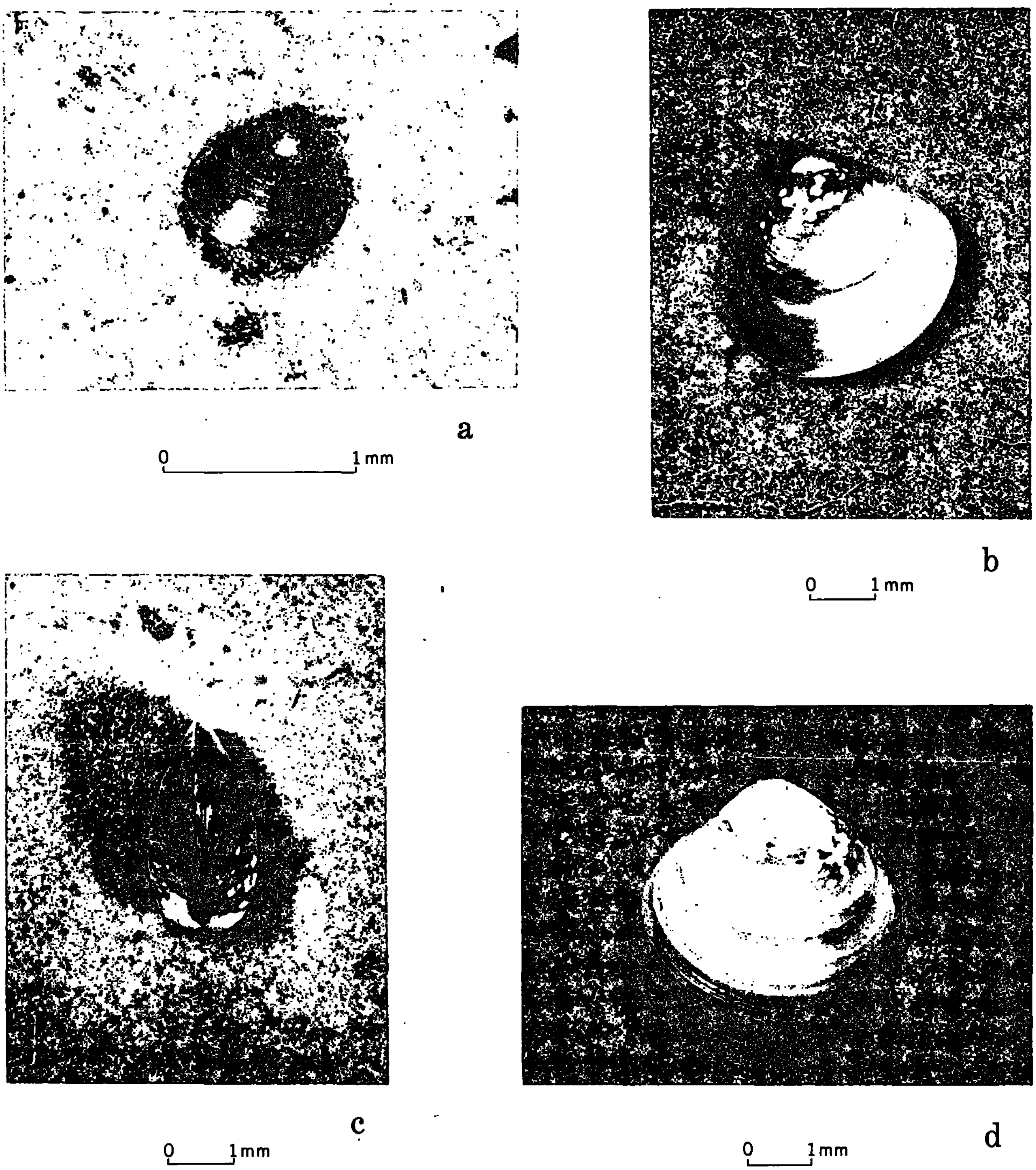

FIGURE 6.—*Gemma gemma* showing first-year form (*a*) with rugose larval cap and clear glassy, deep violet post-larval growth; two-year old individual (*b*) having white, chalky larval cap, chalky blotches on the first year growth, and clear glassy second year growth; posterior view (*c*) of same 2-year old showing the darker violet band close to the margin of the first year's growth; a 3-year old (*d*) showing corroded larval cap, chalky first year growth, sparsely blotched second year growth, and a narrow band of clear third year growth.

A small number of the shells in the living population have obscure growth bands and so their ages are indeterminate. In the ancient *Gemma* population the ages of more shells were indeterminate, principally because the surface layers of shell had flaked off. Only sound shells whose growth zones were clearly marked were used in making the counts listed in table 3.

TABLE 3.—*Age distribution of living, modern dead, and ancient gemmas in the Sagadahoc Bay tidal flat*

Age classes	Living (1949)	Living (1955)	Modern[1] dead (1955)	Ancient
1-year-olds	5	345	30	44
2-year-olds	12	1,208	155	71
3-year-olds	32	32	83	79
4-year-olds	1		8	[2] 8
Totals counted	50	1,585	276	202
Average age (years)	2.6	1.8	2.2	2.25

[1] Those that died in 1955 plus a small but unknown number that died in preceding years.
[2] Includes some 5- and 6-year olds and possibly some still older.

The age distribution of the living gemmas apparently differs somewhat from year to year, although the average age seems to be decreasing progressively. In 1949 it was 2.6 years; in 1955 it was only 1.8 years. Some allowance must be made in this comparison for the fact that in the 1949 age class we determined the ages of only 50 gemmas whereas for the 1955 class we determined the ages of 1,585 (table 3). This table shows that the 1955 population was abnormally deficient in individuals over 2 years old.

Because the climate has been warming progressively for the past 30 years or more, it is pertinent to raise the question whether the life span of *Gemma gemma* along the Maine coast may not be decreasing. Much farther south (Chesapeake Bay), *Gemma gemma* has a life span of only 1 year (J. P. E. Morrison; oral communication, 1955). But many more vital statistics on the Maine *Gemma gemma* than we have collected will be required to determine if such a secular change is taking place.

A less extreme explanation, and perhaps therefore more probable, is that the decrease in life span resulted from the crowding of the gemmas while the population was so dense during 1950 (and possibly 1951–53). Pearl, Miner, and Parker (1927, pp. 293–296) found in their experiments with fruit flies, that density of population markedly decreases life duration, particularly when the density increases greatly over the optimum.

The average at death of both the modern *Gemma* population and the ancient *Gemma* population is essentially the same (2.2 years), despite the fact that the ancient animals grew somewhat more slowly and, at least, a few of them lived longer.

As discussed later (p. 325–27), Comparison of 1950, 1954, 1955, 1956, and 1957 population, the *Gemma* population in Sagadahoc Bay decreased progressively for the years 1954, 1955, and 1956. Moreover, it decreased a proportionate amount between 1950 and 1954, but as we took no census in the years 1951–53 we do not know whether the decline was at a uniform rate (fig. 13).

We wonder whether the apparent decrease in life span shown in table 3, especially the very small number more than 2 years old in the 1955 living population, may not account in part for some of the observed decline in the population. A stable population of animals whose average life span, for example, is 4 years, can be sustained by a 25-percent annual replacement, but if the life span is reduced to 2 years it would require 50-percent annual replacement to maintain that same population. Of course, if the replacement rate remains constant the population must be reduced by half. Clearly, the *Gemma* population in Sagadahoc Bay has declined much more in the interval 1950–56 than the apparent decrease in the life span of the gemmas could account for; hence, other factors must be sought to account for the decrease in the *Gemma* population.

Surely something abnormal is happening in the population, because in each census the number of 1-year olds is markedly less than the number of 2-year olds (table 3), whereas in a stable population it should be the other way around. Even allowing for 25-percent loss of the minute individuals, which is generous in our method of sampling (p. 319–20) the numbers of 1-year olds are discrepantly small. Considering the small size of the youngest gemmas and the fact that most small particles are winnowed out of the sandy part of the flat by waves and currents, it seems probable to us that a sizable percentage of the minute gemmas are similarly winnowed out and either moved up the flat into a muddy and much less favorable environment or moved seaward beyond the low-tide line where they cannot live. This would account for the observed abnormal deficiency of 1-year olds in the population. If this is so, an abnormally high frequency of summer storms would have a depleting effect on the population of *Gemma* and vice versa.

We have very little information on seasonal changes in the abundances of *Gemma* in this bay, but that little suggests no change.

TABLE 4.—*Winter and summer Gemma counts per 3-inch diameter sample*

Stations	February 1956	July 1956
H	60	67
I	98	74
J	132	123
K	50	74
Means	85.0	84.5

Feeding habits

Gemmas that live in the sandy areas have relatively thick, strong shells that are strongly colored, deep violet or purple in the small ones and lighter violet in the mature shells. The mature ones, however, have only about one-half or less of the posterior ends colored. When the clam is feeding in the dark, this colored posterior end rises above the surface of the sand. In the dark, they move around somewhat as *Spisula* does. In subdued light, they feed with only their siphons exposed. It is doubtful whether they feed at all when strong sunlight penetrates to the bottom, that is, in shallow, clear water. But in Sagadahoc Bay the water is generally somewhat turbid so that a few feet of water over the part of the flat where the gemmas are most abundant probably dims even midday summer sun enough so that they feed, at least with only their siphons exposed.

An attempt was made to determine the area over which individual mature gemmas feed. To do this a small aquarium was set up with sandy mud from the flat with its contained gemmas. No running sea water was available, but at appropriate intervals the water was poured off and some hours later fresh sea water was added, thereby roughly simulating the tides.

We found that the gemmas fed much more actively at night, or indeed at any time when kept in the dark. They are so shy of light that observations had to be made within a minute or less after the aquarium was uncovered. In those brief intervals we could make no measurements; only estimate dimensions by visual comparison with the known average dimensions of the shells. In general the siphons protrude about the equivalent of a shell width and most of the time they are kept in, or nearly in, the plane of the valve openings. Occasionally the siphons are moved slowly about in a semicircle. The effective area from which they draw food was estimated to be roughly equal to the area of the side of the shell, about 0.0065 square inch (4.2 square mm.), but this is probably a minimum because gemmas move about, at least in the dark. The longest furrow observed in the aquarium was a little more than 1.2 inches. Where several mature gemmas by chance came into contact they pushed and shoved one another with considerable vigor.

If we assume that the probable minimum area from which each gemma draws food is 0.0065 in.^{2} (4.2 mm.^{2}) and that there are 25 mature gemmas per square inch in the central sandy part of the tidal flat—roughly the average density in 1954—then these gemmas are drawing food from about 16 percent of the bottom layer of water passing over them. The present living *Gemma* population (1950) ranges from 1 or 2 per square inch near the margins of the flat to as many as 190 per square inch in the sandy central part of the flat (fig. 7).

LIVING POPULATION

Distribution

Gemmas live in virtually all parts of the Sagadahoc Bay except a narrow irregular zone around the margins (fig. 8). They are much more numerous in the large areas of the flat where the sediment is relatively clean, fine-grained sand, and they evidently find a nearly optimum environment in the midsection of the flat.

Gemmas that live in the sandy areas, have thick strong shells and are white with violet posterior ends. Those that live in the muddy areas have thin, delicate shells, which are easy to crush between the thumb and finger. The mud-dwellers have paler colors and in some areas are light brown.

Apparently gemmas, like many intertidal species, must be wet virtually all the time, for they are extremely rare or absent from places, either sandy or muddy, that drain out nearly dry between tides. They prosper only in intertidal areas where the slopes are gentle and where the

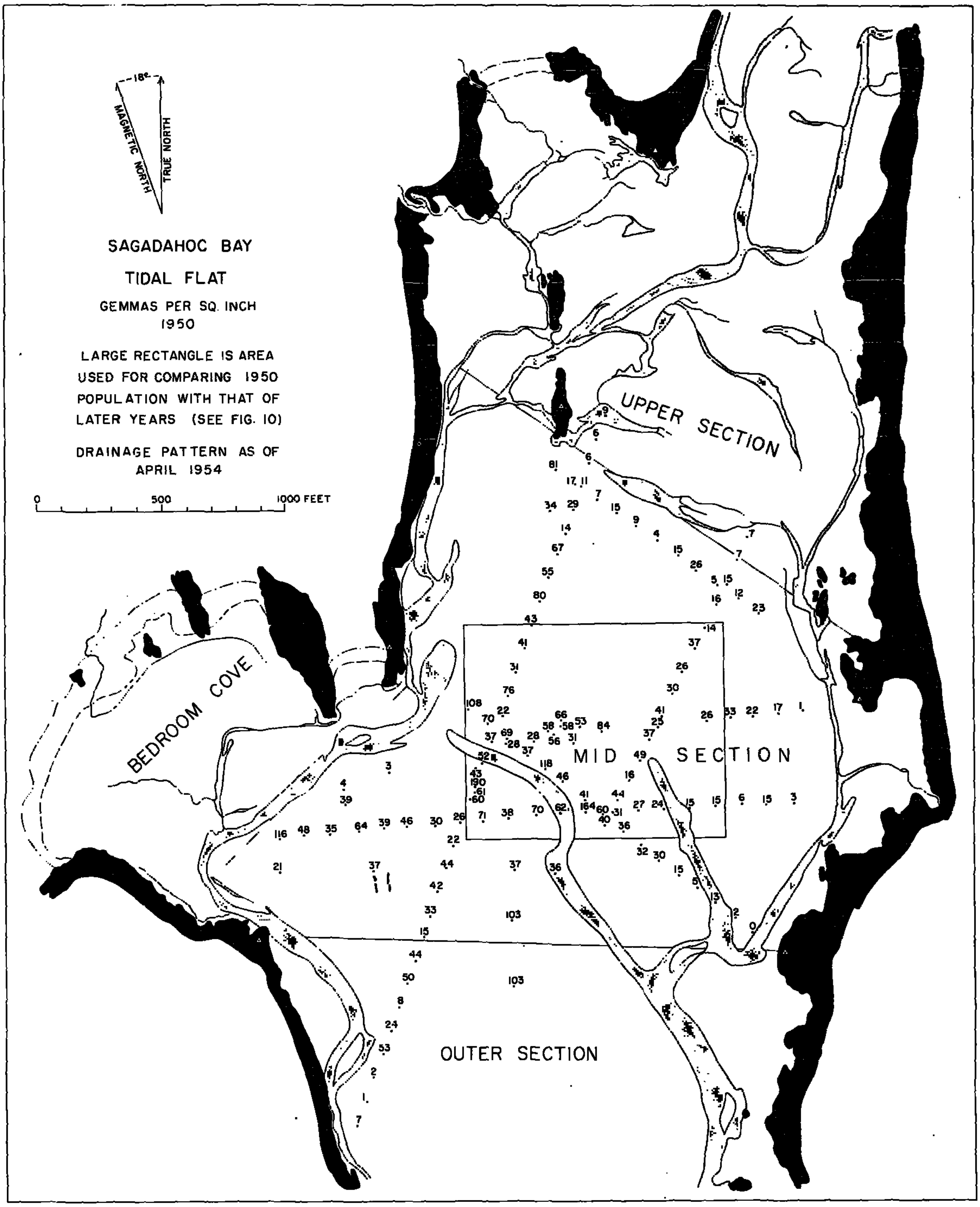

FIGURE 7.—Distribution of sampling stations used in the 1950 *Gemma* census. Numbers are gemmas per square inch. Large rectangle is area sampled in 1955, 1956, and 1957 for comparison with 1950 and 1954 populations.

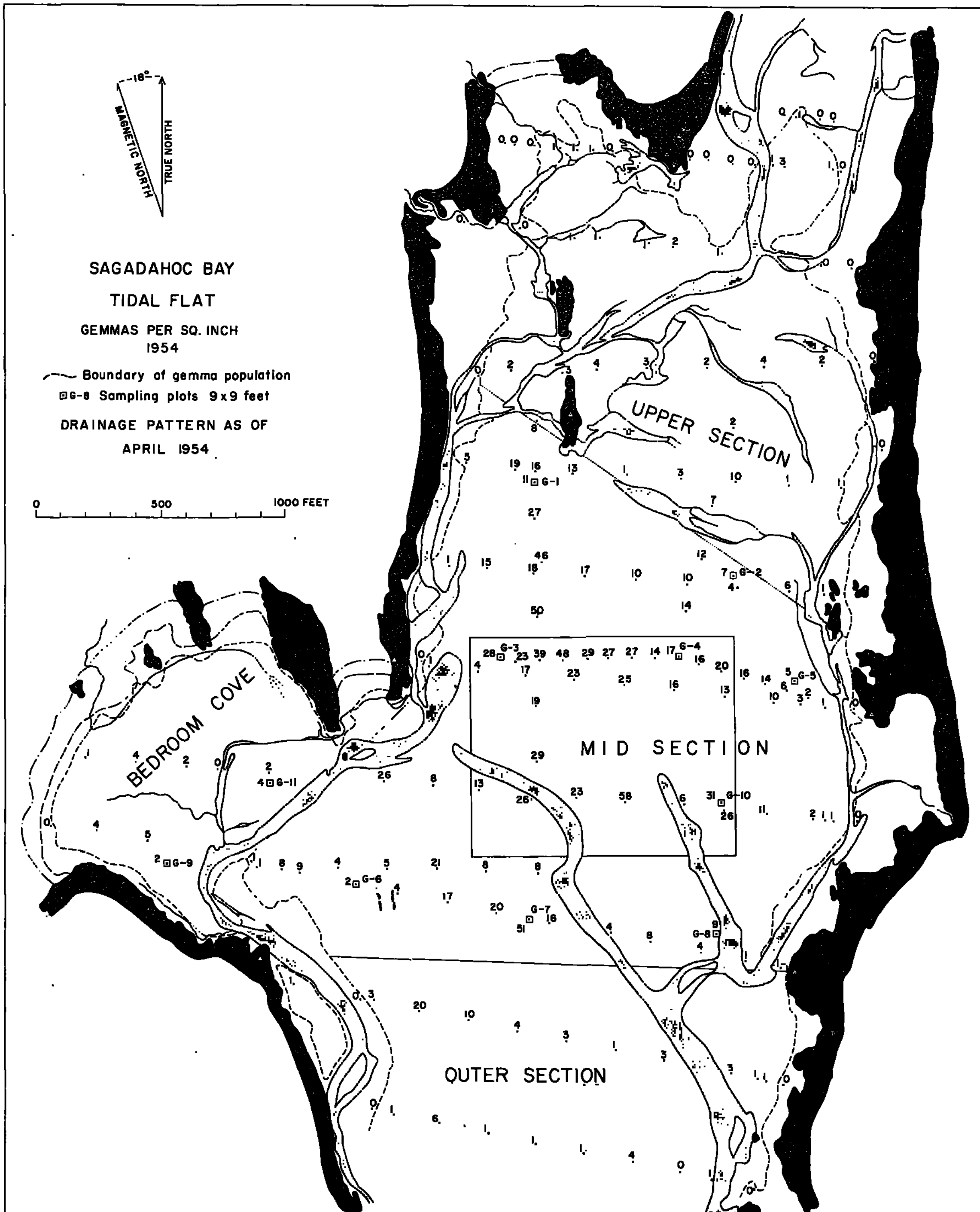

FIGURE 8.—Distribution of sampling stations used in the 1954 *Gemma* census. Numbers are gemmas per square inch. Dashed line around margins of the flat is the outer boundary of the *Gemma* population. The distribution of special sampling plots 9 by 9 feet square (G–1 to G–11) are also shown together with the large rectangle used for comparing the *Gemma* population from year to year.

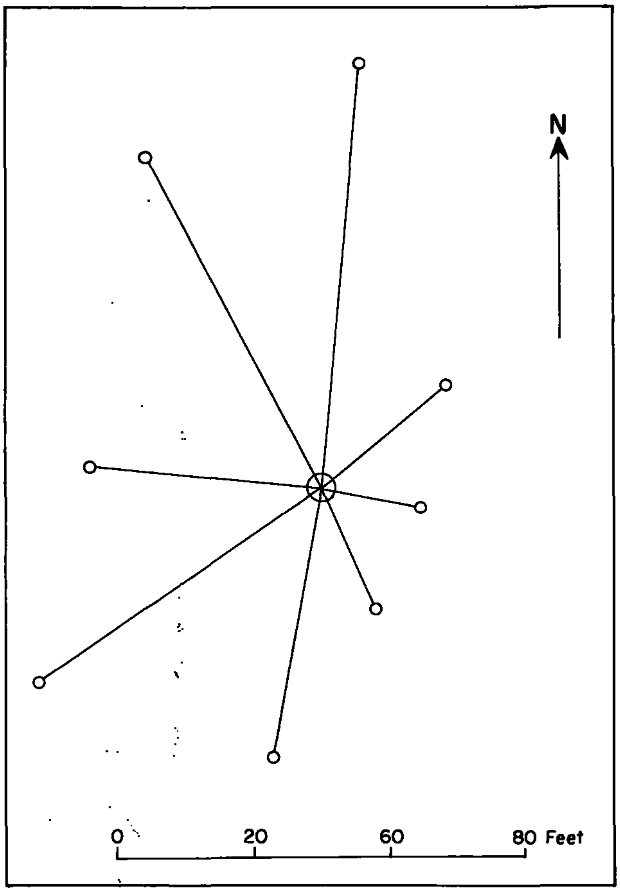

FIGURE 9.—Directions and distances that colored sand grains were moved radially from a point source by waves and tidal currents in 15 days of average summer weather during the summer of 1950. The colored grains were of about the same size and density of the average sand grains in the sandy part of the flat.

sediments are fine grained enough to keep the pore spaces filled with water while the tide is out.

As noted above, gemmas move about while feeding or while searching for better feeding grounds. Perhaps this movement alone could account for their present ubiquity in the sandy parts of the Sagadahoc Bay tidal flat. But waves, especially those generated by big storms, move gemmas in large numbers and probably for considerable distances. Patently, small gemmas are moved about more than the mature ones. Judging by the measured migration of sand grains on this flat (fig. 9), the dominant tendency of the waves is to move gemmas northward up the long axis of the flat. Nevertheless, the sand grains, which average about 0.005 inch (0.12 mm.) in diameter, are also moved in all other directions and doubtless also are gemmas. These and other related observations are discussed in another report (Bradley, pp. 666–669).

A small percentage of mature gemmas acquire tufts of the green alga, *Enteromorpha compressa*, which ensures their transport by waves of even moderate size. Whenever mature gemmas containing young in their mantles are transported to a favorable environment, new centers of relatively greater population density come into being.

Both these saltatory means of distribution help to account for the observed uneven distribution of the *Gemma* population in an extensive, monotonously uniform sandy flat where uniformity of distribution might be expected.

The sandy part of the flat, with the exception of a few small marginal areas, is always rippled, and the ripple crests are nearly normal to the long axis of the bay. The size and shape of the ripples, of course, is determined by the size of the waves and the depth of the water during the preceding high tide. Most common are ripples that are asymmetric and whose wave lengths are 5 or 6 inches from crest to crest. Amplitudes of the ripples differ from tide to tide but rarely exceed one inch.

During one low tide we sampled the number of living gemmas at 18 stations in the midsection of the flat and found that on the average there were 20 per square inch in the troughs, 16 per square inch on the crests, and 24 on the midpart of the long back slope.

The surface of the whole flat is interrupted at intervals of a quarter of a mile or less by low transverse ridges and adjacent broad shallow swales. These features have roughly the same form as gigantic asymmetric ripples whose steep faces are landward. On one of these ridges we found from rather extensive sampling that there are about 22 gemmas per square inch on the ridge and about 15 per square inch in the adjacent swale.

Further observations are needed to determine whether this distribution of gemmas with respect to the sand ripples and larger topographic features, is determined by the waves or whether the gemmas move to those positions because they are in some way more favorable.

The 1950 and 1954 counts (figs. 7 and 8) show that gemmas are much more abundant in the midsection of the tidal flat than they are elsewhere. This environment is evidently more favorable than elsewhere. The favorable factor may be a greater food supply made available to that area by the tidal currents, which flow over it 30 to 36 percent faster than they do farther up the flat. At a depth of 0.1 foot above the bottom the average tidal currents run over this midsection of the flat about 0.3 foot per second during the tides with small ranges and about 0.4 fps. during the large tidal ranges. A little farther up the flat the corresponding average velocities are 0.23 and 0.29 foot per second (Knox and Bradley, 1954, p. 7, table 11). The greater velocities over the midsection of the flat are doubtless due to the fact that the bay narrows here. Tidal velocities were not measured farther seaward, but we infer that they are less until one comes to the low-tide zone where the bay narrows again. Neither gemmas nor myas, however, live in significant numbers near the low-tide line.

In the midsection of the flat polychaete worms are common and locally abundant. Two species, *Spio setosa* and *Pygospio elegans*, which were kindly identified for us by Dr. Marian H. Pettibone of the University of New Hampshire, outnumber all others by an overwhelming margin. Roughly, the larger worm *Spio setosa* is most numerous in the western and northern parts of the midsection of the flat and *Pygospio elegans* is most numerous in the eastern part of the midsection of the flat. In the central part of the midsection of the flat where gemmas are most numerous, neither worm is common.

Methods of sampling

All the counts of the living gemmas were made on the flat after wet-sieving the sample through a 20-mesh screen (diameter of opening 0.033 in. or 0.84 mm.). This quickly removes virtually all the sand but has the disadvantage of losing an unknown number of the smallest gemmas, those between about 0.016 in. and 0.039 in. (0.4 and 1.0 mm.). Nevertheless, a considerable number of these minute forms are found after wet-sieving because they have a strong tendency to be trapped by the capillary film on the wires of the screen. To determine the probable maximum number of minute gemmas that could pass the 20-mesh screen, two 3-inch diameter samples were taken side by side, air dried, and sieved dry. The counts of gemmas caught on the several screens were as follows:

Screen	Gemmas caught	Size ranges
No. 9 mesh	344	0.14 in. (3.5 mm.).
No. 20 mesh	147	0.047–0.12 in. (1.2–3.1 mm.).
No. 32 and 65 mesh	72	0.024–0.39 in. (0.6–1.0 mm.).

Nearly 13 percent passed the 20-mesh screen dry. This undoubtedly represents a maximum for samples with this size range. During the summer of 1950, all the samples were taken with a cylindrical cutter 1¾ inches in diameter (2.4 square inches), which took the top 1 inch of sediment. In 1954, 1955, 1956, and 1957 we used a cutter 3 inches in diameter (7.06 square inches), which took a sample 1⅜ inches deep. The deeper sample is better because we have occasionally found mature gemmas that deep, presumably buried by shifting sand.

The pattern of sampling of the living *Gemma* population was unfortunately not consistent. In 1950 the sampling was incidental to other studies made on the tidal flat, and the pattern of sampling, therefore, was determined in part by the plan of those studies (fig. 7). In 1954 the pattern of sampling was designed to obtain as good a representation of the total living population as possible (fig. 8). In 1955, 1956, and 1957 only a part of the midsection of the flat was sampled (fig. 10), primarily to compare the population of 1955, 1956, and 1957 with that in the same area in 1954 and 1950.

During the summer of 1954 we sampled systematically along rather regularly spaced traverses and at close intervals along the margins of the flat but also sampled 11 square areas 9 feet on a side in some detail. The locations of these squares are shown on the map (fig. 8) as G–1, G–7, etc. Each square was divided into 81 squares 1 foot on a side. Three-inch diameter samples were taken from the centers of 23 of these smaller squares according to the pattern shown in fig. 11. But for one of the 9-foot squares we took samples from alternate 1-foot squares, which yielded a total of 41 samples. This pattern of sampling was adopted to see whether we could evaluate the reliability of our single widely spaced samples taken in traverses roughly normal to the long axis of the flat (fig. 8). We also wished to appraise the spottiness or uniformity of gemmas in relatively small areas, which were selected as typical of various parts of the flat. The distributions are shown in table 5 (see also fig. 12).

After discussions with W. C. Krumbein of Northwestern University about the statistical significance of our 1954 and 1950 sampling, we decided to sample in the summer of 1955 enough of the flat to permit a reliable comparison of the 1950, 1954, and 1955 populations. The pattern of sampling in 1956 and 1957 was like that of 1955. A rectangle, 875 by 1,050 feet, was laid out in the midsection of the flat (fig. 10). Following Krumbein's counsel, we subdivided this into 30 squares 175 feet on a side and took a 3-inch diameter sample from the center of each square. These samples were used as a basis for estimating the 1955 *Gemma* population. Using a table of random numbers, 10 of these 175-foot squares were selected and each was subdivided into 49 squares 25 feet on a side. Then two of these 25-foot squares were selected at random from each of the ten 175-foot squares. Each 25-foot square so selected was subdivided into squares 1 foot on a side. Again using a table of random numbers, two 1-foot squares were selected and from the center of each

TABLE 5.—*Numbers of gemmas in 3-in. diameter samples in 9 by 9 foot square plots, G–1 to G–11 of fig. 8*

Sample plot	Number of samples	Minimum	Median	Maximum	Mean	Standard deviation	Average no. per sq. in.
G–1	23	22	74	244	76	52	11
G–2	23	28	49	85	51	13	7
G–3	23	82	200	382	195	66	28
G–4	23	48	104	208	118	43	17
G–5	23	5	28	77	33	21	5
G–6	23	7	33	75	33	16	5
G–7	23	208	324	644	357	118	51
G–8	23	19	62	138	64	27	9
G–9	23	2	14	41	16	10	2
G–10	41	105	212	456	221	78	31
G–11	23	9	27	41	24	8	3

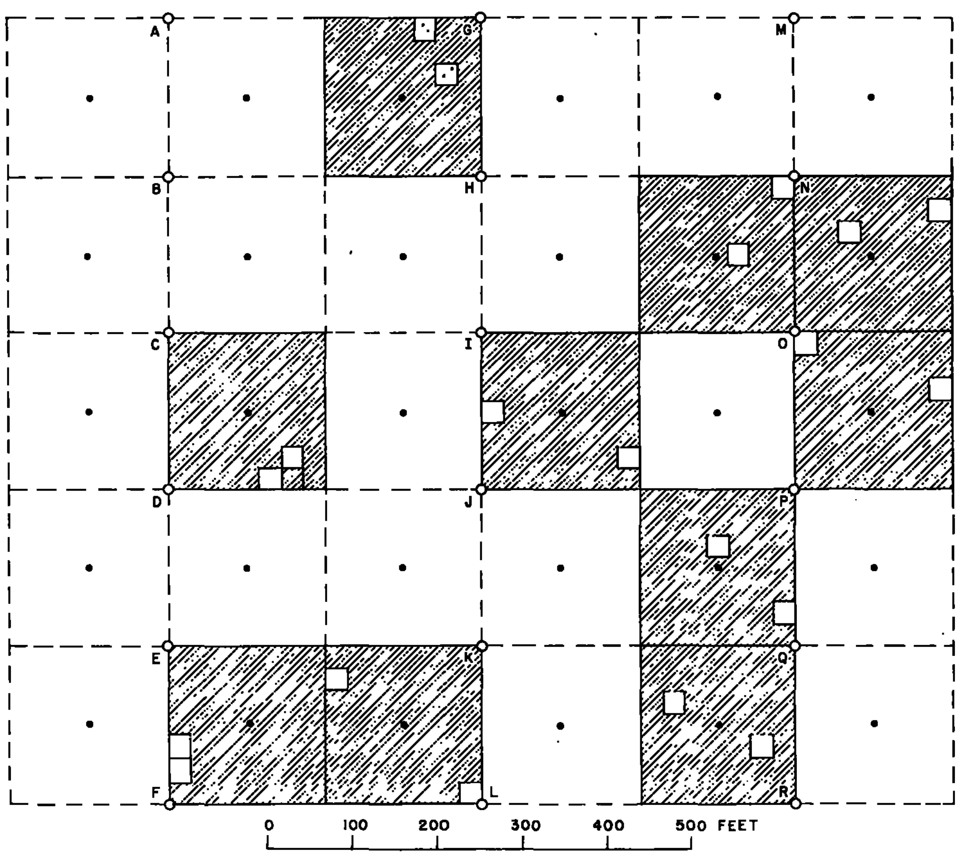

FIGURE 10.—Plan of detailed sampling for 1955 designed by W. C. Krumbein. The rectangle is 1,050 feet by 875 feet, the larger squares are 175 feet on a side, and the smaller squares are 25 feet on a side. Three lines of stakes, lettered A through R, were fixed on the tidal flat by plane table survey. All other positions in the rectangle were measured from those stakes. Sampling procedure is described in the text.

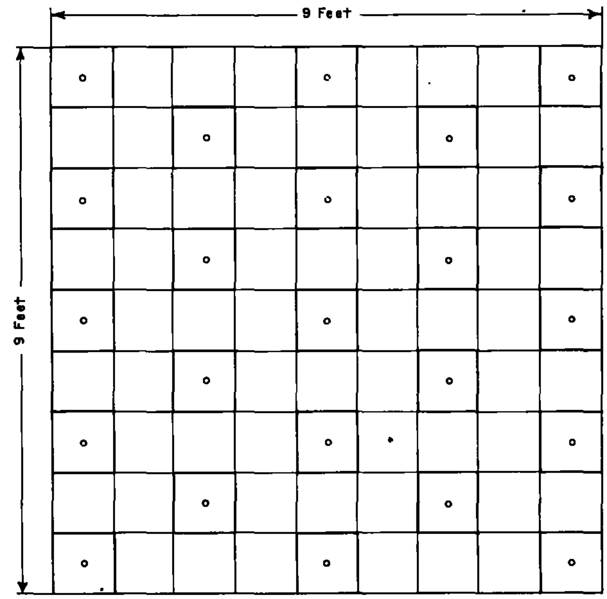

FIGURE 11.—Plan of 1954 sampling plots designated G–1 to G–11 located on map figure 8. The smaller squares are 1 foot on a side and samples were taken from the center of 23 such squares as indicated. In plot G–10 samples were taken from alternate 1-foot squares making a total of 41 instead of 23.

of these 1-foot squares we took a sample 3 inches in diameter.

Analysis of nested samples

Table 6 shows the distribution of gemmas in the 40 nested samples. We wanted to get a measure of the variability with different sample spacing. From the raw data we found the following average differences in numbers of gemmas counted: Between 175-foot squares 229.2; between 25-foot squares 95.3; and between 1-foot squares 30.9. To test the significance of the differences, W. C. Krumbein kindly made an analysis of variance and reported as follows:

The nested samples give some information about the variability with different sample spacings. I used logs directly and obtained the following mean squares in log terms.

TABLE 6.—*Numbers of gemmas per 3-inch diameter sample taken from the randomized and nested plots (fig. 10)*

25-foot squares	1-foot squares	175-foot squares									
		I	II	III	IV	V	VI	VII	VIII	IX	X
A	1	175	129	118	181	227	147	104	115	159	75
	2	98	123	105	213	222	88	44	102	161	61
B	1	199	72	128	325	126	116	76	63	80	24
	2	109	47	111	259	82	114	30	99	84	32

TABLE 7.—*Analysis of variance*

	Sum of squares	Degrees of freedom	Mean squares
Between 175 foot squares	1.6062	9	0.1785
Between 25 foot squares	0.5458	10	0.0546
Between 1 foot squares	0.3249	20	0.0162

Two F tests can be made. The first is 0.1785/0.0546= 3.27, which is significant at the 5-percent level. It suggests that there is greater variability between large squares than there is between small squares in a large square. Similarly, the test 0.0546/0.0162=3.37, which is significant at the 1-percent level, and it states that there is more variability between small squares in a large square than there is between samples in a small square.

The differences between the 175-foot squares probably reflect an already recognized decrease in the numbers of gemmas in all directions away from an area of peak abundance (fig. 8). This area of peak abundance is northwest of the center of the sandy part of the flat and presumably represents optimum conditions for *Gemma*. The differences between 25-foot squares may also reflect in part this same "regional" distribution but in larger measure they, like the differences between the 1-foot squares, reflect the general spottiness of the *Gemma* distribution.

A crude measure of the scale of the spottiness is shown by the average range in the numbers of gemmas. Within the 175-foot squares the mean range is 81.2; within the 25-foot squares it is 95.3; but between samples within the 1-foot squares, it is only 31. The bunched groups of gemmas occupy areas between the area of the 25-foot squares and the 1-foot squares. (See fig. 12.)

Pattern of distribution

The 9-foot-square plots sampled in 1954 provide data that reveal something of the pattern of *Gemma* distribution in the Sagadahoc Bay tidal flat. In analyzing these data we follow G. E. Hutchinson's illuminating paper, Concept of Pattern in Ecology, (1953, pp. 1–12). He defines pattern (p. 3) as "the structure which results from the distributions of organisms in, or from, their interactions with, their environments", and visualizes five kinds: Vectorial patterns, which are distributions of organisms determined by external forces, such as light, temperature, humidity, or density gradients, changes of state in certain directions, currents, and winds; reproductive patterns, which are determined by genetic continuity, offspring remaining near the parent; social patterns, which are determined by signaling of various kinds, leading either to spacing or aggregation; coactive patterns, which are determined by interaction between species in competition; and stochastic patterns, which are determined by random forces.

From the fact that *Gemma* is ovoviviparous it is reasonable to expect that the organism continually tends to establish a reproductive or superdispersed pattern. The reproductive pattern, however, continually tends to be destroyed by the action of waves and currents and this disturbing vector is enhanced to some extent by the plumes of *Entero-*

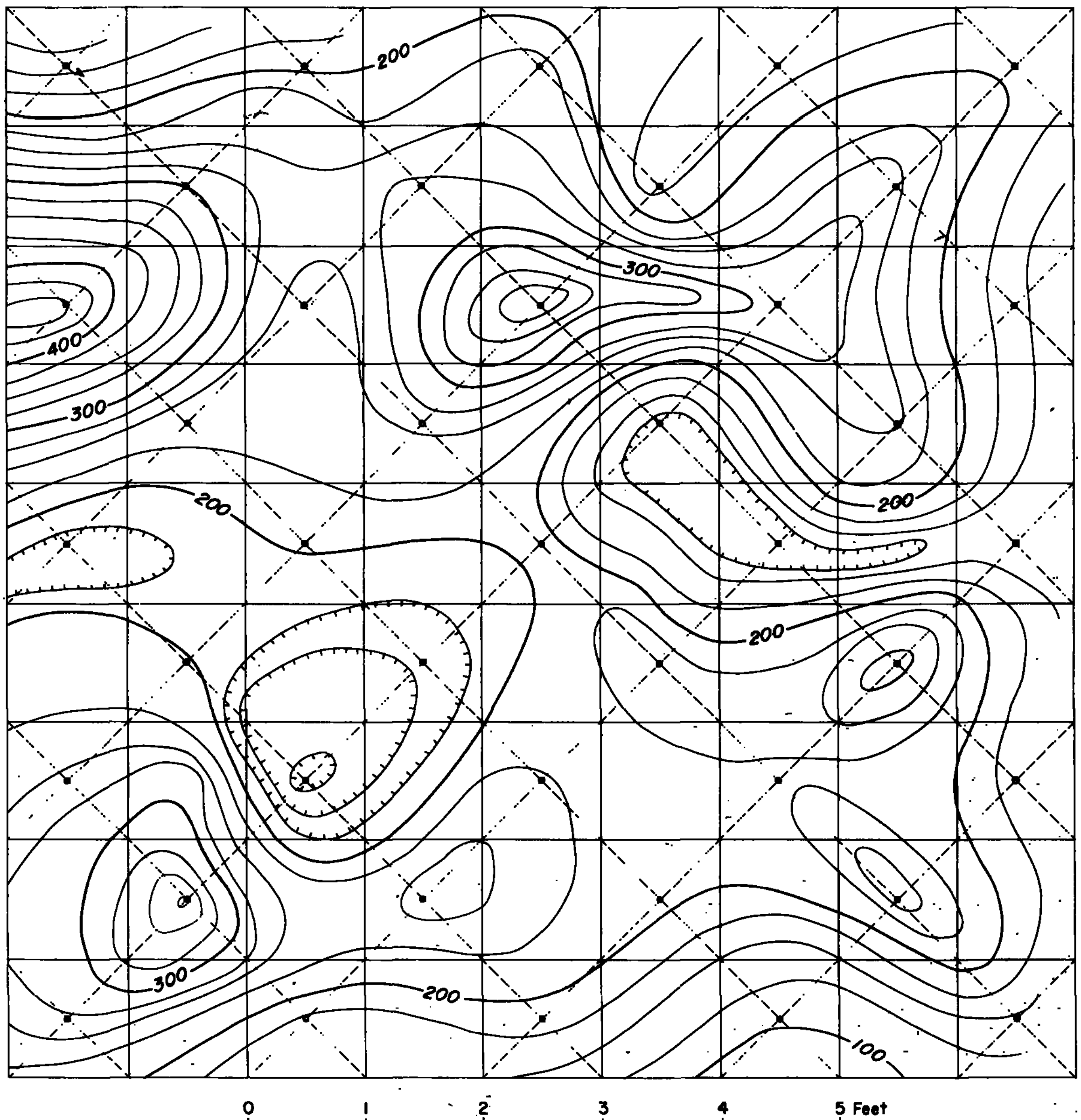

FIGURE 12.—Bunched distribution of gemmas in a 9 by 9 foot square, G–10. Contours represent lines of equal numbers of gemmas and are based on counts of the clams in 3-inch diameter samples indicated by the black dots in the centers of 41 alternate 1-foot squares. In drawing the contours, it was assumed that the numbers of gemmas decreased, or increased, at a uniform rate across the spaces between samples. Hachured contours indicate closed "depressions".

morpha compressa, which the gemmas acquire during the summer.

The resultant of these several factors is a population that has a bunched, or modified reproductive pattern of distribution (fig. 12). The bunches range in size from a little more than 1 square foot to several square feet. Because the contours were spaced uniformly between control points (samples) the bunchiness is to some extent minimized, but it is doubtful whether there is a bunched pattern of still smaller scale superposed on the pattern shown by the contours in figure 12.

A more significant aspect of the *Gemma* population is that it has a log normal distribution. This was suggested by W. C. Krumbein and demonstrated by my colleague John T. Hack who plotted the data on log probability paper and ran a chi-square test of fit. Standard statistical tests can therefore be applied to the data provided they are first converted to logs.

If *Gemma* and *Mya* are in any sense competitors one might expect that gemmas would find the areas close to large myas less favorable than farther away. Moreover, as both clams get their food from water that flows over them, the least desirable places for gemmas should lie along lines representing the dominant direction of flow of the tidal currents. In Sagadahoc Bay, this direction is roughly north-south, hence the least favorable spots for gemmas should be just north and just south of each mature mya. The same reasoning would apply if the inimical factor were metabolic wastes from the mya. Of these two critical spots, the one in the lee of the mya siphon during incoming tides should be the less desirable, on the assumption that the mya would always be robbing the gemma of the best nutrients brought in from the sea by the rising tide. To test this idea the senior author, in July 1956, sampled 5 areas around individual myas living within the large sampling rectangle shown in figures 10 and 7. The samples (3 inches in diameter) were taken at fixed intervals along 8 rays of a star whose center was the siphon hole of a living mya. The innermost ring of samples was 5 inches from the center, the next ring 1 foot, and the third ring 2 feet. At some of the stations, rings of samples at radial distances of 3, 4, and 5 feet were also added, but the larger number of samples required more than one tide to count the contained gemmas, and it seemed highly desirable to restrict the sampling of each plot to one low tide to avoid movements of the gemmas. Areas of this size are not likely to contain other undetected myas because in this part of the flat myas occur almost always as individuals spaced several to many feet apart.

We have assumed, perhaps unwarrantedly, that if the proximal positions along the north-south line through a mya siphon are the least favorable spots for gemmas there will be, on the average, fewer gemmas in those spots. To determine if this is so, the number of gemmas in each pair of north-south proximal samples were averaged (col. 3, table 8) and then the rest of the samples at each station were averaged to give the average number of gemmas per sample (7.06 square inches) at that station. This is referred to hereafter as the station population (col. 2, table 8). The table shows that the number of gemmas in each pair of north-south proximal samples is consistently smaller than the respective station populations. The last column of table 8 gives the differences as percentages of station populations. Each percentage figure is preceded by a negative sign to show that the average number of gemmas in each pair of north-south proximal samples is smaller than the corresponding station population.

TABLE 8.—*Distribution of gemmas around individual myas*

Station	Number of samples	Station population	Average number gemmas per pair in north-south proximal samples	Differences	Differences as percent of station population
1	36	115.6	86.5	28.9	−25.0
2	32	62.6	46.0	16.6	−26.5
3	25	99.0	63.0	36.0	−36.4
4	24	114.2	101.0	13.2	−11.6
5	22	82.0	62.5	19.5	−23.8
Means		94.6	71.8	22.8	−24.6

Because the station populations differ considerably in density and because at each station the ranges in numbers of gemmas are rather large (table 9), it may be that the consistently low counts found in the 5 pairs of north-south proximal samples are the result of chance. To test this we made a T test of the significance of the differences between the means of the north-south proximal pairs at the 5 stations and the means of the respective station populations. By pairing the observations and analyzing only the differences we get rid of the station-to-station differences that are presumably due to small differences in favorability of environment and, also, we need not assume that the variance of each north-south proximal pair equals the variance of its respective station population (Dixon and Massey, 1951, p. 106). As the *Gemma* population has a log normal distribution, logs are used throughout.

TABLE 9.—*Ranges and medians of the total numbers of gemmas counted at each of 5 stations*

Station	Minimum	Median	Maximum
1	45	108	177
2	15	61	144
3	32	106	176
4	54	103	202
5	17	77	166

Table 10 shows that the observed differences between the north-south proximal pairs and the mean population at each station are significant at the 98-percent level and we can rule out chance.

The deleterious influence of the myas extends north and south beyond the north-south proximal pairs of samples. This is shown by the fact that the counts in all four proximal samples (2 north and 2 south) are consistently lower than the respective station population means. Indeed, the average difference for all 5 stations is 23.7 percent less. By contrast the percentage differences of the east-west proximal pairs from their respective station populations are decidedly erratic (+10.4, −10.4, −50.0, +1.3, +2.0). So also are the percentage differences for a pair of samples selected at random from each station population (−19.6, +23.2, +36.5, −30.2, +18.8).

TABLE 10.—*"T" test of differences between the means of the north-south proximal pairs at the 5 sampling stations.*

Stations	log N.-S. proximal pairs	log Station populations	Differences
1	1.935	2.04	0.105
2	1.66	1.75	.090
3	1.80	1.96	.160
4	2.00	2.03	.030
5	1.63	1.86	.230
Means	1.805	1.928	0.123

Mean 0.123.
Total squares 0.0985.
t=3.64.
t_4d. f. (0.9875)=3.50.

Inspection of the five pairs of north-south proximal samples shows that the numbers of gemmas in four of the five samples lying north, or landward, from a mya siphon are smaller than those lying seaward, or south. As mentioned above, this is what would be expected if the mya were indeed robbing the gemmas just north of it of the best (or greatest amount of) food being brought in from the sea by the incoming tides. Whether so few samples can give reliable testimony on this point is certainly debatable. For what they are worth, the actual counts are given in table 11, along with the sizes and approximate ages and conditions of the five myas at the stations sampled.

TABLE 11.—*Numbers of gemmas north and south of individual myas and lengths and ages of the myas*

Stations	Gemmas north of a mya	Gemmas south of a mya	Differences	Length of myas (inches)	Approximate ages (years)	Condition of mya siphon
1	87	86	+1	2.0	?	Limp.
2	41	51	−10	3.25	6	Active.
3	61	65	−4	3.5	7	Active.
4	92	110	−18	3.75	9+	Very limp.
5	17	106	−89	3.0	6	Very active.
Means	60	84				

The smaller numbers of gemmas living within a foot north and south of mature mya individuals seems to support the inference that *Mya* and *Gemma* compete for food. To be sure, diminished food supply might not be the only factor that adversely affects the neighboring gemmas. Conceivably metabolic wastes expelled by *Mya* have an undesirable effect. But whatever may be the inimical factors, it seems to us reasonable, since both *Mya* and *Gemma* are filter feeders, to turn the argument around and postulate that a dense population of gemmas might have a similarly bad effect on newly set minute larval myas. The difference in size (length) between mature gemmas and minute larval myas is very nearly the same as that between mature mya and mature gemma. But the difference in body weight (soft parts), and hence the energy requirements, between the mature mya and the mature gemma is probably many times greater than the difference in body weight between the mature gemma and the minute, newly set larval mya. (Average weight fresh meat of 5 myas=38.9 gms.; average weight fresh meat 6 gemmas=0.0065 gms.; ratio 1:6000; weight of newly set larval myas is unknown but is probably much more than 0.0065 gms.÷6000). But this body weight difference may be more than offset by the close spacing of the gemmas (fig. 18) and the fact that the gemmas raise their siphons appreciably above the sediment surface while feeding. We believe it probable that the dense population of *Gemma* in the large sandy part of the flat during the past decade, or more, has been largely the cause of the vanishingly small set of *Mya* in that part of the flat. See page 332.

It may be that the sandy part of the Sagadahoc Bay flat, during the past thousand years, has been subjected to an alternation of variable external factors that favored first, *Mya* and then *Gemma*, and vice versa. Conceivably, abnormally dry summers may have favored *Gemma* and abnormally wet summers caused high mortality among its juveniles. Conceivably also, extended intervals of unusually calm weather at times of *Mya* set may have favored *Mya* whereas storminess at times of set or when the juvenile myas are quite mobile in the spring[1] would have a correspondingly adverse effect on *Mya* populations. In general, factors such as these would favor or inhibit one species without much affecting the other and vice versa.

Though we have no knowledge about *Mya's* heat tolerance it may be that abnormally warm, dry summers, or the progressive rise in mean annual temperature observed over the past few decades raises the mud temperature during the daytime low-tide intervals above the point where *Mya* can prosper. In Chesapeake Bay *Mya arenaria* lives below the low tide. Does it do so because the high summer temperatures in the intertidal zone are too unfavorable? *Gemma gemma* also lives below the low-tide zone in Chesapeake Bay. The heat tolerance of *Mya* seems to us worth investigating for if it is increased summer heat in the tidal flats of New England that is the cause of declining *Mya* populations, then no remedial measures will be effective. In the summer of 1955 we measured temperatures between 63° and 64° F. for depths of 6 to 8 inches, the depths at which large myas live. For depths of 2½ inches we measured temperatures between 66° and 67° F.

During the past few decades two additional external factors have been operating against the *Mya* population, first, man and then the green crab, *Carcinides maenas*. Young green crabs may prey also on *Gemma*. We have seen a little evidence of this in the form of chipped and broken gemma shells. Such chipped shells were found only close to the Black Rocks Islands, never out in the midsection of the flat. Today *Gemma* is in almost sole possession of the sandy part of the flat, the *Mya* population having become very small.

[1] I am indebted to John Glude of the U. S. Fish and Wildlife Service for calling my attention to the spring mass migrations of juvenile myas. Indeed, Glude and his colleagues at Boothbay Harbor, Maine, now believe that such sandy flats as make up a large part of the one in Sagadahoc Bay are more likely to acquire and sustain a *Mya* population by such mass migrations of juveniles than by direct set of spat.

Comparison of 1950, 1954, 1955, 1956 and 1957 populations

Because the bulk of the *Gemma* population is concentrated in the central part of the flat, we selected a large rectangle (see figs. 7 and 10) to use as a basis for comparing the population from year to year. This procedure is open to criticism because it takes no account of the fact that the gemmas living in the muddy sediments at the head of the bay and in Bedroom Cove, for example, are not represented. Conceivably the factors that cause fluctuations in the numbers of gemmas living in the sandy part of the flat may not operate in the muddy areas or may operate in a less decisive manner. But it is the sandy parts of the flat we are primarily concerned with rather than changes in the total population of the Sagadahoc Bay tidal flat.

In the 1950 *Gemma* census, 51 samples fell in the large rectangle; in 1954 only 29 samples fell in the same area but they were more regularly spaced. A simple comparison of the means of the numbers of gemmas counted in these two years showed that the population in 1954 was only about half what it had been in 1950. A more rigorous analysis of these data was made for us by W. C. Krumbein who found that the population in 1950 was 2.07 times that in 1954 and that the 95-percent confidence limits on the ratio of the population in 1950 to the population in 1954 were 1.81 and 2.37.

To compare the 1954 population with that found in 1955 we used the 29 samples within the large rectangle counted in 1954 and the 30 regularly spaced samples counted within the rectangle in 1955 (fig. 10). The nested and randomized samples counted in 1955 were not used for this comparison. The ratio of the means of the 1954 and 1955 counts shows that the population within the rectangle had decreased by a factor of 1.24 between the summers of 1954 and 1955,

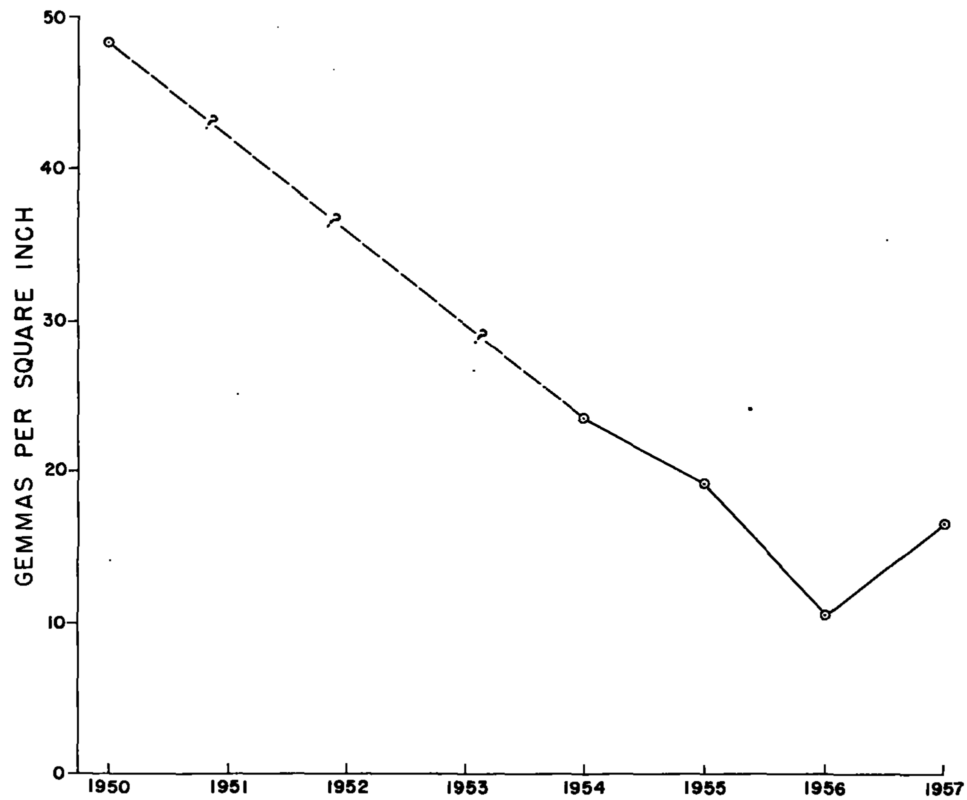

FIGURE 13.—Changes in the *Gemma* population in the interval July 1950 to July 1957.

that is, by about 20 percent. We also analyzed these data by the same procedure Krumbein used in comparing the 1950 and 1954 populations and found that the 1954 population was 1.27 times that in 1955 and that the 95-percent confidence limits on the ratio of the population in 1954 to the population in 1955 were 1.20 and 1.34.

The close correspondence found between the ratio of the means and the values found by the statistical analysis (2.0 vs. 2.07 and 1.24 vs. 1.27) suggests that for comparison of annual changes in such a population the additional effort of making a statistical analysis is not warranted.

In July 1956, the senior author again took a census of the *Gemma* population in the large rectangle laid out in 1955 (fig. 10), but this time the samples were taken at all the corners of the 175-foot squares. This gave 42 regularly spaced samples instead of the 30 taken in 1955 from the center of each of the 175-foot squares. The 1956 pattern also extends the sampling area to the full area of the large rectangle. This change in sampling pattern did not impair the comparability of the two sets of data, because it was found that the largest difference between the 1955 and 1956 counts comes in the internal part of the large rectangle rather than in the peripheral parts. One might have expected that the peripheral samples would be generally low, because the *Gemma* population is known to decrease toward the margins of the tidal flat.

The mean number of gemmas per sample (3 in. diameter, 7.06 square inches) found in these 42 samples in 1956 was only 77, which contrasts markedly with the mean number 135 found in 1955 and 346 in 1950.

From the sampling done in 1950, 1954, 1955, and 1956 it is evident that the *Gemma* population was decreasing rapidly. The *Gemma* population was 4.5 times larger in 1950 than in 1956 (fig. 13). But in July 1957 the senior author took another census of the *Gemma* population, following the 1956 pattern, and found that this downward trend had reversed. The mean number of gemmas per sample (3 in. diameter, 7.06 square inches) was 119. Only additional counts can reveal the future trend of the *Gemma* population.

The progressive and marked decline in the *Gemma* population between 1950 and 1956 may have resulted from successively larger losses of minute gemmas by winnowing-out of newly born gemmas by wave action. See page 318.

Whether this marked decline in the *Gemma* population is casually involved we do not know, but in July 1956 for the first time since the senior author started to study this flat in 1949 he found juvenile myas in the sandy part of the flat where gemmas have been most numerous in the past 8 years. These juvenile myas ranged in length from about 0.25 to about 0.75 inch (6 to 20 mm.). In 1957 he found no juvenile myas.

Total population

The total *Gemma* population in Sagadahoc Bay (summer 1954) was about 11.5 x 10^9 and was distributed as shown in the following table.

TABLE 12.—*Percentage distribution of the* Gemma *population by subdivisions of the tidal flat* (fig. 8)

Subdivision	Percent of total area (191 acres)	Percent of *Gemma* population
Upper section	23	4.9
Mid-section	51	89.5
Outer section	17	5.4
Bedroom Cove	9	0.2

The population was estimated from 146 sampling stations distributed more or less evenly over the flat as shown on the map (fig. 8), but included also the averages obtained from counts in the 9- by 9-foot squares (G–1 to G–11). In all, more than 42,000 gemmas were counted during the summer of 1954. In making this estimate it was assumed that the mean of all the observed numbers of gemmas per square inch in each of the subdivisions of the flat represented the actual average number per unit area for each subdivision. This assumption is probably more nearly valid for the midsection of the flat because of the greater number of counts made there.

ANCIENT GEMMA POPULATION

Late geologic history of the flat

One of the primary objectives of studying the Sagadahoc Bay tidal flat was to determine, if possible, its late geologic history. By this we meant the last few hundred, or few thousand years, depending upon our luck in finding evidence of successive events that we could date. During the summer of 1950, the senior author, assisted by William Fairley and Herbert Schneider, then graduate students at the University of Maine, dug more than 50 test pits in the flat to depths of 3 feet or more. The pits were distributed approximately along the long axis of the flat and along a line transverse to this axis.

In these pits we found two highly distinctive layers, which we called shell-pavement layers (fig. 15). These have been described in detail in another paper (Bradley, 1957, pp. 670–678). All that need be repeated here is the senior author's belief that these two layers, which are remarkably uniform over most of the sandy part of the flat, each probably formed as a result of an

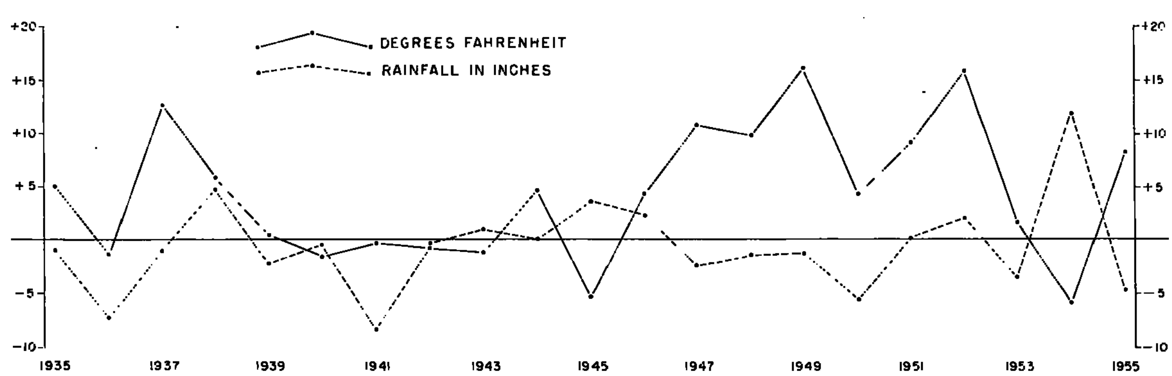

FIGURE 14.—Departures from normal mean temperatures and rainfall at Portland, Maine, for the months of May through September of each year. The values shown are the algebraic sums above or below the normal mean. Only the summer months, May through September, are shown because most of the life activities of *Gemma* occur during those months.

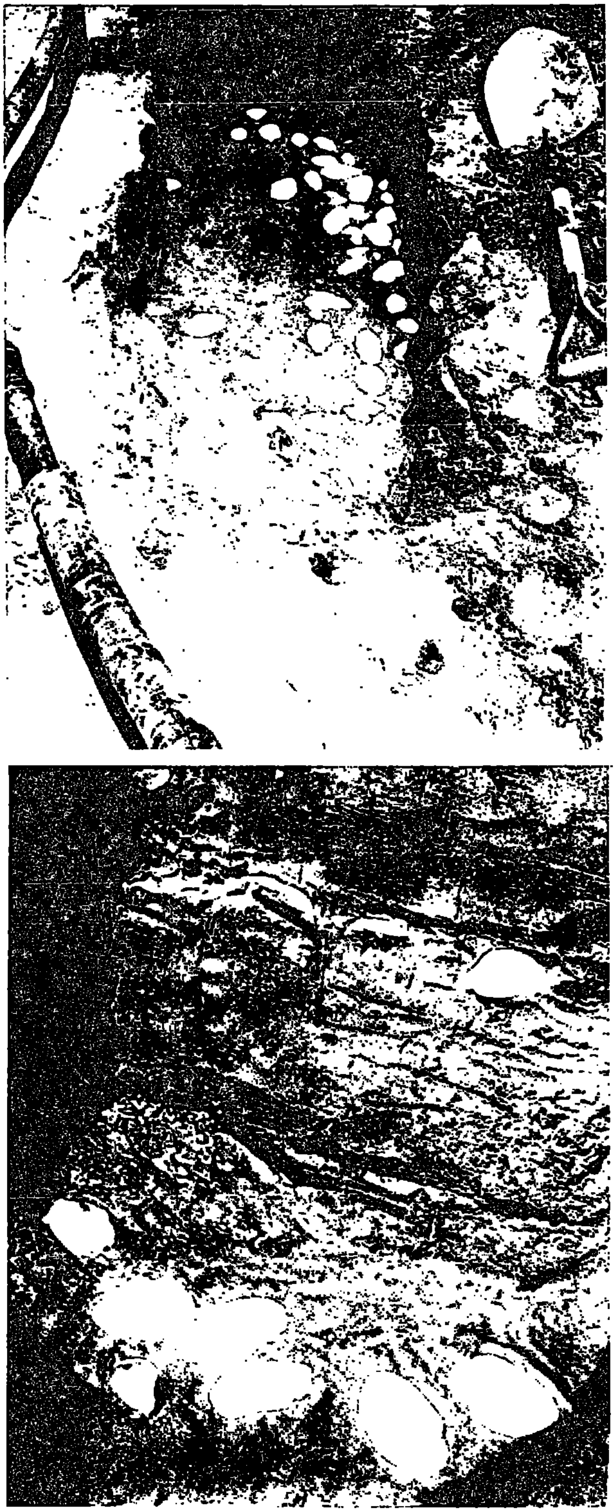

FIGURE 15.—Distribution and attitude of large *Mya* and other shells in a portion of the upper shell pavement layer (*above*); and (*below*) a section through the same shell pavement. Below that is a portion of the lower shell-pavement layer. For discussion of these shell pavement layers see text and an earlier paper by the senior author (Bradley 1956, pp. 670–678).

earthquake that happened at high tide and that jolted a layer of sand 1 or 2 feet thick into loose packing so that most of the loose stuff ran down the gentle slope into the sea. Presumably this flow followed the slumping into deep water of a large prism of submerged sand that partly filled the outer part of the bay, as it does today. Evidently the shells in this fluid sand layer and and many of the more dense mineral grains settled to the bottom where they came to rest to make the shell pavements.

Mya shells from the lower of the two layers (roughly 3 feet below the present surface) have been determined by the C^{14} method (by Meyer Rubin, U. S. Geological Survey) to be 1,050 ± 160 years old (sample W–40). After this catastrophic event the flat built up its sand surface again and new populations of *Mya*, *Gemma*, and other organisms reestablished themselves. Then, about 600 years later, a similar catastrophe occurred and the upper shell pavement was formed in the same way. This now lies 20 to 24 inches below the present surface of the flat and has a radiocarbon age of 390 ± 160 years (sample W–328) or about 400 years. After this last catastrophe the sand built up to its present level and was again repopulated. We infer, from geologic evidence, that the lower part and perhaps much of it filled in rather rapidly. Mya shells are scarce in the lower two thirds of the sandy sediment that covers the younger shell pavement layer. Nevertheless, the *Mya* population that occupied the uppermost 6- to 9-inch portion was really large and produced a rewarding commercial yield for several decades until it began to fail soon after the end of World War II. Gemma shells, on the contrary, are scattered through this layer from top to bottom. In the summer of 1955 we collected, from a depth of about one foot, a small group of mya, gemma, and gastropod shells for C^{14} age determination (sample W–329), but our laboratory report indicates that they are less than 200 years old. In other words, these shells are so young that the uncertainties of the radiocarbon dating procedure are about as large as the absolute age.

FIGURE. 16.—Piston-type core sampler in operation.

Sampling the ancient population

In the hope that the numbers and distribution of the gemma shells in the sandy sediment overlying the 400-year-old shell-pavement layer might reveal something about both the size of successive ancient *Gemma* populations and the rate at which the sediments accumulated, we took 33 core samples (summer of 1954) distributed over the sandy part of the flat and counted their contained gemma shells.

The coring device (fig. 16) was designed and built for this project and used the piston principle of Kullenberg (1947, pp. 1–46). The apparatus was designed to take cores 22 inches long and 1½ inches in diameter. Because of one difficulty or another the first several cores taken were short, but 20 of the 33 cores had lengths ranging between 17 and 22 inches. The locations of these are shown on the map (fig. 3), and the discussion in following paragraphs is based wholly on data obtained from these 20 cores.

During the coring operation, portions of the core were extruded an inch at a time. Each such portion was wet-sieved through a 20-mesh screen to remove the sand, and then gemma shells were counted. Gemma shells are so constructed that the valves tend to hold together after death and many were found thus in the cores. Paired valves were, of course, counted as one individual but we also counted all the complete or nearly complete single valves. In reckoning the total number of once-living individuals, we divided the total number of single valves in each sample by 2, thereby arbitrarily pairing them. To this number we added the number of naturally paired valves. No attempt was made to evaluate shell fragments but this introduced no significant error because, with the exception of one sample, shell fragments were uncommon. This procedure in reckoning the total number of once-living gemmas seems to be warranted by the remarkably close proportionality of naturally paired ancient shells to the numbers of accompanying single valves, which we paired arbitrarily (fig. 17). This proportionality held through all the cores.

The numbers of living gemmas were counted separately in the top inch of each core.

The abrupt and locally large changes in numbers of ancient gemma shells with depth in the cores (fig. 17) suggest that it would be relatively easy to correlate the layers of abundance from one core to another. This proved to be wholly illusory, and we were forced to conclude that the peaks of abundance represent small lenticular accumulations of shells and that these lentils have a random distribution. The only systematic relation we could find was that in those parts of the flat where gemmas are abundant today they were also abundant during the past 400 years.

Being unable to correlate layers of ancient gemma shells from core to core we cannot say, for example, that there were recurrent episodes during which the *Gemma* population flourished and was of such and such a magnitude with respect to the current population. We may infer, by analogy with the living populations, that the past populations, fluctuated, but we can furnish no proof.

Comparison of ancient and living populations

We do have a means, nevertheless, of determining with some assurance that the *Gemma* population of 1954 was greater than the mean ancient *Gemma* population that inhabited the flat during the past 400 years. We know, surely, that the *Gemma* shells we found in the cores are the actual accumulation of the past 400 years or so, the resultant of a long *Gemma* succession and of whatever factors operated during that long interval to destroy, or remove, gemma shells. We know from many repeated observations and counts that, on the average, living gemmas are 3.9 times as abundant as contemporary dead shells (reckoned as above). This means that about two-thirds of the shells are removed from the area of the flat wherein they grew. Waves and wave-generated currents move most of them landward up the flat but during large storms large numbers move seaward beyond the low-tide zone. As we have no reason to believe that this same winnowing did not go on in the past and at essentially the same rate, we feel reasonably safe in concluding that the ancient shells we find in the cores represent, on the average, roughly one-third of the ancient population.

To compare this ancient population, whose shells accumulated over about 400 years, with the living population, we can assume that the living *Gemma* population (1954) persisted unchanged in time for 400 years and calculate how many shells that hypothetical, and constant, population would be expected to have left. In making this calculation we let the 22-inch cores equal the full 400 years. But not all the cores were 22 inches long; they ranged from 22 to 17 inches. So for each inch less than 22 we reduced the time equivalence of each shorter core by 1/22 x 400. This is open to question because it assumes a uniform rate of accumulation of the sand, which we do not know to be true. Nevertheless, it seemed better to make some adjustment for the shorter cores, and it results in minimum estimates of the numbers of shells to be expected. We then took the number of living gemmas per cross sectional area of the core found at and close by the top of each core, divided by 2.2, the life expectancy of the gemmas, multiplied this by the number of years the core represents, and divided the result by 3.9, which is the average number of times greater the living population is than the associated dead shells (table 13). These values should be, within the limits of our knowledge, directly comparable with the total number of dead shells (ancient and modern) found in each core.

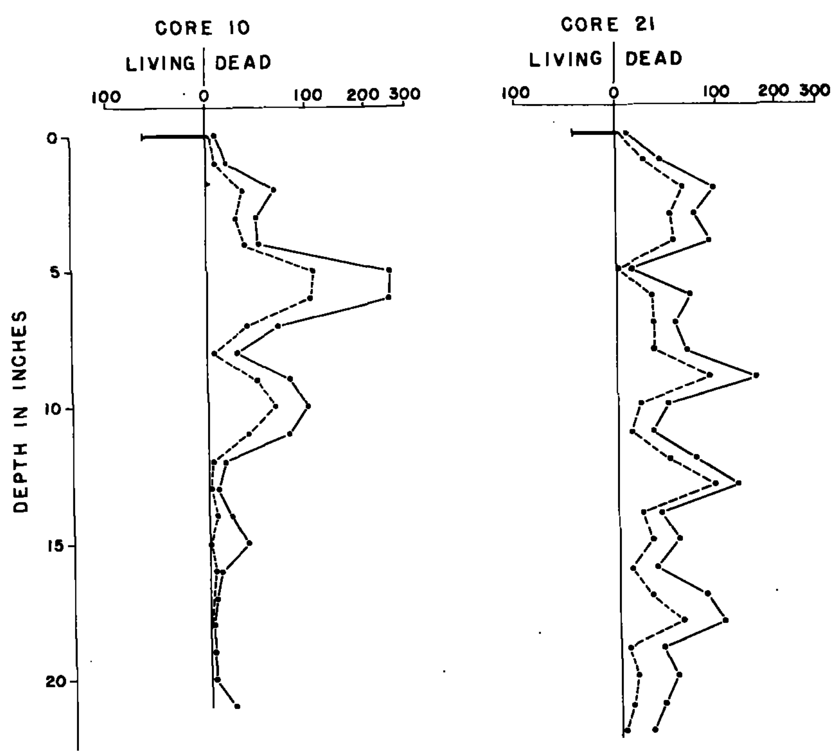

FIGURE 17.—Number and distribution of dead gemmas in two cores and the number of living gemmas at the top of each core. Dotted lines indicate complete gemma shells with both valves in place; solid lines indicate total number of dead gemmas; i. e., naturally paired valves plus all single valves arbitrarily paired.

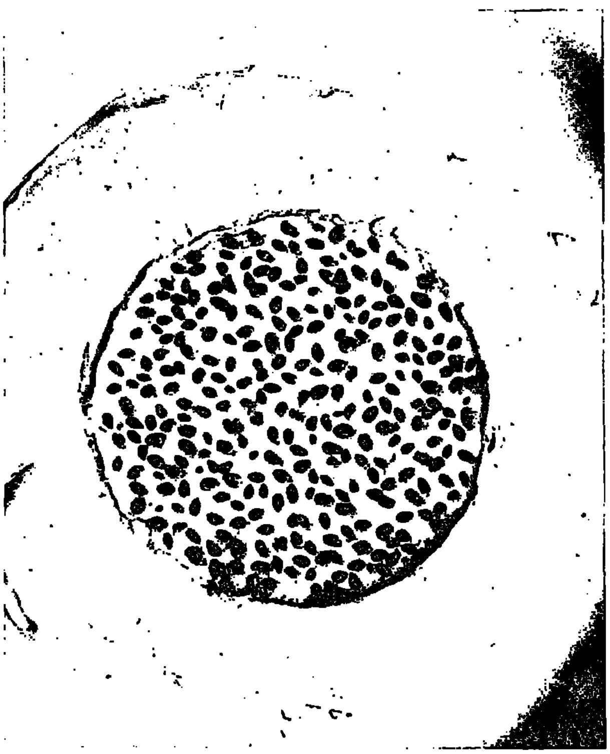

FIGURE 18.—About 200 gemmas, mostly mature, screened from one sample 3 inches in diameter (7.06 square inches) and mounted in putty within a ring 3 inches in diameter. They are mounted in feeding position and, though arbitrarily distributed rather uniformly, give a good idea of what the sandy bottom of Sagadahoc Bay looks like where the *Gemma* population averages 28 to the square inch.

The ratios of expected shells to the numbers actually found differ through a wide range. This was expected from the spotty pattern (modified reproductive) of the living gemmas, the spotty vertical distribution of the dead gemma shells, and the small cross section (1.76 square inches) of the cores that sampled both. The numbers used for the living gemmas, however, are somewhat better representations of the living population because they are the means of the number found in the top of each core and the number found in a sample 3 inches in diameter taken close by and at the time the core was taken. Because of the variables in these factors, and the relatively small number of cores, we are inclined to believe that only the mean of all 20 ratios (2.0) is likely to be significant. It indicates that the 1954 population was about twice as large as the average population over the past 400 years. Actually this factor 2 is probably

TABLE 13.—*Comparison of ancient Gemma shells, D, with the number, E, to be expected from projecting the 1954 living population (held constant) back over 400 years*

[The projection is made in accordance with the formula $E = T\left(\frac{n}{2.2}\right)/3.9$ where n is the number of live gemmas per area of the core barrel found at, and close by, the top of each core; 2.2 is the life expectancy of the gemmas; T is thespan of years represented by each core; and 3.9 the ratio of living to dead gemmas found on the flat today.]

Core Number	n	D	E	$\frac{E}{D}$
10	52	1,087	2,300	2.30
11	35	1,257	1,480	1.18
12	96	884	4,065	4.60
16	72	722	3,360	4.66
17	79	907	3,180	3.50
18	56	1,247	2,470	1.98
19	49	836	2,285	2.74
20	15	1,206	665	.55
21	21	1,290	980	.76
22	40	1,156	1,865	1.61
23	28	449	1,130	2.52
24	21	802	760	.95
25	16	227	645	2.84
26	23	840	970	1.15
27	18	406	725	1.79
28	14	339	565	1.64
29	3	120	115	.96
30	31	813	1,185	1.46
31	29	913	1,225	1.34
32	25	519	1,008	1.94
Mean Ratio				2.02

a minimum figure because the number of dead shells found in the whole 400-year column of sediment was used in the calculations and certainly this includes a definite, but unknown, number of dead shells from the *Gemma* population of the past decade. The intensive work of the clam diggers alone would have ensured this, but, in addition, there have been several hurricanes in the past decade and at least one very large winter storm (Feb. 1952) that blanketed the flat with a layer of new sand, which ranged from a fraction of an inch thick at the extreme northern (landward) end of the flat to more than a foot thick in the low-tide zone.

If the 1950 *Gemma* population had been used for the comparison, the mean ratio would have been approximately 4, because the 1950 *Gemma* population was twice as large as that of 1954. If the 1956 population were used, the ratio would be only about 0.9.

CONCLUSIONS AND RECOMMENDATIONS

Our study of the past and present *Gemma* populations in the Sagadahoc Bay tidal flat show that *Gemma gemma* and *Mya arenaria* have occupied the flat jointly for at least 1,000 years. Our interpretation of the subsurface evidence indicates that twice during this 1,000-year interval the *Mya* and

Gemma populations were removed catastrophically from most of the sandy part of the flat and that the two populations each time reestablished themselves. We infer, but cannot prove, that during this long interval various external factors such as storminess or protracted calms and summer drought or summer rains, or overcrowding, and the increase or decrease in numbers of predators, may have alternately favored or inhibited one species or the other. We assume that both species of clams are nourished by the same kinds of organic substances, living or not, that are brought to them suspended (or perhaps even dissolved like sugars and amino acids, Lucas 1955, pp. 142–145) in the water that flows over them. Research is needed to determine whether this assumption is valid.

We have shown by analyzing the population densities of gemmas in the immediate vicinity of mature mya individuals (pp. 323–25) that the myas exert some sort of unfavorable effect on the gemmas; either depriving them of food or in some other way creating an unfavorable environment. Other field evidence seems to support our findings of incompatibility between the 2 species.

On the Little River flat, which is just east of Sagadahoc Bay (fig. 1), casual examination showed that there is a marked inverse relation between the abundance of *Gemma* and the abundance of *Mya*.

Observations made during the summer of 1950 suggest that *Gemma*, when present in great abundance, may create an environment that is unfavorable to even mature myas. During that summer we dug more than 50 pits and, as these pits were 2 feet or more in diameter and a few were trenches several feet long, we had an opportunity to see a fair sample of the *Mya* population, particularly in the sandy part of the flat. Before the summer was over, we became impressed with the number of myas that had recently died or were in such a weakened condition that they could not retract their siphons, which hung down limply. These dead, dying, and abnormally weak clams were in the sandy part of the flat where they had once been numerous but where, at that time, gemmas were extraordinarily abundant, up to 190 per square inch in one place.

The *Gemma* population that summer was, on the average, twice as dense as it was in the summer of 1954 and 4.5 times as dense as in 1956. It may have been only coincidence, but this was near the middle of a series of abnormally warm and dry summers (fig. 14). We have inferred that warm dry summers favor *Gemma* because Sullivan (1948, p. 3) has shown that juvenile gemmas are killed rather quickly by fresh water. Heavy rains at low tide flood the flat with fresh or nearly fresh water, which stands for several hours in the troughs between sand ripples. We must not, of course, ignore the possibility that the same series of abnormally warm, dry summers may have had an adverse effect on the myas, either through elevated temperature directly or perhaps indirectly through increased metabolic rates and essentially fixed food supply. Research is needed on the tolerance of *Mya* for moderately elevated temperatures applied intermittently (i. e. tidal cycles). If *Mya* is adversely affected by such elevated temperatures, their moribund condition may have been independent of the presence of an extraordinary abundance of gemmas. An undetected disease of the myas might also have accounted for their lack of vitality.

After witnessing this unusual *Mya* mortality and knowing that the *Mya* population has gone through a marked decline, one wonders whether the decrease in density of the population has gone below a critical value, which alone might have raised the death rate, as it did in the *Drosophila* population that Pearl and his associates (1927, pp. 293, 316) studied.

Other observations on the Sagadahoc Bay flat reinforce our belief that *Gemma* and *Mya* tend to be incompatible. During the seven summers, 1949–55, we found no new set of *Mya* juveniles on the sandy part of the flat except (and we believe this is significant) in a few well-drained areas where *Gemma* is absent or extremely rare. But in July 1956 a small number of juvenile myas (6 to 20 mm. long) were found in the sandy part of the flat where gemmas have been most numerous. This may be significant in view of the fact that the *Gemma* population in 1956 was less than a quarter of what it was in 1950 (fig. 13). Plankton studies carried on by the biologists of the U. S. Fish and Wildlife Service during these years showed that the waters of Sagadahoc Bay contained about the expected abundance of *Mya* larvae throughout the summer. Moreover, new sets of *Mya* have continued during these years in the muddy parts of Sagadahoc Bay where the *Gemma* population is sparse, although, according to the U. S. Fish and Wildlife biologists the total *Mya* population, even in the muddy areas, has continued to decline with the years.

We believe that the balance between these two species has been seriously upset by the greatly intensified digging for *Mya* during, and for several years after, World War II and, to a much lesser extent, by increased depredations on the *Mya* population by the mounting numbers of the green crab *Carcinides*. Both factors have tended to deplete the *Mya* population and permit rapid growth of the *Gemma* population.

Our inquiry has led to several inferences and suggestions but few conclusive results. This must be so until more research is undertaken—mostly in the laboratory. The principal deficiency in our knowledge is the food of both *Gemma gemma* and *Mya arenaria*, not only the specific kinds but the amounts that each require. It is desirable also to know whether the kinds of food differ with the ages of these two clams. A promising line of inquiry would be to explore the reactions of each species to the metabolic wastes of the other. These wastes may contain substances that are inimical to the welfare of potentially competitive species. Only when we understand these things can we say in what ways *Gemma* and *Mya* tend to be incompatible with one another. The marked decline in the *Gemma* population from 1950 to 1956 suggests the possibility that the gemmas may cyclically increase in numbers, become overcrowded, and then decrease in numbers, thereby providing first unfavorable summers for the set and growth of *Mya* spat and then a series of summers that are more favorable. Progressive loss of minute gemmas by wave action may, as noted earlier in this paper, have caused the present decline of the *Gemma* population. Significant decrease in the numbers of gemmas, regardless of cause, will according to our view increase the capacity of the sandy part of the flat to support a larger clam population, either *Gemma* or *Mya*. If the *Gemma* population becomes very small, say less than half of the 1956 density, it will be interesting indeed to see whether *Mya* or *Gemma* first succeeds in taking advantage of the newly enlarged capacity.

Another subject that perhaps warrants investigation is the heat tolerances of both *Gemma* and *Mya* in both early juvenile and mature stages of growth. Our reasons for suggesting that heat may be a critical factor is that the climate has been growing progressively warmer and the fact that for a time, while the *Mya* population was falling off most conspicuously, we had in New England a succession of abnormally warm, dry summers. Then there is the fact that farther south, in Chesapeake Bay, both these clams live below the low-tide zone, but whether or not high summer heat determines this is unknown to us.

If heat is a critical factor one might expect its effect to be most telling during summer daylight low tides. We found that the flat absorbs considerable heat from the sun and sky and that appreciable amounts of heat are conducted in a few hours to depths of 6 to 8 inches where mature myas live.

The heat tolerances of such mollusks, at various stages of growth, should be readily determinable in any well-equipped marine laboratory. If the secular warming of the climate accounts in any significant degree for the decreasing *Mya* population of New England then remedial measures are, of course, futile.

We recommend that research on the food, temperature tolerances, and metabolic wastes of both *Gemma* and *Mya* be undertaken to gain a better understanding of the fundamentals involved. Once the dominant foods are determined, some effort should be made to appraise the amounts contained in the waters that flow over the surface of the flat. The current velocities of these bottom waters are already known in Sagadahoc Bay. If we knew the kinds and amounts of foods used, a good estimate of the carrying capacity of the bay could be made. We also recommend that a census of both *Gemma* and *Mya* be continued for a few more summers to test the suggestion that the present decline in the *Gemma* population may provide optimum opportunity for a natural set and growth of *Mya* spat in the sandy part of this flat.

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