MOVEMENTS OF MICHIGAN HERRING GULLS

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By

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AN ABSTRACT

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ABSTRACT

The 1143 recoveries from 37,414 Herring Gulls banded as juveniles in colonies in the Great Lakes by Claud C. Ludwig and his two sons are analyzed. Details of the dispersal are presented on five maps, seven graphs, and four tables.

Dispersal begins in late summer and early autumn. There is great individual variations in the distances flown, but generally speaking second-year and older birds tend to remain within 300 miles of the colonies, while first-year birds show much greater variation and may travel much farther. Most movements take place along the Great Lakes-St. Lawrence system, the Atlantic seaboard, and the Mississippi River system, although there is a possible northward component. Autumn movement shows a decided eastward tendency and is followed by a southward shift, mainly of first-year birds, to Florida or the Gulf of Mexico. Waterways and coasts are followed, apparently because they provide a source of food and of upward air currents used in soaring. The correspondence between the pattern of prevailing winds and the seasonal and directional movements of the gulls is noted, and several cases of the use of wind by soaring and non-soaring birds in migration are cited in support of the proposal that wind is a major factor in controlling the direction of Herring Gull dispersal.

A comparison of the data in this paper with other published banding studies of the Herring Gull in North America, and with accounts of the movement of the species in Europe, reveals essentially similar habits

of wandering throughout. Related Larus species also tend to disperse and wander with considerable intraspecific variation, and fixed migration patterns are, on the whole, not well-developed.

Causes of mortality are listed in so far as they are recorded by the persons submitting the recovery reports. Mortality is highest among first-year birds.

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INTRODUCTION

Since July 1931 Mr. Claud C. Ludwig of 279 Durand Street, East Lansing, Michigan, and his two sons, Dr. Frederick E. and Dr. Claud A., (and sometimes a small crew of helpers) have banded a total of 37,414 juvenile Herring Gulls, Larus argentatus Pontoppidan, in 17 Michigan colonies. Mr. Ludwig recently has made his carefully kept records of this work available to Dr. George J. Wallace of the Department of Zoology, Michigan State University, for analysis by a student. This report is that analysis. Sincere thanks are due to Mr. Ludwig for supplying these data, and for his patient help in answering my queries about the field work in which I had no part. The nearly one hundred and five thousand birds of many species banded by the Ludwig team stand as a truly remarkable tribute to the service these men have done ornithology. To Dr. Wallace I should also like to express my gratitude for his constant advice, suggestions, and careful criticism during both the analysis and literature-search that preceded the writing of this report and the period of writing itself. Dr. P. J. Clark, also of the Department of Zoology, has instructed me on the use of the contingency chi-square method and helped in its application to the data.

The banded gulls have to date yielded some 1,143 recoveries, not including those young birds recovered on or within a few miles of the colonies shortly after being banded. The high mortality of juvenile Herring Gulls still in the colony is too well known to require

discussion here; and the inclusion of such recoveries would obviously tell us nothing new concerning the species' life history, but rather would serve only to distort our picture of its movements. These 1,143 recoveries, representing 3.06% of the birds banded, provide a large sample from which has emerged a clear picture of the seasonal distribution of Michigan-born Herring Gulls. Other banding studies of this species in North America and Europe have been published and will be referred to below, along with studies on closely related Larus species for comparison.

Location of Colonies

The banding was done in 17 colonies. The nine in Lake Huron, from north to south, are as follows: St. Martin Shoals, off St. Martin Bay, Upper Peninsula, about 8 miles north-northeast of St. Ignace; Goose Island, about 10 miles to the east off Marquette Island; Thunder Bay Island, Sugar Island, Gull Island, Sulphur Island, and Scarecrow, in Thunder Bay or just off North Point by Alpena; Black River Island a mile and a half off Black River 17 miles south of Alpena; and Little Charity Island in Saginaw Bay, 32 miles northeast of Bay City. On these nine Lake Huron colonies 20,468 gulls, 54.71% of the total, were banded. On the seven Lake Michigan Islands 16,791 gulls, 44.88% of the total, were banded. Four of these islands, Gull, Pizmire, Hatt, and Shoe, are in the Beaver Island group, Gull and Pizmire lying to the west of Beaver Island beyond High Island, and Hatt and Shoe lying north and a bit east above Garden and Hog Islands. Bellow Island is in the

mouth of Grand Traverse Bay north of Traverse City, and Green Island lies in the western Straits of Mackinac, about 6 miles northwest of Mackinaw City. There remains Grass Island, a low island in the Beaver group on which only five gulls were banded, and none of these five has been recovered. In Lake Superior the Ludwigs banded only on Round Island, just east of Brimley at the head of St. Mary's River and only 155 birds in one year, 0.41% of the total.

Table 1 shows the number of gulls banded each year in each colony, and the total number banded in each colony in the 24 years. No banding was done from 1943 to 1945 inclusive. Fig. 1 shows the locations of colonies or groups of colonies except for Round Island from which there has been only five recoveries.

MOVEMENTS

Five maps (Figs. 1 to 5) show the distribution of the 1,143 recoveries. In some ways it might have been preferrable to present this material as a unit and to use only one map for each of the three age groups recognized. The large number of recoveries, however, could not have been properly represented on the small scale this would have required. Accordingly, these age groups are presented separately only on those three maps showing the United States (except Maine), Ontario and part of Quebec. All recoveries from eastern Quebec, the Atlantic Provinces and Maine are shown together on one map, and all recoveries from south of the United States on another. The areas in which groups of colonies or single colonies are located are marked on the maps of the United States, but no attempt has been made to indicate each colony in a group as I felt the desirability of using a large symbol for place of origin outweighed any advantage the alternative might have. A centre of origin to which to relate the linear distance flown has been chosen and is indicated.

The advisability of dividing the data into age groups was recognized after completing a preliminary plotting, and the groups were chosen in accordance with their correlation with obvious distributional tendencies (see Table 2). These groups, then, are as follows:

1) birds recovered between the time of banding and December 31st of their first year, except, as noted above, those recovered on or within a few miles of the colonies shortly after being banded,

2) birds recovered in the six-month period between December 31st of their first year and the following June 30th,

3) all birds over one year old. These have been indicated on the map by figures showing the year of life in which each was recovered. In some cases the group of birds in their second year will be mentioned separately.

Of the 1,143 recoveries, 724 or 63.34% were of first-year birds. To be more specific, 42.16% of the total was of birds recovered before December 31st of their first year, and 21.2% between December 31st and June 30th. Thus some 419 birds, or 36.6%, were recovered subsequent to their first year, and of these 32.2% (135 or 11.8% of the 1,143) were second-year birds. The high mortality of first year birds, particularly up to December 31st, will be discussed below.

Michigan Recoveries

The home state of Michigan yielded 425, or 37.18% of all recoveries. About half, 50.35%, were first year birds. If we analyze the Michigan recoveries by month we see that many Herring Gulls leave in

Month	J	F	M	A	M	J	J	A	S	O	N	D
Percent of the Michigan recoveries	2.9	2.7	2.2	2.8	7.6	9.3	9.8	20.2	13.3	11.9	11.9	5.2

December and some at least return at the end of April, although many over-winter in the state. Certainly part of the reason for the larger number of summer returns is that more people frequent beaches then, and from July on we must further consider the appearance of young of the year, among which mortality is high. This latter point may be

demonstrated by dividing the percentage of the recoveries in each month into two categories, percentage of first year birds and percentage of older birds:

Month	J	F	M	A	M	J	J	A	S	O	N	D
Percent of recoveries (1st year)	1.9	1.0	1.0	1.4	2.4	0.0	1.7	10.7	10.2	8.6	7.6	3.1
Percent of recoveries (older)	1.0	1.7	1.2	1.4	5.2	9.3	8.1	9.5	3.1	3.3	4.3	2.1

This does show a heavy mortality of young in August, September, October and November, and indicates either that this rate of mortality drops quickly by December or that the young birds scatter out of Michigan. The maps show the latter to be at least partly the case, and probably both causes are operative. Considerably more adults than first-year birds appear to winter in home waters. The increased number of recoveries of adults in June, July and August may largely reflect the distribution of people who find the gulls.

Twenty birds banded in the colonies were recovered there in later years as shown below. Note that 13 of the returns were of fully mature

Colony Where Banded	Recovered in Same Colony	Recovered in Another Colony (Ages and colony of recovery in brackets)
Hatt	1 (1)	
Gull (L. Huron)	1 (7)	2 (2, Bl. River; 10, Sulphur)
Pizmire	2 (6,9)	2 (4,4, both at Gull, L. Mich.)
Green	1 (11)	
Scarecrow		2 (1,1,both at Bl. River)
Black River	5 (2,1,5,4,3)	1 (4, Little Charity)
St. Martin Shoals		2 (12, Sugar; 15, Bl. River)
Bellow	1 (19)	
	11	9

birds, four years or older. If the birds recovered were breeding, then there is at least some exchange between colonies, although perhaps not much between lakes. This is further shown by two birds recovered by the Ludwigs but not banded by them: one banded by A. D. Trempe in 1932 at Hatt Island and found dead in 1940 on Black River Island, and one banded by W. I. Lyon in 1932 on Big Gull Island, Lake Michigan, and recovered in 1938 on Sugar Island, Lake Huron. The list also shows some return to the colony of birth, and this is further substantiated by a bird banded by W. I. Lyon in 1935 on Green Island and recovered there in 1936 by the Ludwigs.

Linear Distances of Recoveries from Colonies

To examine the distances at which recoveries were obtained I have drawn circles of 300,500, 1000, and 1500 miles radii from the center point. Below are listed the numbers and percentages of the total of recoveries within each circle.

	First-Year Birds Until Jan. 1st.		First-Year Birds Jan. 1st to June 30th		Total, First-Year Birds	
	No.	Percent	No.	Percent	No.	Percent
Within 300 miles	359	31.4	77	6.7	436	38.1
300-500	53	4.6	26	2.3	79	6.9
500-1000	61	5.3	43	3.8	104	9.1
1000-1500	7	0.6	56	4.9	69	5.5
Over 1500	2	0.2	40	3.5	48	3.7

	Second-Year and Older		Second-Year Birds		Third-Year and Older		Grand Total
	No.	Percent	No.	Percent	No.	Percent	
Within 300 miles	345	30.2	79	6.9	266	23.3	781
300-500	43	3.8	17	1.5	26	2.3	122
500-1000	19	1.7	14	1.2	5	0.4	123
1000-1500	6	0.5	3	0.3	3	0.3	69
Over 1500	6	0.5	5	0.4	1	0.1	48

Obviously first-year birds, particularly in the period between January 1st and June 30th, fly farther than older birds. This is in agreement with the calculations made by Gross (1940) for mean distances flown by different age groups of Herring Gulls from colonies both in the Great Lakes and at Kent Island, New Brunswick.

Dispersal Pattern

Recoveries were most frequent from the shores of the Great Lakes, in particular Michigan, Huron and Erie with considerable, however, from Lake Ontario, and relatively few from Lake Superior. Most Michigan recoveries were from the lake shores, and the remainder almost all from river systems. Out-of-state recoveries fall into two categories, both well-represented:

1) the Mississippi River and its tributary system accounting for virtually all of the inland records west of the eastern mountains,
2) the sea-coasts, including:
    a) the Atlantic coast and the rivers leading to it, as well as the coasts of Cuba and the Bahamas, and
    b) along the coast of the Gulf of Mexico, including Nicaragua and Honduras. Of the 38 records, exclusive of the West Indies, from south of the United States only one from Monterrey, Mexico, was any appreciable distance inland (although one from the West coast of Mexico represents a bird that had crossed that country,

perhaps at the Isthmus of Tehuantepec in the company of such other soaring coastal species as the Magnificent Frigate Bird, Fregata magnificens Mathews, which Dalquest [1951] observed over the Isthmus).

Exactly how the gulls reach the Atlantic coast cannot be determined from the recoveries, but probable routes can be shown. Of the 57 recoveries in this group (West Indies excluded; the St. Lawrence River below Father Point included), five on the mainland could not be located from the data available. Of the other 52, 39 were on or near the coast, or on islands, such as Newfoundland, off the coast. Sixteen in the Gulf of St. Lawrence area show this river to be a main artery to the coast. The remaining 11 were on rivers flowing to the coast south of the St. Lawrence. Four on the upper Hudson may indicate another link between the Great Lakes-St. Lawrence system and the coast, a possibility considered below. There are six records from rivers in Georgia, the Carolinas, Virginia and Pennsylvania, and one from very near the St. John River in Maine. These could represent birds that have flown overland to these rivers, as Gross (1940) believes, or birds that have been on the coast and followed these rivers upstream. In view of the fact that inland recoveries away from major river systems are practically nonexistent, and considering that mountain barriers lay in the paths of these seven gulls, the second alternative appears more likely. The Bonaparte's Gull, Larus philadelphia (Ord), a bird perhaps more accustomed to forests than the Michigan Herring Gulls of the Great Lakes, has been observed by Brooks (1952) to fly over the Alleghenies

but he does not mention the Herring Gull. If the Herring Gull does not usually cross the mountains, then access to the Atlantic coast is primarily by way of the St. Lawrence and, perhaps, the Hudson Rivers.

A similar explanation might well be valid for the five recoveries of birds on rivers which are not tributaries of the Mississippi but which do flow into the Gulf of Mexico. In these cases, however, the headwaters of the rivers concerned are all very near tributaries of the great river, and there are no mountainous barriers involved.

Use of Waterways and Coasts

That Herring Gull movements should be confined to waterways is not surprising, since their food (Bent, 1921, Mendall, 1939, Otterlind, 1948, Pimlott, 1952, Spärk, 1951, Witherby, et al., 1941, give the most comprehensive accounts) is primarily found in or near water. Herring Gulls are omnivorous, however, and could presumably travel overland, feeding primarily on insects and vegetable matter, and even refuse at garbage dumps. That they do not appear to do this may be traceable to certain other inducements that rivers and coasts hold for them.

The Herring Gull is a soaring bird, in fact such an accomplished soaring bird that it has been met with by aircraft at heights up to 3500 feet (Ingram, 1919, and further observations by Mitchell, 1955, and Woodcock, 1942, the latter not concerned with aircraft). When travelling it prefers to make use of up-currents of air (Tinbergen, 1953), and, indeed, will often not travel when it cannot soar—Woodcock (1940,1942) reports that Herring Gulls are not seen 100 miles or more at sea off the east coast until the autumn when cold continental air

flows out over the warm sea and creates thermal conditions. A movement of any distance is undoubtedly facilitated by up-currents, for Griffin (1943), while conducting a homing experiment with 176 Massachusetts Herring Gulls, found that rapid homing was favoured by unstable air and strong updrafts to permit soaring.

Forster (1955) has examined the use by birds of ascending air currents of two origins:

1) those due to the effects of wind blowing up a slope or rise in the ground (slope currents and wave currents), and

2) those due to the effects of air being heated (thermal currents).

He suggests that "birds will tend to follow slope and thermal up-current lanes," and that "the use of up-currents partly accounts for the tendency to drift with the wind during migration," so that suitable thermal and drift conditions could combine to be an aid to covering distance. I shall examine the problem of drift below, but should first like to speculate on the use of up-currents by travelling Herring Gulls. During the day a gull could find not only thermal currents over beaches and shores, but also slope currents created by wind on the banks or dunes and would thus have an up-current lane beside most large waterways. Further, due to the high thermal capacity of water there would be, once the air was colder than the water, a thermal effect over all unfrozen rivers and lakes, as well as over the sea as mentioned by Woodcock (1940,1942). McMillan (1938) states that a quartering wind on a seacoast will create a surf that will give both lift (Forster's "wave currents") and direction, and this would presumably be the case

on the Great Lakes as well. If, then, the Herring Gull does follow up-current lanes because it is a soaring bird, rivers and coasts would provide another inducement, besides food, to travel along them. In support of the notion that the gulls would follow such lanes I might cite a few instances of this in other species.

In the Suez region thermal activity in the atmosphere is marked. Goodwin (1949) tells of from less than 1,000 to 4,500 birds of prey a day for seven days in October all using thermal migration. MacKintosh (1949) writes of the same phenomenon in which he says tens of thousands of Accipiters pass over Suez in the autumn. The hawks are careful to avoid crossing the Gulf over which they would have to flap, probably because they have low food reserves, but storks, herons, and pelicans which also migrate on the thermals do use flapping flight to cross the water. At the western end of the Mediterranean area Moreau (1953) found that soaring birds would converge at the Straits of Gibraltar to make the water crossing (which would be without the aid of thermals) as short as possible. He felt that the coastline guided them to the Straits.

In southern Sweden Rudebeck (1951) has observed a "very close correlation" between weather conditions suitable for soaring and the migration of several species of hawks, "particularly those species which are most inclined for soaring." In an earlier paper (Rudebeck, 1950) he stated that these hawks allow themselves to drift within the limits of the leading lines provided by the coasts of Sweden and Denmark. Thomson (1953) calls the tendency to be deflected by topographical features which act as "leading lines" an intrinsic factor of orientation which

is probably a reaction to a barrier between a favourable and an unfavourable habitat. This, then, is an example of a group which combines migration by soaring with the following of leading lines. Brown (1939) noted that hawks passing over Hawk Mountain, Pennsylvania, in the autumn flight coast on the up-currents of air caused by wind striking the flanks of the mountain.

The Factor of Prevailing Winds

From the maps showing first-year birds it can be seen that recoveries in the autumn and early winter tend to be from the east, northeast and north, whereas winter and spring recoveries are from the south and west. Although the over-all dispersal pattern seems to include all points of the compass, few birds travel far before January that do not go east. It is probably more than coincidence that the prevailing winds at this season are from the southwest.

To be more precise, in August the prevailing wind is west over Lake Superior and southwest down the Great Lakes-St. Lawrence system. In September and October it is similar with a north to northwest tendency down the East coast which continues at least into February—although with frequent westerly components. In December, however, there is a shift to northwest across the Great Lakes, northerly components are frequent down the Mississippi, while the prevailing wind on the Gulf of Mexico coast is north or northeasterly and remains so through February. The January winds of the southern Great Lakes tend to be west or southwest, a condition which is common both winter and summer,

but which may give way to northwesterlies particularly in the spring. In March the winds on the Gulf of Mexico, including the Mexican coast, become south to southeast but remain the usual northeast over Yucatan, Central America, Cuba and the Bahamas. By April there is a good degree of southerly flow up the Mississippi and up the East coast (Kendrew, 1953; Baker, 1936; Bartholomew et al., 1899, and Climatological Data, U. S. Department of Commerce Weather Bureau).

This pattern fits, in general, the seasonal movements of Michigan Herring Gulls rather well. The possible use of the Hudson as a lane to the coast may be further considered here as recoveries are fewer than might be expected if it were used to any extent. It may be that it does not get much use for the prevailing autumn winds are upstream from the south, both at the surface (Baker, 1936) and at an altitude of 500 metres (U. S. Department of Commerce, Weather Bureau, 1941).

I have already mentioned Forster's (1955) statement that "the use of up-currents partly accounts for the tendency to drift with the wind during migration." For some reason, though, early accounts such as Cooke (1910,1913a), and even Thomson (1936) and Allen and Peterson (1936), considered that wind is not important, other than accidently, as a determining factor in migration. This attitude was long lodged in the literature. That wind is important to birds using thermal migration has been attested to by MacKintosh (1949) who noted that migrant Accipiters in the autumn may find themselves considerably south of Suez on the wrong side of the Gulf and have to turn north to Suez to avoid flapping over water. He attributed this southward drift to the fact

that the prevailing north wind of the autumn season carries the birds south with the thermals themselves. Regarding Herring Gulls, Griffin (1943) in his homing experiments noted that rapid homing was favoured not only by strong updrafts and good visibility, but moderate to fresh "favorable winds."

That winds do cause birds to go far out of their intended way has been long known, but has been thought to be a relatively rare tragedy when it occurred on a large scale, as in the case, for instance, of the wind of an unseasonal anticyclonic pressure system in the spring of 1948 that carried thousands of Redwings, Turdus musicus L., to Britain and to their deaths in a snow storm (Suffern, 1949). The unsuspected enormity of unintentional wind drift has now been realized by Williamson (1952), however, who believes that "such passage migration as we encounter over the greater part of Britain is largely due to. . . . . displacement by easterly winds from their [the birds'] Continental coastal 'guiding lines' between Skaggerak and northern France." These migrants are so regular that they were formerly thought to be on a particular over-water flyway in order to explain their occurrence. Williamson argues that anticyclonic conditions over North or Central Europe initiate southward autumn migration on the part of large numbers of birds, and that the easterly airstream south of the anticyclone creates a certain amount of westward drift—enough to result regularly in wastage on a "colossal scale" of those birds carried beyond the British Isles. An example in North America of the effect of a shift in the prevailing wind is given by McCreary (1934). During the first

half of May, 1933, in East Wyoming the prevailing wind, normally south-west, blew almost continuously from the east, southeast or northeast, and pushed birds west which normally pass further east. The birds he mentions were all small species except for Franklin's Gulls, Larus pipixcan Wagler.

From such evidence it would appear that wind does have a very major effect on the direction of bird migration, if only to hamper the birds in following their usual course. Further recent papers, however, show very definite correlations between wind patterns and normal migration routes and behaviour. Landsberg (1948), for instance, has pointed out that there is a close resemblance between certain generalized trajectories of air currents and the migration routes of the Arctic Tern, Sterna paradisaea Pontoppidan, Wheatear, Oenanthe oenanthe (Linnaeus), Pacific Golden Plover, Pluvialis dominica fulva (Gmelin), and Greater Shearwater, Puffinus gravis (O'Reilly), (northward). This has also been noted by Allen, 1948, for two of those species, the Arctic Tern and the Golden Plover, P. d. dominica (Muller), but in this case the claim is made for the flight of the latter from Nova Scotia to South America. Landsberg further suggested that prevailing conditions would account for the scatter that occurs, that is, the deviations individual birds or flocks make. MacMillan (1938) has also proposed that whenever possible migrating birds ride the wind, and that migration routes are thus correlated with prevailing wind. Clear quantitative demonstrations of this have been given by Lowery and Newman (1955) from their studies of nocturnal migration, and Devlin (1954) who also studied

nocturnal migration. Dennis (1954) has observed that southerly winds generally attend the northward departure of migrants from the Gulf of Mexico coast, and that northerly winds in the spring result in an arrested wave. Dennis and Whittles (1955) have noted that autumn migrants reach Nantucket on northeasterly or northwesterly winds, and Stanford (1953) that many birds arrive from over the desert in Cyrenaica in spring with a south wind, sometimes very strong, behind them, and further migration across the Mediterranean is held up by north or northwest winds. Broley (1947) usually found that his Bald Eagles, Haliaeetus leucocephalus (Linnaeus), migrated north from Florida up the Atlantic coast after the breeding season. In April, 1945, however, the prevailing wind, which normally is from the south up the Florida coast in April and May, shifted and blew across Florida and then swung north up the Mississippi valley. That year he got four inland recoveries.

Not all observations correlating the arrival of birds with tail-winds can be used to support the notion that birds deliberately migrate with the wind, of course. Some are cases of drift out of preferred migratory paths, and it could be that the birds involved were not using the winds as tail-winds but were (as Williamson has postulated) actually heading across the winds. Such is likely the case in the hawk migrations at Cape May Point described by Allen and Peterson (1936). Here birds which normally pass southwestward somewhat inland are crowded into the narrow cape by a northwest wind. The flights observed by Ferguson and Ferguson (1922) for five fall seasons on Fishers Island, New York, show a good correlation with northwest wind for the

partly-soaring Sharp-shinned Hawk, Accipiter striatus Vieillot, but not for the stronger flying falcons which could fly into opposing winds. The Sharp-shins flew "slightly sideways" because of the wind. Smith's (1908) observation of over 10,000 Purple Martins, Progne subis (Linnaeus), migrating south down a quarter-mile wide strip along the east shore of Lake Michigan would indicate by virtue of sheer numbers that the birds were migrating with the northeast wind and were being turned across it to follow the guiding line of the shore by the water barrier. Had they not begun by flying with the wind could such a concentration have occurred, that is could drift alone, acting on birds flying with a southerly heading, be responsible? Bennett (1952), on the basis of five year's study of migration at Chicago during which every important autumn wave was associated with an advancing cold front followed by northwest winds, concluded that birds migrate with the wind. A clear case of migrating with the wind is recorded by Brown (1939,1951) for the hawks soaring on the slope-currents of Hawk Mountain, Pennsylvania. Of those counted in September and October from 1934 to 1938, 61.9% passed on a northwest to northeast wind, and many more hawks were aloft on days with northerly winds than on any other days.

Whether Michigan Herring Gulls seek westerly winds with which to fly, or are simply put adrift by them, it does not appear unlikely to me that the eastward tendency of their autumn dispersal is to a large degree correlated with the prevailing wind. The situation is complex, though, and the influence of the Great Lakes-St. Lawrence system as a guiding-line might be even more important. If it were, however,

I should expect more birds to scatter west along the shores of Lake Superior than are indicated by the recoveries.

There is perhaps a further consideration. Deelder and Tinbergen (1947)cite Lorenz's observation that crows, geese and gulls migrate low against the wind but high with a tail-wind. The reason for the latter Lorenz supposes to be that a gust from behind would cause these large birds to lose relative airspeed temporarily and descend, hence they must be well above obstructions. Now Dobben (1953) adds that since birds react less to topographical features as they fly higher a following wind serves to weaken the guiding-line effect. If this is the case, then the guiding-lines could here be drawing the gulls either east or west, but the prevailing wind would tend to send them east, and would actually weaken the effect of the guiding-line on days when it reached a high velocity.

Dispersal and Colony of Birth

In order to see if there was any relationship between the colony of birth and the direction of dispersal (see Table 3) the contingency chi-square method was applied to a table listing numbers of recoveries by areas with the colonies where the birds had been banded. To have numerical values sufficiently large for the use of this method a certain amount of grouping was necessary, so that colonies geographically close together were grouped, and the places of recovery were lumped into five areas with Michigan and Ontario considered separately. Since the probability of a chi-square greater than that obtained was less than 0.5%,

there is apparently some relationship. This appears to be largely that more birds banded in Lake Michigan tend to be recovered in Wisconsin, Illinois or Indiana than in Ontario, while birds from Lake Huron show the opposite tendency. This might be expected since the birds commence to wander on the lake of their birth. Birds from the St. Martin Shoals colony on the Lake Huron side of the Straits of Mackinac show no relationship which would support this idea, although birds from the Beaver group of colonies in Lake Michigan show a marked tendency not to go to Ontario. There is variation from colony to colony significant at the 5% level for the Lake Michigan colonies and at the 10% for Lake Huron, either to show the tendency characteristic of the colonies as a whole in that lake, or to show no tendency at all. It is difficult to know whether these tendencies indicate a slight genetic difference between some of the colonies (recall, however, that nine birds banded in one colony were recovered in another) or are merely an imperfect reflection of the geographical influence. A less marked tendency for more Lake Huron gulls to go to the East coast rather than the Gulf of Mexico, the Lake Michigan birds again showing the opposite tendency, is probably a reflection of their original dispersal on the later southward movement. It would follow if birds which have wandered to the lake shores of Ontario continue to drift down the Great Lakes-St. Lawrence system with the winds, while birds which have reached southern Lake Michigan would have to let the wind carry them away from the shores and across the southern part of the state of Michigan.

Southward Movement

Figure 2, graphs 2 and 3, and Table 4, reveal that most recoveries from southern states and Mexico occur in the period from January 1st to June 30th, the graphs showing that birds actually begin to appear at least in the southern states in December. The southward movement (characteristic only of first-year birds) is probably due to a number of factors such as the prevailing north winds of December and January, the freezing of northern rivers and the new difficulties shore ice brings to finding food, and perhaps a simple movement in the direction of greatest warmth as proposed for many European species by Drost (1929). Lincoln (1950) has suggested that this southward movement is the product of a "directive migratory impulse," but I should like to point out that (a) the movement begins very late in the year, and, more important, (b) only the first-year birds take part to any extent. As sexual maturity is approached and attained, wandering of more than two to three hundred miles is largely given up (see Figure 3). It is noteworthy that the two southernmost recoveries, a bird from Honduras on February 2, 1935, and one from Nicaragua on February 8, 1938, are both first-year birds. Rather than a migratory impulse it would appear that sexually immature gulls may simply experience less of an attraction to the breeding grounds than do adults, and are thus more free to wander as weather and comfort direct.

Western Recoveries

The most westerly inland recoveries (except one from Monterrey, Mexico) are 11 first-year birds recovered west of 95° west latitude in

Minnesota, South Dakota, Iowa, Nebraska and northern Texas. All are from tributaries of the Mississippi and ten are recoveries in April, May or June (one in January in Texas) and probably represent birds attempting to return to the Great Lakes but led astray by mistaken guiding-lines, their tendency to return to the colonies not yet fully developed.

Coastal Recoveries

Having now examined the distances flown by the different age groups, discussed the recoveries from Michigan, and remarked at length on the inland routes followed by the birds I should like to examine the coastal recoveries beginning with the Gulf states and Mexico. On graph 4 are plotted recoveries from the coastal regions of Texas and Louisiana, and these are summed in graph 5. First-year birds account for 90.80% of the 87 recoveries. Of these 87, 74 or 85.06% were first-year birds taken after January 1st--there are only five from December: one in Mexico, one in Louisiana, and three in Texas. The remaining eight birds were older than one year: two from Texas were in their second year and one in its fifth, four from Mexico were in their second and one in its sixteenth.

Correspondence between these two graphs and graph 1 showing the totals banded per year is only superficial. On graph 5 a recovery peak in the year 1936 is prominent. This consisted of 25 recoveries of birds banded in 1935, a year when 1,535 were banded. A banding peak of 4,027 individuals was attained in 1939, but 1940 saw only four recoveries

from the Gulf region, and only one of these (Mexico, January) was banded in 1939.

Since some 9,277 birds had been banded by 1938 and not recovered by 1940 as compared with 853 banded by 1934 and not recovered by 1936, there was ample opportunity for three more recoveries of older birds in 1940. If, then, we do not consider these three older gulls we find a ratio of about 1/65, that is 1/25 as many recoveries of first year birds from 2 2/3 more banded (a significant difference). Thus, placed in perspective, it is obvious that these recoveries indicate that a much larger proportion of first-year birds (not necessarily as great as 65:1, of course) reached these southerly regions in 1936 than in 1940. This is consistent with the recoveries of Caspain Terns, Hydroprogne caspia (Pallas), banded in the Great Lakes in 1935 (Ludwig, 1942). In contrast to recoveries from other years, great distances were covered by the terns in short times as shown by four recoveries: one in Alabama (September 14, 1935), one in Cuba (November 5, 1935), one in Colombia (December 15, 1935), and a final one in Colombia (April 1, 1936). It is worthy of note that of the total of 36 Mexican recoveries of Herring Gulls in this study ten are from 1936. I have been unable to discover any environmental causes for this phenomenon, the exceptional cold of late January and early February in the southern Great Lakes region that winter being unlikely as an influence on avian movements which preceded it. Note that only very minor recovery peaks follow the postwar banding peaks and that total recoveries for the region are fewer. For some reason, however, total recoveries from all birds are lower after the three-year gap in banding.

Turning to the East coast recoveries, I have plotted those from Quebec, the Atlantic Provinces and Maine, and Georgia and Florida on graph 6, and summed on graph 7. Close in number to the previous group, there are 85 recoveries so comparison can be direct. Seventy-one or 82.4% are of first-year birds: 15 out of the 16 from Florida and Georgia, 44 out of the 56 from Quebec, and 11 of the 13 from the Atlantic provinces and Maine. In this case a major recovery peak in 1940-1941 does follow the major banding peak of 1939, indicating that different unknown factors affected the birds which went to the Gulf of Mexico. However, the second highest banding peak (3,206 in 1950) is not followed by a recovery peak, and there is a low percentage of recoveries from all areas (see graph 1) thereafter.

Briefly we may say that there are numerous recoveries from both the East coast and the Gulf of Mexico, and that they are primarily, being far from the colonies, birds in their first winter (see Table 2).

Recoveries North of Breeding Colonies

From the maps it is obvious that dispersal carries a number of Michigan Herring Gulls to the north of the breeding colonies. Along the lower St. Lawrence River and in Newfoundland this can probably be explained by a combination of the prevailing winds and leading-line effect, but many of the northern Ontario records, especially the one from James Bay, and a few of the Quebec records do not fit such an hypothesis. Probably, too, there are many more Michigan birds that stray into these areas than the maps would suggest, for the human population is thin and largely localized, leaving vast lake and river

areas virtually uninhabited. Dispersal including northward directions is known for other Herring Gull colonies both in North America and Europe, and for various other Larus gulls, as will be mentioned later in this paper. Herons are notable for a northward post-breeding dispersal (Cooke, 1913b, Coffey, 1954, and many other papers) which may be somewhat different, however, in that in herons the trend seems quite pronounced. Lowe (1954), however, noted no directional tendency for the dispersal of British herons Ardea cinerea Linnaeus. The dispersal of at least part of the northern population of Barn Owl, Tyto alba (Scopoli), in North America is also in all directions (Wallace, 1948, and Stewart, 1952). Lincoln (1950) calls the northward movement both of the herons and of the Herring Gull "vagrant migration," "governed only by the availability of food" which seems to me to be supposing a great deal. Another North American bird which goes north after breeding (apparently both adults and young) is the Bald Eagle of Florida (Broley, 1947) which, as I mentioned above, seems to rely for the direction of this movement upon the prevailing winds.

Regarding the northward component of the dispersal of Michigan Herring Gulls, then, I can only say that we do not know sufficient about the numbers of individuals involved to characterize it properly. It may be simply a function of the influence of good habitat on erratic dispersal, or there may be a variably inherent tendency to go north.

COMPARISON WITH OTHER AMERICAN HERRING GULL STUDIES

The movements of Michigan Herring Gulls as revealed by this study can now be stated briefly. In late summer and early autumn there begins a dispersal with great individual variation in the time of leaving the colonies and in the distances traversed. Second-year and older birds with a few exceptions tend to remain within 300 miles of the colonies, although some move up to about a hundred miles farther along Lake Ontario. First-year birds, however, show much greater variation. Although some 60.2% are recovered within 300 miles the remainder wander widely. During the autumn this dispersal shows a decided eastward tendency (perhaps a function of the prevailing winds) and possibly a slight degree of northward tendency. With the advent of winter, however, many first-year birds, including many of those still in the Great Lakes area, move southward along the East coast or the Mississippi and its tributaries. Some stop in Florida and a few get to Cuba or the Bahamas, but a concentration occurs on the Gulf coast of Louisiana and Texas, from which a number straggle into Mexico or, occasionally, even farther. These birds gradually drift northward in the early spring, a few wandering off to the west along tributaries of the Mississippi, and many probably reach the Great Lakes or even the breeding colonies, although they are, of course, immature and do not breed. Very few spend the summer as far south as the Gulf of Mexico.

The most valuable study for comparison is work done by Gross (1940) on 1,409 recoveries of Herring Gulls banded in the Great Lakes by H. C. Wilson and William A. Lyon. Most of the gulls were banded by Wilson on the Sister Islands, Wisconsin; Lyon banded in 50 comparatively small colonies in Lakes Michigan, Superior and Huron. The different colonies showed much similarity of dispersal pattern. As noted above, the younger, non-breeding brids as a whole flew farther from the colony than did the older birds. Dispersal was erratic but Gross noted a "distinct tendency for them to concentrate on the shores of the Great Lakes and the river courses such as the St. Lawrence, Mississippi, Ohio and their tributaries." Those which go down the Mississippi to the Gulf of Mexico fan out along the coast forming a concentration--as do the Ludwigs' birds--along the Texas coast. A "distinct movement up [down] the St. Lawrence to Labrador and Newfoundland" is explained by Gross as a "tendency to cling to the shore lines of the lakes and to follow the river course." As I have indicated above, I feel that this is only part of the explanation and that prevailing winds play a major role. He also noticed a certain northward tendency which he felt to be merely part of a "preliminary explosive dispersal" followed later by a southward movement. He felt this to be the same situation as in other species such as the Black-crowned Night Heron Nycticorax nycticorax (Linnaeus), a subject upon which I have commented above. The map on which these 1,409 recoveries are plotted reveals a close correspondence with the dispersal pattern of the Ludwigs' birds, although the Sister Islands are somewhat more westerly than any upon which the Ludwigs banded.

Gross showed that fourth-year birds do breed, and that younger birds usually do not.

Lincoln (1928), on the basis of fifty some recoveries from the Beaver Islands, was able to discern the autumn dispersal with its northward tendency, the later, often extensive southward movement, and the erratic first spring return which leaves some of the young birds in the south. From such a small sample, however, he could not give a more precise picture. These recoveries again fit the pattern presented here, but I find Lincoln's map (Figure 3 in his paper) showing recoveries between January 1st and the following midsummer to be rather misleading as presented. This is due to the use of arrows running from the colony to the point of each recovery. Arrows tend to give the impression of direct flight and I strongly suspect that many of the birds involved were returning north. The western recoveries in particular probably represent, as I have already suggested for similar recoveries of the Ludwigs' birds, cases in which the returning gull took the wrong tributary while coming up the Mississippi.

Eaton (1933) divided the Herring Gulls of the Eastern United States and adjacent Canada into three populations on the basis of what he considered to be their migratory patterns. In most cases he was working with very few recoveries and his conclusions, as he recognized, are highly speculative. These proposed populations are: (1) the Atlantic which migrates down the coast, (2) the Laurentian (St. Lawrence River) which he felt didn't migrate, but which, according to color-banding work (Poor, 1943) apparently does pass through the Gulf of St. Lawrence

then south down the East coast, and (3) the Lacustrine. The latter he described as showing wide dispersal with the first-year birds tending to winter wherever there is open water on the southern Great Lakes drainage system, a lesser fraction following the Mississippi to the Gulf of Mexico, and a few wintering on the Atlantic seaboard.

His Lacustrine population is based on recoveries from birds banded in the following colonies: Red Bay (Bruce Peninsula), Ontario (9), Green Bay, Wisconsin (33), and the Beaver Islands, Michigan (89). He suggests several interpretations of the "wide dispersal" of this group. The first is that the colonies possess "no fixed habit of migration" but individuals merely "wander indiscriminately in search of a food supply and open water." With this wandering I should agree, whatever the reason why the gulls wander, as I feel that the pattern which is more-or-less recurrent annually is largely forced on the gulls' movements by such environmental factors as the direction of the prevailing winds and the location of thermal lanes. Individual recoveries from the West Indies, Central America, and the western tributaries of the Mississippi are frequent enough to suggest that if there is a "fixed habit" it is not well-fixed. The tendency to disperse, however, is perhaps inherent.

Eaton's second interpretation is that the colonies may be a "mixture of two or more strains possessing different migratory traits." He derived this notion from his analysis of the "Atlantic population" in which, on the basis of very few recoveries, he believed he could detect fairly distinct wintering grounds for birds of different colonies.

The work of Gross (1940) at Kent Island suggests that this is true for the Atlantic colonies at least to the extent that birds from northern colonies winter in the vicinity of more southern colonies while the occupants of the latter are father south. I fail to see much indication, however, of two or more inherent tendencies toward "different migratory traits" in the dispersal pattern of the Michigan Herring Gulls. As I have said, that some birds from certain Lake Huron colonies tend to go to the Atlantic while some from the more southerly Lake Michigan colonies tend to go to the Gulf of Mexico is likely traceable to their original dispersal on the shores of the lakes of their birth, although this itself may be genetically governed.

His third suggestion, namely that the Lacustrine population might be divisible on the basis of migratory tendencies into an "eastern" and a "western element" is probably unnecessary if the tendency for more birds from certain Lake Huron colonies to go to the East coast than to the Gulf of Mexico, or the opposite in the case of certain Lake Michigan colonies, is dependent upon their original dispersal on their home lakes. Environmental factors provide a much more likely explanation of the eastward, northeastward, and southward movements, and the straying of birds into the west on tributaries of the Mississippi is a function of their tendency to follow water courses. Eaton's maps of this dispersal introduce no new tendencies to the maps presented herewith.

Gross (1940) analyzed 773 recoveries (3.29%) from 23,434 Herring Gulls banded on Kent Island, New Brunswick. He found a dispersal at the end of the breeding season, but of a less erratic nature than that of

the Great Lakes birds. The Kent Island Gulls tend to cling to the Atlantic coastline. Fewer go northward than southward, and the northward migration is followed later by a general southerly flight. A large number return to the natal colony to breed, but he found none banded as young in other colonies, nor any Kent Island birds breeding elsewhere. There was always a number of non-breeders of all ages at the colony in summer. Although few Kent Island birds winter on their breeding grounds, color-banding studies (Poor, 1944) indicate that many go no farther than the New York region and reproductively-active individuals leave there in January to be back at the colony by the last week in February.

MOVEMENTS OF THE EUROPEAN HERRING GULLS

Banding studies of North European colonies, such as those of Mortensen (1950) and Paludan (1953) in Denmark, indicate erratic dispersal but quite restricted movement. In the case of Paludan's two colonies the average distances of dispersal were only 90 and 217 km., and the farthest of the 426 recoveries was only about 800 km. Tinbergen (1953) states that neither the Dutch nor the German North Sea population is really migratory--i.e., there is "no shift in population area from north (east) to south (west) in winter"--but that there is mass movement along the coast. This movement is to find a safe habitat. High tides in combination with strong westerly winds completely cover the beach and the gulls' food, and the gulls shift to broad beaches where they can rest and wait for the storm to pass. Southwesterly winds are most frequent, and the gulls sail to the southwest using the rising air above the seaward slope of the coastal dunes, "and sail for hours and hours, practically without a single wing-beat." Tinbergen believes that the reason the whole population does not move southwest is that there is considerable back migration in calm weather out over the open sea--perhaps they use the soaring methods described by Woodcock (1940, 1942). When the wind is at right angles to the coast, two streams of gulls travel along the dunes in opposite directions.

Herring Gulls of the British Isles show at most only a "very moderate dispersal" (Matthews, 1952). Witherby et al. (1941) remark

that they are "more or less sedentary, a few seem to be completely so, but [the] majority move away, though movement is almost entirely one of dispersal in any direction and [the] majority do not travel more than 200-300 miles." A distinct tendency for more extensive movements, especially of birds from the more northerly colonies, toward the south or south-west has carried a few birds to North France and the Biscay coast (Witherby et al., 1941), but according to Matthews (1952), doesn't alter the general picture of moderate dispersal. Fisher (1954) credits the British subspecies, L. a. argentatus, which also breeds in Iceland, the Faeroes, N. W. France and the continental North Sea coast to S. Norway, with reaching the Mediterranean. None of the few recoveries of Irish birds show movement "other than short distance dispersal" (Witherby et al., 1941).

Matthews (1952) reports a "strong southerly bias" for the British birds, and notes that recoveries are largely restricted to the coast on which the colony is situated. Although the most sedentary birds may scarcely leave the colony—Lockley (1942) states that on Skokholm Herring Gulls may be feeding young as late as October, and are "back at the nesting terraces on the first fine day in November"--dispersal from the colonies commonly takes place between the end of July and mid-August with return from the end of February or early March to mid-May. During the autumn and winter their movements in British waters are greatly influenced by migrations of the herring (Witherby et al., 1941). Immature birds often pass the summer south of the home colonies. Some continental birds from Norway, Holland, Denmark, Frisian Islands,

South Sweden and North Germany come to the British East coast in the autumn (Witherby et al., 1941), but the incidence of this is not known as the immatures of the subspecies cannot be distinguished in the field (Leach, 1944) and ringing recoveries have not as yet been numerous.

It would appear, then, that the Herring Gulls of northern Europe and North America have essentially similar habits of wandering, although the former may make fewer long flights and show less southward tendency. Even though the spatial patterns vary from one region to another all appear to include a dispersal from the breeding colonies, particularly by the young birds, the directions and distances of which are largely controlled by environmental factors. Return to the colonies is for many individuals dependent mainly upon degree of maturity, and for those that return in their first year may be simply a function of a gregarious tendency.

COMPARISON WITH RELATED LARUS SPECIES

In a number of related species many of the same dispersal tendencies are evident. In the closely related Ring-billed Gull, Larus delawarensis Ord, for instance, banding recoveries from Great Lakes colonies (Ludwig, 1943) indicate that many of the birds go south to Florida and the Gulf of Mexico, largely by way of the Mississippi or Great Lakes-St. Lawrence systems. Some winter in the Great Lakes but most immature birds at least (recoveries of adults were few) remain south of the colonies for one or two years. Florida appears to be the site of the chief concentration.

Color-banding studies of gulls on the Pacific coast of the United States (Woodbury and Knight, 1951) show no real migration pattern, but a wandering back and forth along the coast. Recoveries from the Western Gull, Larus o. occidentalis Audubon, for example, show a dispersal north and south from the Oregon colonies (Ferris, 1940) in which individuals may become resident where they spend their first winter, but probably return as adults to the general region of their birth. Woodbury and Knight recognize that there is "great variation in the distance travelled by young gulls, not only among members of the same colony but also among colonies, populations or species." California Gulls, Larus californicus Laurence, from Klamath Falls, Oregon, and Mono Lake, California, for instance, do not travel as far as those from Utah. The Utah birds, banded at Great Salt Lake (Woodbury, Behle, and Sugden, 1946) present

an interesting case of longitudinal migration. The first-year birds fan out, mostly towards the West coast, and most of them reach the Pacific, descending to it along various waterways. In their winter absence they are replaced in Utah by Ring-billed Gulls presumably (Woodbury and Knight, 1951) from Canadian breeding grounds, although why one leaves and the other comes to Utah has not been answered. Since most of the California Gulls from Utah go to the Pacific coast, they may have a genetically fixed directional tendency of the sort shown to be much more clearly present in some European birds such as Storks, Ciconia ciconia (Linnaeus), (work reviewed by Mayr, 1952). They would not be aided by the prevailing winds, and the authors noted no other environmental factors which could serve to direct them. However, their original dispersal is erratic both in time of inception and in direction and some remain in the interior--a lack of consistency is thus apparently common to at least several Larus species.

The British Larus gulls, as described by Witherby et al. (1941), also show a pattern of erratic dispersal of immature birds and a certain amount of drifting with little actual migration. Some such as the Common Gull, Larus canus Linnaeus, are partially sedentary or do not go "any great distance" (Danish population treated by Munk, 1951), while the Lesser Black-backed Gull, Larus f. fuscus L., shows a definite migration (Thomson, 1924) in which most birds participate, and its immatures disperse to greater distances. Matthews (1952) experimentally compared the homing ability of Herring Gulls and Lesser Black-backed Gulls. He found both to be inefficient, but felt that there were more

able navigators among the latter. In North America probably only the Franklin's Gull has a true migration.

Just why there is a dispersal tendency in the Herring Gull, and why it is pronounced only in some first-year birds, is difficult to see. Lincoln (1939) thinks that the tendency, which he calls "migration," may be inherited by the individual as a "recessive character which it largely outgrows as it reaches maturity." He further suggests that it may represent vestigial migration. Possibly it should be called migration only in a very broad sense since its direction and timing may be largely due to external environmental factors. Perhaps the young birds do not really display Zugunruhe (as reviewed by Farner, 1950), but simply are not strongly attracted to the vicinity of the colonies. Perhaps natural selection favours those which do simply drift with the wind and eventually proceed to the south, for these avoid the harshness of winter with which, in their inexperience, they might not be able to cope. Later, when more experienced, they are also more sexually mature and many feel an attraction to the vicinity of the colony, even if this be just a rather broad vicinity. Once fully adult and breeding there may be less incentive to wander and more to return to the nesting sites early in the year--a tendency frequently found in colonies where the best (i.e. central) sites are occupied by the older birds (Fisher and Lockley, 1954).

MORTALITY

Some idea of the causes of death of the banded birds can be gained from the details usually submitted with the recovery reports, but equal significance cannot be given to all the recoveries. As Paynter (1947) has made clear, fates closely allied with human activities will be amply recorded, but birds killed by predators, disease and other causes will be recovered only by chance. He illustrates this, and to repeat his illustration using the figures from this study, 3.02% of the 1,127 recoveries for which data were furnished were caught by fishermen. This does not mean that 3% of all Michigan Herring Gulls meet this fate, for these 34 birds probably represent most such catches of the entire 37,414 banded. Thus the mortality rate due to this cause is more nearly 0.09%.

Listed herewith are the causes of mortality recorded for both the Michigan birds and Paynter's Kent Island birds. Of the latter group, 37,557 were banded as young. Recoveries of gulls which were banded as adults at Kent Island are not considered here.

	Michigan		Kent Island	
	No.	Percent	Percent	
Found dead	693	61.49	53.51	
Captured and released	60	5.32)	1.99	(during banding, not
Captured	37	3.28) 13.84%	9.02) 14.76%	comparable)
Captured by fishermen	34	3.02) captured	4.31) captured	
Trapped	25	2.22)	1.43)	
Shot	85	7.54	5.35	
Injured, sick, or wounded	76	6.74	7.58	
Found	50	4.44	4.63	
Killed	24	2.13	2.14	
Band only	4	0.35	0.87	("band recovered" perhaps
Miscellaneous	39	3.46	3.17	not comparable)
Total	1,127	100%	2.71	(prob. found dead)
No information	16		1.19	(collected
	1,143		1.83	(no information)
			100%	

Most birds are reported as "found dead." This category, and those of "found," and "killed," furnishes us with no information.

Some 13.84% of the Michigan birds recovered were captured in one way or another as compared with 14.76% of the Kent Island recoveries. Those Michigan birds reported as captured by fishermen were taken on a line, by a hook or in nets. A somewhat higher percentage of the marine Kent Island birds met this fate, but more of the inland Michigan birds were taken in animal (mainly muskrat) traps.

Of the 85 Michigan birds shot, 48 (56%) were in their first year (35 were shot before their first December 31st). Probably many of the recoveries reported as "found dead" really represent birds shot as the persons sending in the bands may have feared prosecution. European banding studies show much higher percentages of recoveries from shot birds (Drost and Schilling, 1940, record 51.2% shot and 34.5% found dead, Paludan, 1953, 60.4% shot and 30.8% found dead), along with correspondingly fewer birds recorded as found dead.

The three recoveries given as "band only" are instances in which a band has been picked up in a field or on a shore perhaps after being lost by the bird which bore it. Paynter's category "band recovered" is probably not comparable. I have lumped all recoveries of birds reported as "injured," "sick" or "wounded" because of the likelihood that the person finding the bird was unable to distinguish which was the case.

The miscellaneous group is worthy of mention. Included here are two birds which were shot, one for a specimen and one, a four-year-old,

at a state fish hatchery. Two were reported as killed by owls, and one by an eagle (Paynter records two as killed by eagles). Losses to animal predators include one killed by a "fox or coyote," one by a dog, and one killed "probably" by a mink. It is to be expected that the number of recoveries from such sources will give a very incomplete picture of the actual predation rates. Three were hit by automobiles, three by trains, and one died in a collision with a jet aircraft at an airbase. Of Paynter's similarly sized sample eight deaths resulted from collisions with aircraft, eight with automobiles, and one with a train. Two birds, reported as being "tame," were "picked up," and a first-year bird was taken when it flew into a porch. Two birds were found exhausted, six frozen, two drowned, and one with oil on its plumage. Not all of these diagnoses, of course, are necessarily correct, and some, such as a bird found "paralyzed" and one which died of "lead poisoning" leave considerable doubt as to the cause of death.

One report of considerable interest, however, tells of a four year old gull which pecked at its leg until the band fell off. Although a certain amount of forcible removal shortly after banding might be expected, this seems to indicate that some birds at least do not become accustomed to wearing bands. Paynter (1949), is of the opinion that loss of bands by wearing and breaking probably is not great in the Herring Gull, at least up to ten years of age, since many bands survive ten years in good condition. Recall, however, that in three cases bands of Michigan gulls were found lying in fields or on beaches, and bands found on nesting islands have not been considered. These birds had

been banded one, six, and eight years before the bands were found. If the bands did not wear through and fall off, then either the birds themselves removed them or the bands were separated from the birds' carcases by some agency. The number of instances in which these isolated bands are found can certainly give no idea of how many are lying on beaches and fields, as they are much less likely to be found than are dead gulls. If, then, many Herring Gulls do remove their bands, older age groups will yield proportionately fewer returns than younger, but the extent of the bias thus introduced, if, indeed, such a bias does exist, is unknown. This bias could be partly responsible for the failure to reconcile attempted calculations of mortality rates and longevity with known productivity rates on the basis of North American banding recoveries (reviewed by Farner, 1955).

The remaining recoveries are likely unusual instances; a bird was found "stuck in [an] asphalt bed" in Mexico, another flew into the cargo hold of a freighter, one became caught between two timbers on a dock, one broke its wing by flying into a ship's life line, while one in Chicago was killed when it flew into a flagpole. Finally, in the course of feeding one took poisoned corn and one "choked on a fish."

The oldest bird yet recovered in this group was a 19-year-old found dead by the Ludwigs in 1954 on Bellow Island, Lake Michigan, where they had banded it in 1935. It may be the oldest Herring Gull yet recovered in North America. A Herring Gull banded in Denmark in 1925 and recorded just over 28 years later is claimed by Bergstrom (1956) to have set a new longevity record for any species in the wild.

Captive Herring Gulls, however, have reached considerable ages. Pearson (1935) records a captive pair which attained 49 and 45 years of age, and Flower (1938) one which reached at least 41 years.

I have already mentioned that mortality is highest among first-year birds and stated that 63.34% of the recoveries in this study were of that age group, 42.16% of the total being before December 31st. This feature has been common to all the banding studies of Herring Gulls in Europe as well as in North America referred to previously in this paper and to studies of other species of gulls. Paynter (1947) has suggested that first-year birds are relatively weak. Lack (1943) shows that the number of first-year Black-headed Gulls, Larus r. ridibundus L., which are shot is disproportionately higher than for older birds. He suggests that they become "warier and harder to shoot as they get older." Later (Lack, 1946) he suggested on the basis of recoveries from a number of species that the higher mortality among juvenile birds is due to general inexperience.

SUMMARY AND CONCLUSIONS

1. Between 1931 and 1957 Mr. Claud C. Ludwig and his two sons banded 37,414 juvenile Herring Gulls in colonies in the Great Lakes adjacent to Michigan. The 1,143 recoveries are analyzed herein.

2. Dispersal begins in late summer and early autumn. Most birds in their second year or older tend to remain on the shores of the Great Lakes within 300 miles of the colony.

3. There is some evidence of a northward tendency in the early autumn, but recoveries from sparsely-settled northern Ontario and Quebec are too few to characterize it properly.

4. First-year birds, particularly in the period between January 1st and June 30th, fly farther than older birds. There is great individual variation in the distances they cover, however, and in the time they quit the vicinities of the colonies.

5. Recoveries are most frequent from the shores of the Great Lakes. Other recoveries fall into two categories: 1) the Mississippi River and its tributaries, and 2) the Atlantic and Gulf of Mexico coasts. Access to the Atlantic coast is probably mainly <u>via</u> the St. Lawrence River.

6. Waterways and coasts are followed because they provide a source of food, and it is suggested that they function further to supply lanes

of upward air currents used in soaring. This contention finds support in the literature at least to the degree that numerous other soaring species make use of thermal lanes during migration.

7. Prevailing winds probably are a major factor in controlling the direction taken by the gulls, that is, they superimpose a direction upon the dispersal. This direction coincides with autumn movement down the Great Lakes-St. Lawrence system, a winter movement to the south down the Mississippi or the East coast, and spring return northward. Many other birds are known to use tail winds extensively or exclusively on migration, thus it is likely that a soaring species such as the Herring Gull would follow suit. Since many Herring Gulls are relatively sedentary, though, it is quite possible that a condition of Zugunruhe is not typical of the movements of the species. These movements, then, should perhaps not be considered as migratory, but merely as a wandering governed directly by environmental factors. It is possible that immature birds are less attracted to the vicinity of the breeding grounds than are sexually mature birds.

8. The most westerly inland recoveries in the study are probably cases of young birds returning home in the spring and taking a western tributary as they move up the Mississippi. They do not represent a tendency to disperse to the west.

9. The southward movement of late December, characteristic only of first-year birds, carries the gulls on the East coast to Georgia and

Florida and rarely into the West Indies. It also takes other birds from the Great Lakes down to the Gulf of Mexico, a concentration occurring in Texas and Louisiana. Quite a few reach Mexico, and there is one record from Honduras and one from Nicaragua.

10. In 1936 a much larger number of first-year birds reached the western part of the Gulf of Mexico than in any other year of the study. No reason for this movement has been offered herein.

11. A relationship between colony of birth and place of recovery exists to the extent that relatively more birds born in Lake Huron colonies are recovered in Ontario than in Wisconson, Illinois and Indiana, the opposite being the case for birds born in Lake Michigan colonies. Since dispersal is originally for short distances and is probably largely on the lake of birth, and since mortality is highest among the youngest gulls, this is not really surprising. It is reflected to a lesser degree in the winter movement to the south, since Lake Huron gulls, of which more have drifted east, provide relatively more East coast and fewer Gulf of Mexico recoveries than do Lake Michigan gulls. Colonies vary individually in the degree to which they are characteristic of colonies in their lake as a whole.

12. Twenty Herring Gulls banded by the Ludwigs and three by other banders were recovered in the breeding colonies. Thirteen of these were recovered in the colony where banded and ten in other colonies

(one actually in another lake). These indicate both return to the colony of birth, and, if they were breeding birds, some exchange between colonies which would reduce genetic isolation.

13. Other published banding studies of Herring Gulls breeding in the Great Lakes show similar dispersals, as do those of birds banded on the East coast, although the latter do not wander inland to any extent. European studies reveal dispersal of short distances, usually in all directions and often confined to the coasts. Again, it is the young birds which do most of the wandering, and enrivonmental factors may largely control what directional tendencies there are.

14. Many of the same dispersal tendencies are evident in related Larus species. Erratic dispersal of first-year birds, with great individual variation, followed by some degree of drifting usually without a fixed migration pattern, while the adults largely remain relatively close to the breeding colonies is apparently characteristic of most of the group.

15. Over half of the birds recovered were listed as "found dead." The next highest categories were of birds captured, usually by fishermen or muskrat trappers, of birds shot, and of injured, sick, or wounded birds. One very interesting case of a band recovery came after the person submitting the report watched the gull, a four-year-old, remove the band from its leg by pecking at it.

This observation introduces the consideration that if such action is not infrequent, then a bias exists in the recoveries of older birds that will be difficult to calculate.

16. Mortality is greatest in first-year birds up to December, the rate declining rapidly thereafter.

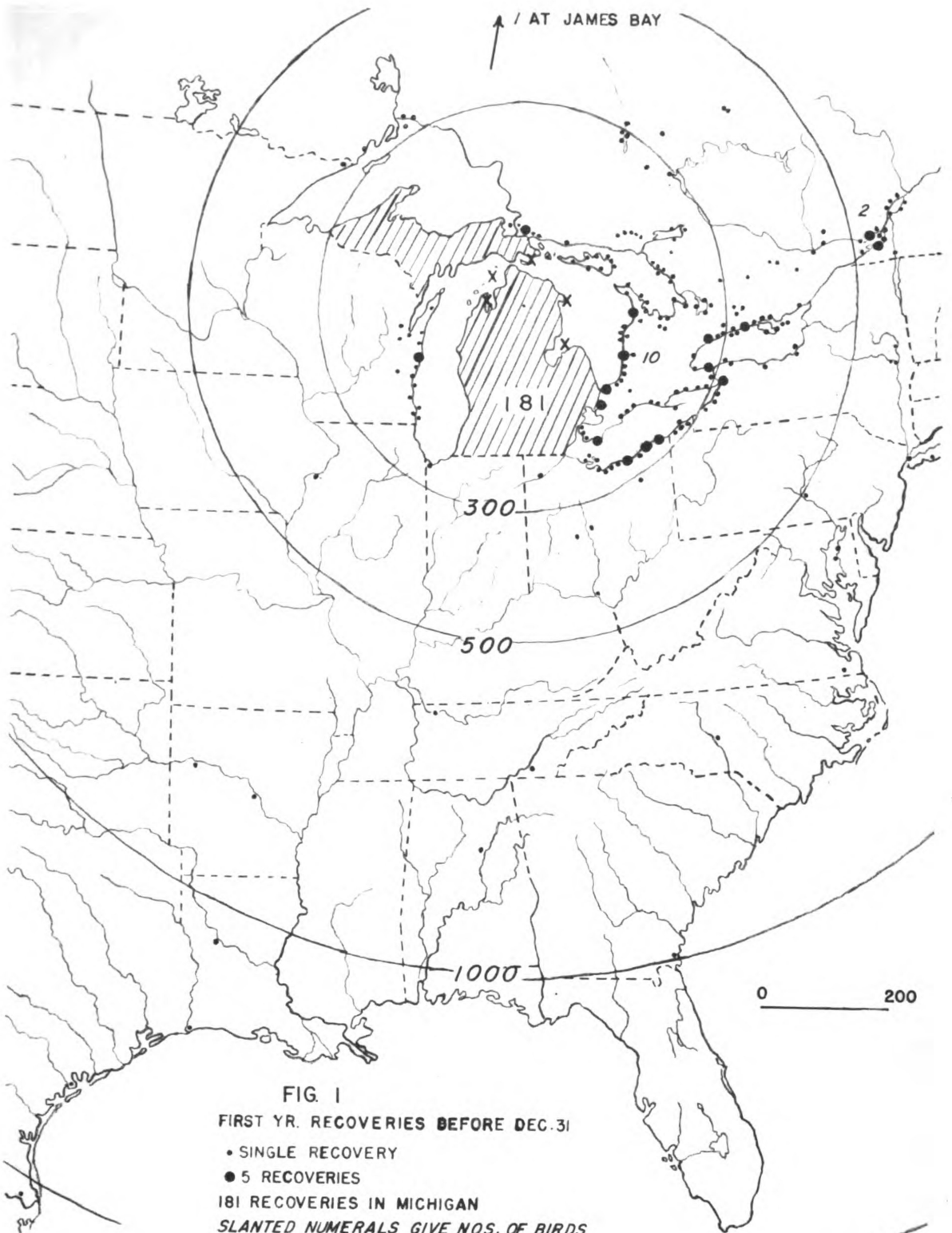


FIG. 1

FIRST YR. RECOVERIES BEFORE DEC. 31

• SINGLE RECOVERY

● 5 RECOVERIES

181 RECOVERIES IN MICHIGAN

SLANTED NUMERALS GIVE NOS. OF BIRDS WHICH COULD NOT BE LOCATED

X SITES OF COLONIES

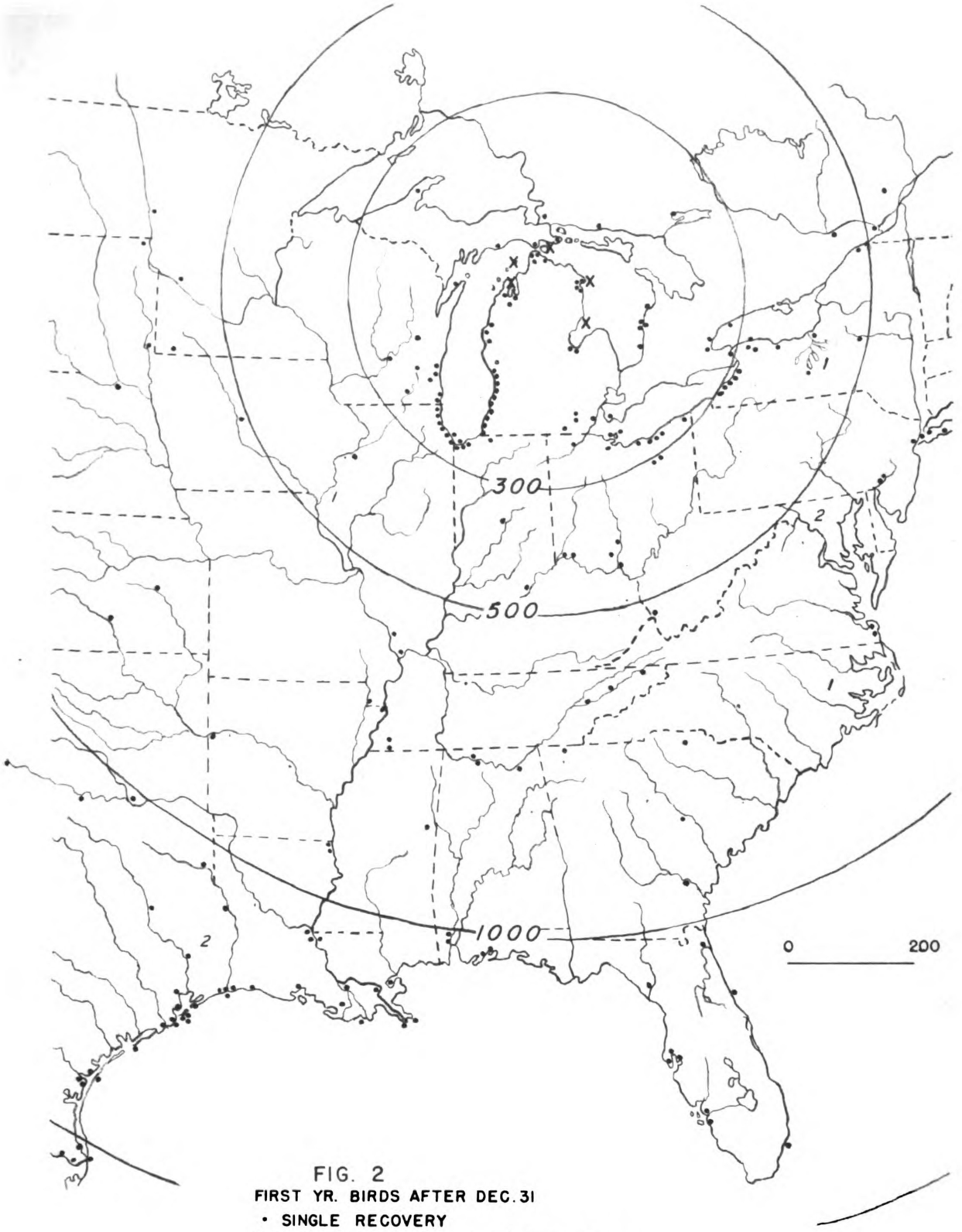


FIG. 2

FIRST YR. BIRDS AFTER DEC. 31

• SINGLE RECOVERY

SLANTED NUMERALS GIVE NOS OF BIRDS WHICH COULD NOT BE LOCATED

X SITES OF COLONIES

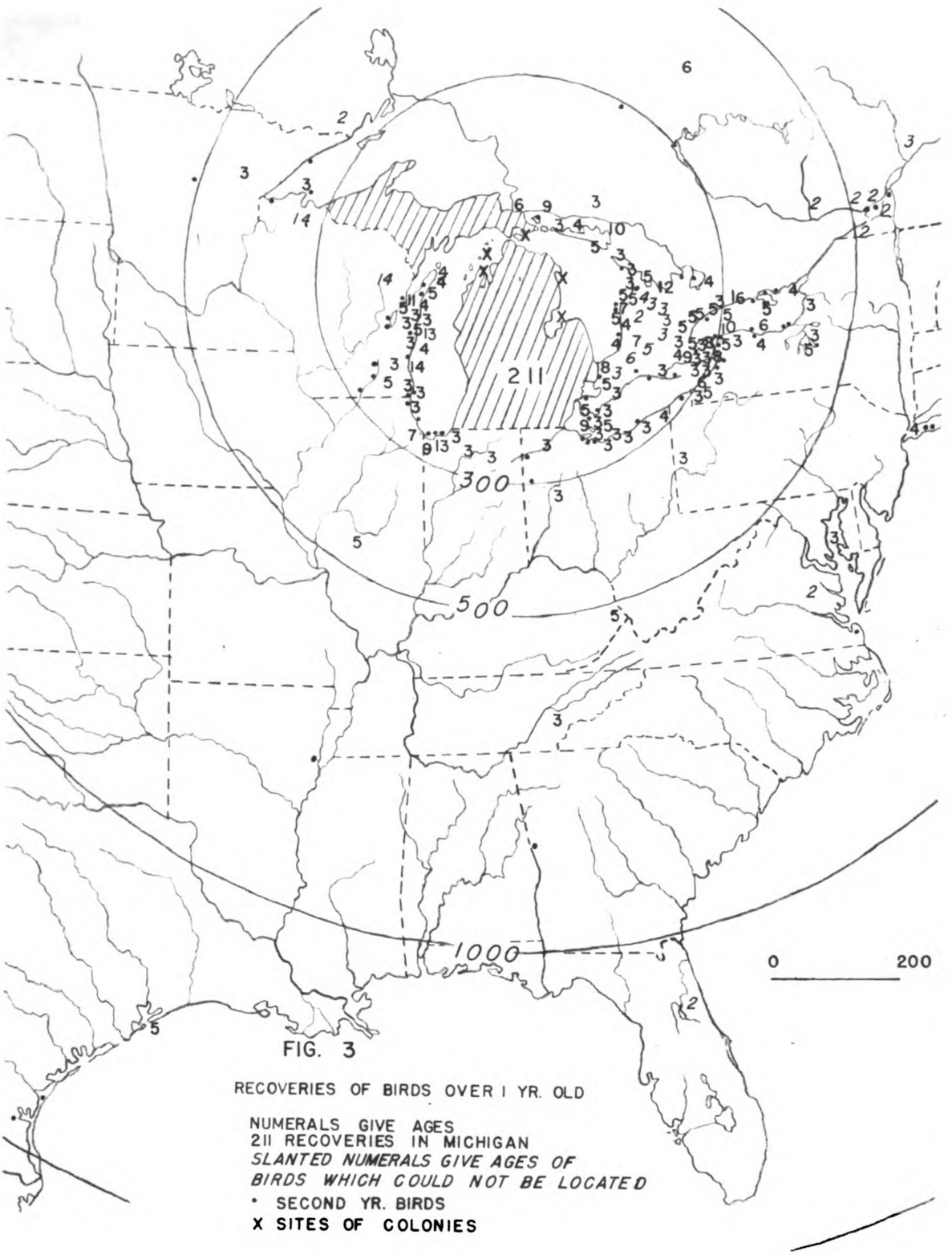


FIG. 3

RECOVERIES OF BIRDS OVER 1 YR. OLD

NUMERALS GIVE AGES
211 RECOVERIES IN MICHIGAN
SLANTED NUMERALS GIVE AGES OF BIRDS WHICH COULD NOT BE LOCATED
• SECOND YR. BIRDS
X SITES OF COLONIES

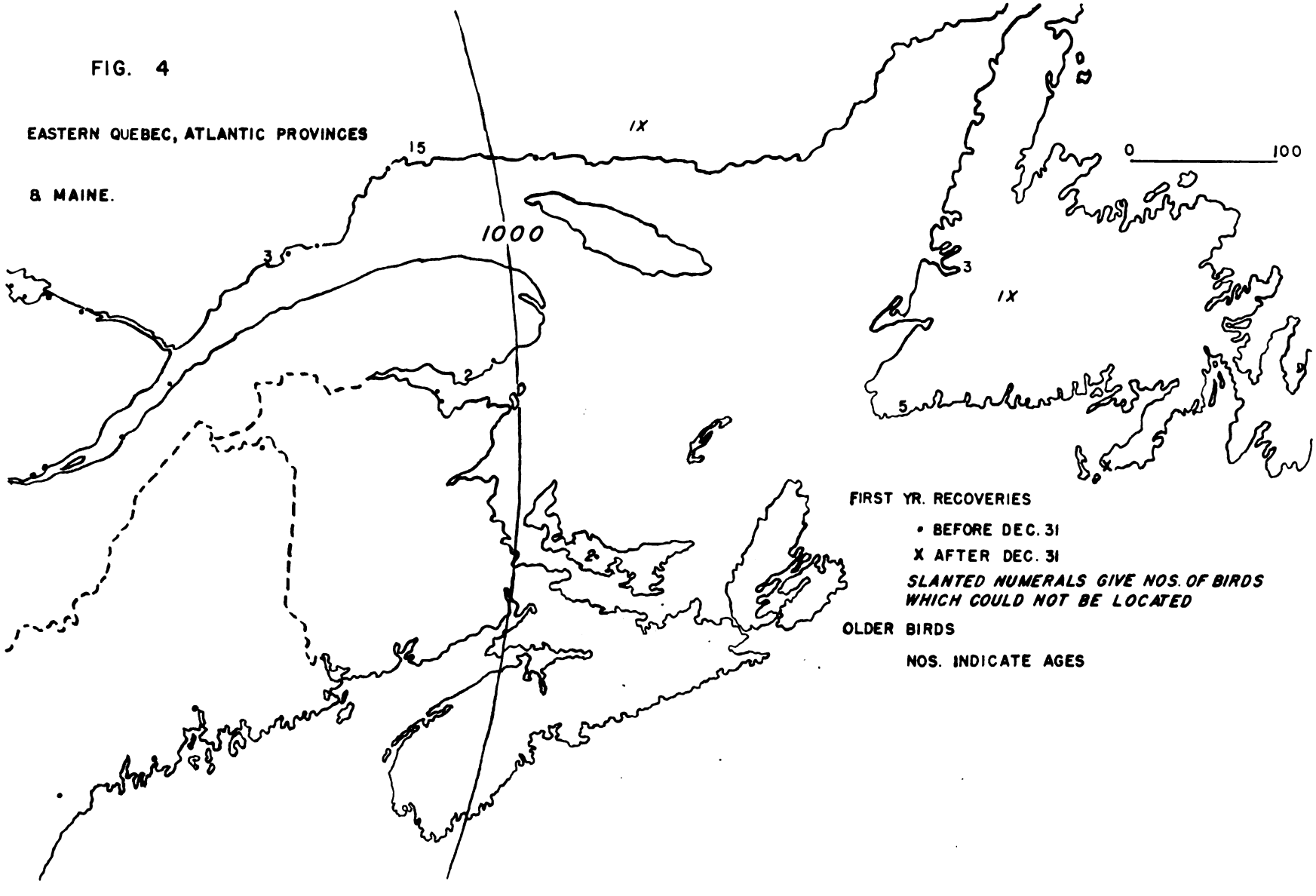
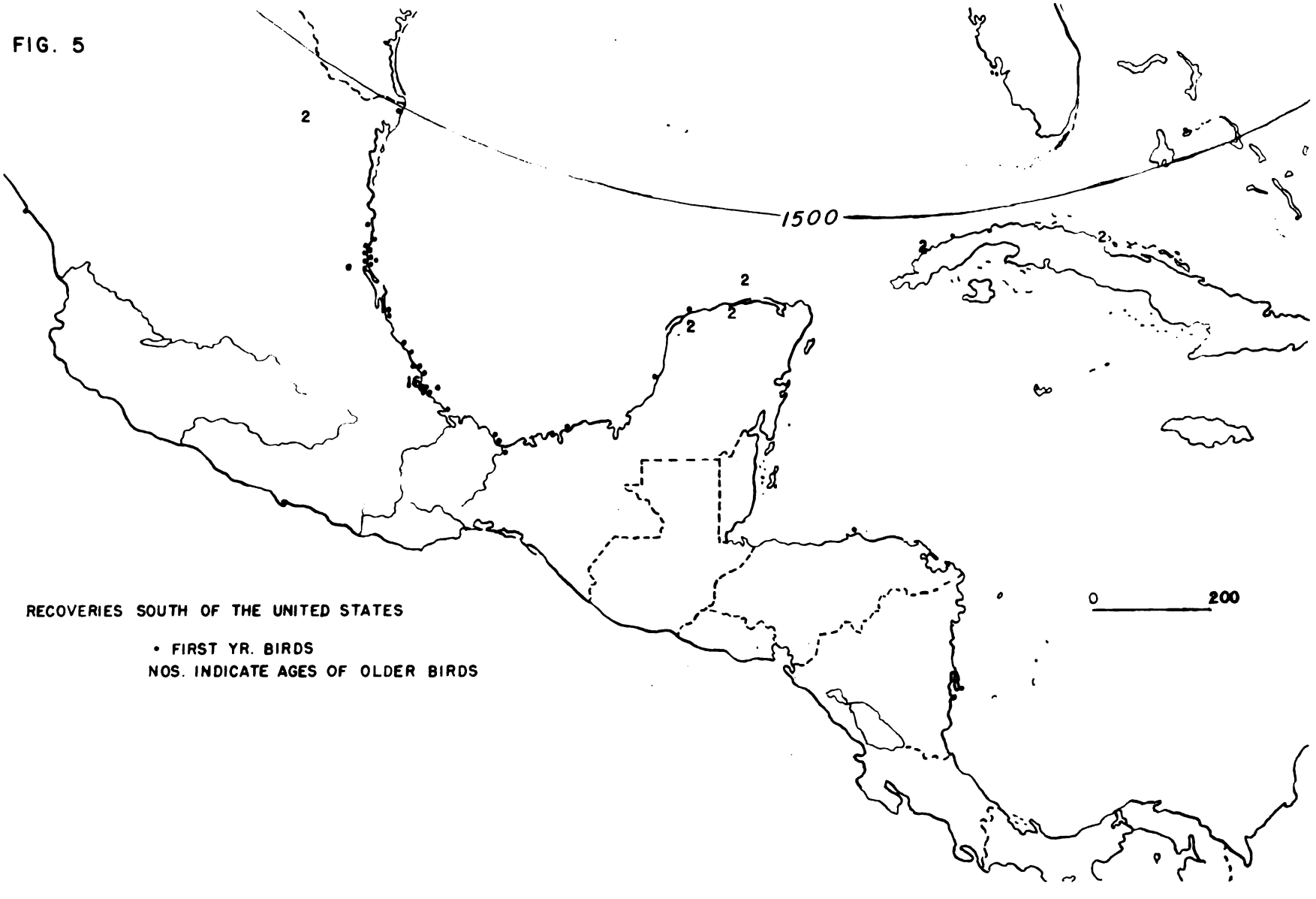


FIG. 4
EASTERN QUEBEC, ATLANTIC PROVINCES
& MAINE.
15
IX
1000
3
3
IX
5
0
100
FIRST YR. RECOVERIES
• BEFORE DEC. 31
X AFTER DEC. 31
SLANTED NUMERALS GIVE NOS. OF BIRDS WHICH COULD NOT BE LOCATED
OLDER BIRDS
NOS. INDICATE AGES

FIG. 5



RECOVERIES SOUTH OF THE UNITED STATES

• FIRST YR. BIRDS
NOS. INDICATE AGES OF OLDER BIRDS

TABLE I Nos. of gulls banded in each colony.

	Lake Huron									Lake Michigan							
	BLACK RIVER	SULPHUR	SCARECROW	SUGAR	GULL	THUNDER BAY	ST. MARTIN SHOALS	GOOSE	LITTLE CHARITY	SHOE	HATT	PIZMIRE	BIG GULL	GREEN	BELLOW	ROUND IS. LAKE SUPERIOR	NO. OF BIRDS BANDED EACH YEAR
1931	14																14
1932	9	11															20
1933	18	8	43	69													136
1934	10		4	160						3	578						755
1935	107		121	483	298	5				7	167	347					1535
1936	46		149	353		514				12	430	49	376				1929
1937	240		157	210	331		439	30		1	223	380		174			2185
1938	46		196	391	640		443	16		1	545	435	240	193			3146
1939	301		249	866	711		409			6		431	398	253	401		4027
1940	264		248	396	575		281		8	3	151	232	152	131	202	155	2798
1941	260		185	229	582		492		145	10	129	408		164	394		2988
1942	9								2								11
1946	331	4	161	231	262									169			1158
1947	465													373			838
1948	518		204											39	459		1220
1949	400														401		801
1950	1087		85								101	439	381		1113		3206 *
1951	719														1228		1947
1952	460						182				116	52			1096		1906
1953	860																860
1954	478		566												1522		2566
1955			56												1054		1110
1956	261		306						27						617		1211
1957	402								640								1042
	2001	23	926	3390	3399	519	2236	46	822	43	2440	2773	1547	1496	8487	155	37409
										* GRASS IS. L. MICH., 1950, 5							5
										TOTAL NO. BANDED							37414

NONE BANDED 1943-1945 INCLUSIVE

TABLE 2 Recoveries by age groups.

	FIRST YR.		BEFORE DEC. 31	JAN. 1 TO JUNE 30	OVER 1 YR.	
	NO.	%			NO.	%
MICH.	214	50·3	181	33	211	49·7
ONT.	177	67·8	162	15	84	32·2
WISC.	29	46·8	19	10	33	53·2
ILL.	12	70·6	1	11	5	29·4
IND.	8	50	1	7	8	50
OHIO	44	74·6	29	15	15	25·4
PENN.	6		5	1	2	
N.Y.	33	56·9	16	17	25	43·1
ME.	4		4			
P.Q.	44	78·6	42	2	12	21·4
N.B.	3		3			
P.E.I.	2		2			
NFLD.	2			2	2	
N.J.	3		1	2		
MD.	4		2	2	1	
VA.	3		1	2	2	
W.VA.	1			1		
N.C.	2		1	1		
S.C.	1			1		
GA.	4		1	3	1	
FLA.	12	92·3		12	1	7·7

	FIRST YR.		BEFORE DEC. 31	JAN. 1 TO JUNE 30	OVER 1 YR.	
	NO.	%			NO.	%
ALA.	6		1	5		
KEN.					1	
TENN.	7		2	5	1	
MISS.	1			1	1	
MINN.	4		1	3	5	
SO. DAK	2			2		
TEX.	33	91·7	3	30	3	8·3
IOWA	1			1		
NEBR.	1			1		
KANS.	2			2		
MO.	1			1		
ARK.	4		2	2	1	
LA.	15	100	1	14		
OKLA.	1			1		
CUBA	2			2	2	
MEXICO	32	88·9	1	31	4	11·1
HONDURAS	1			1		
NICARAGUA	1			1		
BAHAMAS	2			2		
TOTALS	724	63·3	482	242	419	36·7

TABLE 3 (next page) Recoveries by colonies of banding.

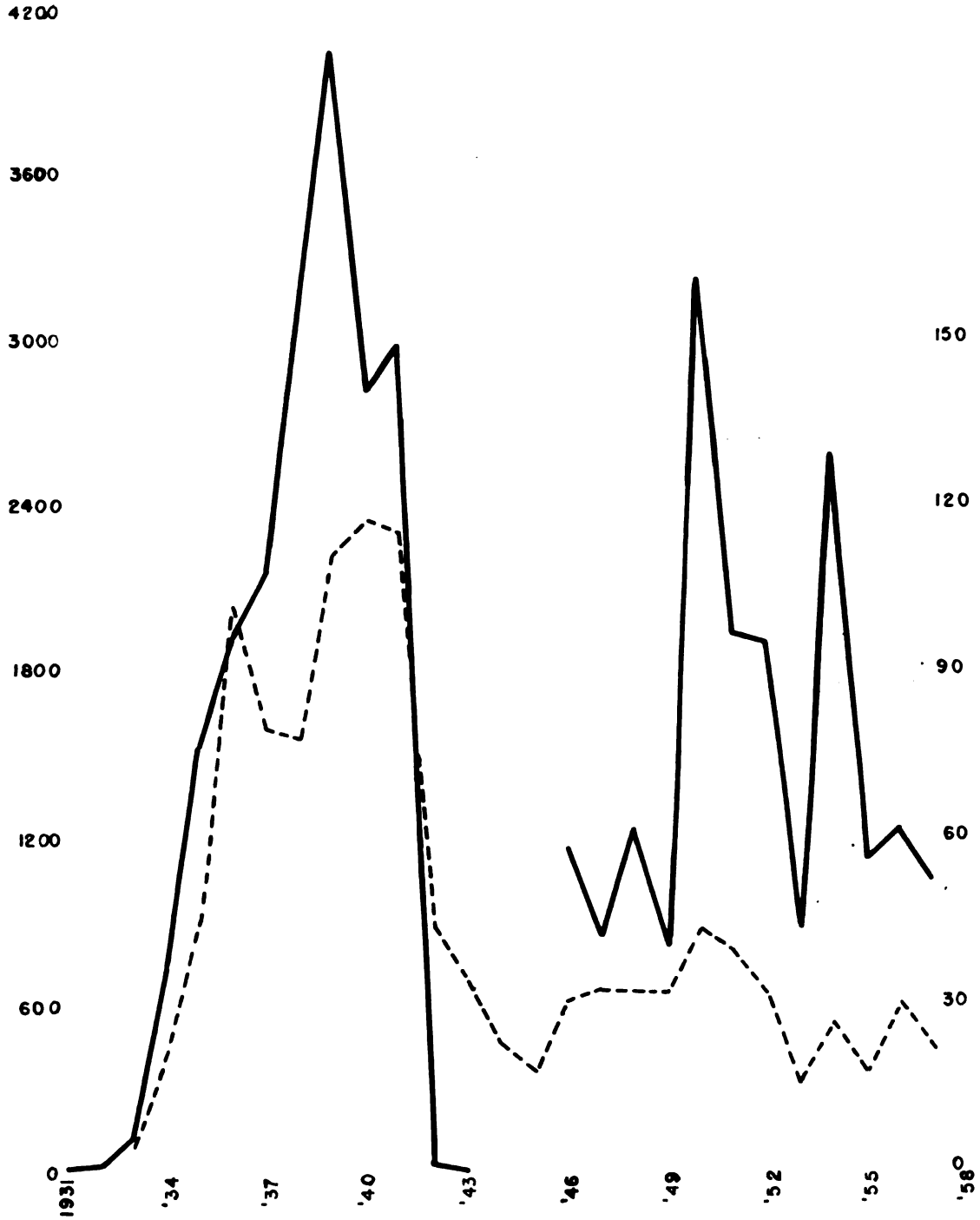
TABLE 3

	TOTALS	BLACK RIVER	SULPHUR	SCARECROW	SUGAR	GULL	THUNDER BAY	ST. MARTIN S.	GOOSE	L. CHARITY	SHOE	HATT	PIZMIRE	BIG GULL	GREEN	BELLOW	ROUND
MICH.	425	56		36	38	49		38	1	13	1	28	52	45	24	39	5
ONT.	261	32	1	24	53	56	2	22	1			18	11	16	9	14	2
WISC.	62	1			6	5		5				4	18	10	7	4	2
ILL.	17	3			1			1				5	3		2	2	
IND.	16	4						2				2	5		1	2	
OHIO	59	6		6	12	7		3				6	4	6	7	2	
PENN.	8	2		1	2							1				2	
N.Y.	58	4		7	13	12		8		1		1	4	3	2	3	
ME.	4					2				1				1			
P.Q.	56	11		1	10	16		5		1		2	2	4		4	
N.B.	3	2		1													
P.E.I.	2	2															
NFLD.	4	2				1						1					
N.J.	3					3											
MD.	5	1		1	2							1					
VA.	5					1							2		1	1	
W. VA.	1															1	
N.C.	2			1												1	
S.C.	1													1			
GA.	5				2	1		1					1				
FLA.	13	2		1		4		1				1	3	1			
ALA.	6	1			1			1				1	1	1			
KEN.	1													1			
TENN.	8	1			1	2		1					1	1		1	
MISS.	1			1													
MINN.	9	1				1		2				2	1	1	1		
SO. DAK.	2											2					
IOWA	1	1															
NEBR.	1													1			
KANS.	2				1											1	
MO.	1												1				
ARK.	5	1				1						2		1			
LA.	15				5	1						3	2		2	2	
OKLA.	1				1												
TEX.	36	1		3	6	4		3		1		8	3	3	1	3	
CUBA	4	1										1				2	
MEXICO	36	5		3	1	6		3				4	4	3		7	
HONDURAS	1											1					
NICARAGUA	1	1															
BAHAMAS	2					1							1				
TOTALS	1,143	141	1	86	155	173	2	96	2	17	1	94	119	99	57	91	9

TABLE 4 Total recoveries by month for those in which date of recovery was reported.

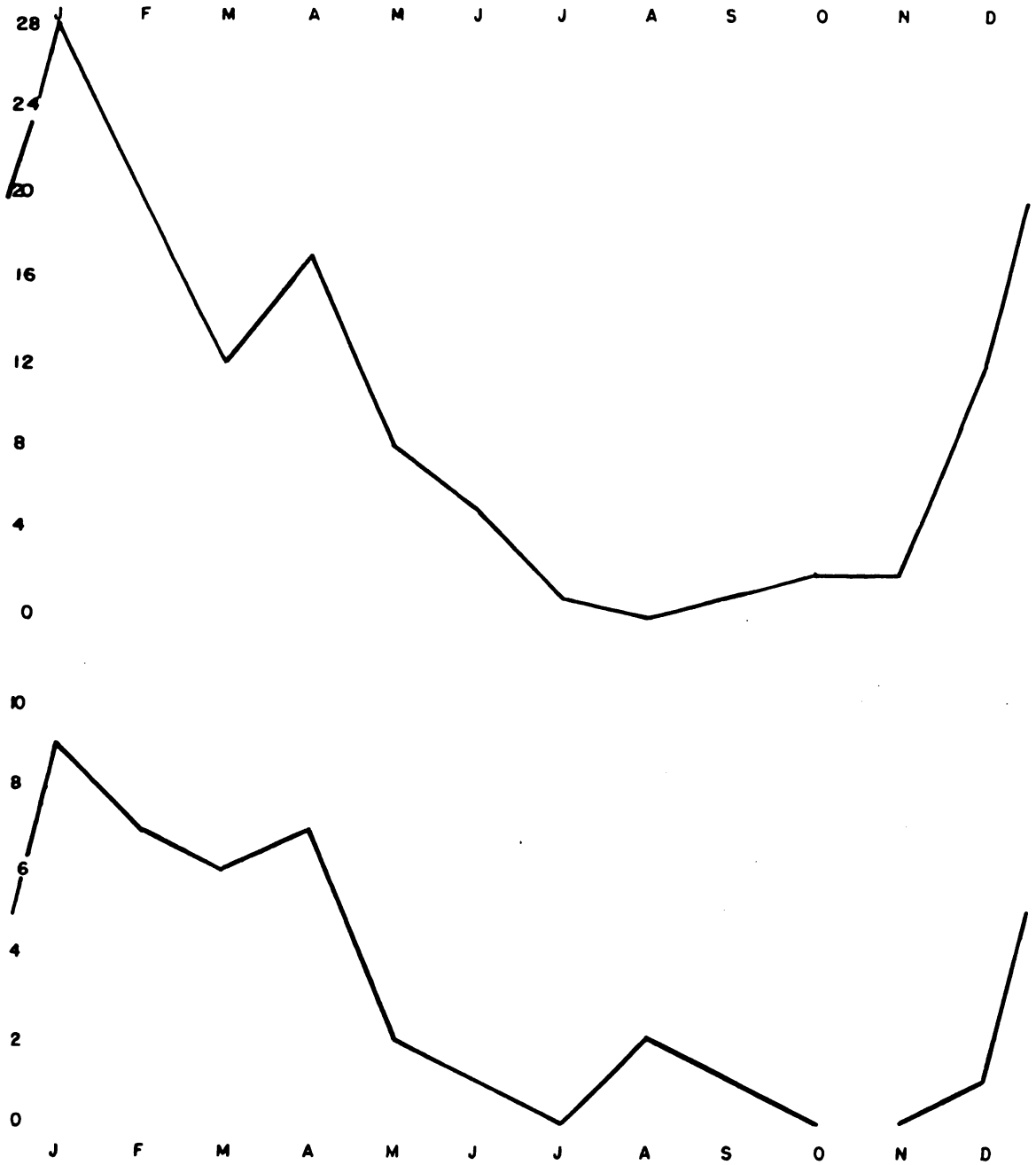
	J	F	M	A	M	J	J	A	S	O	N	D
MICH.	12	11	9	12	33	39	41	85	56	50	50	22
ONT.	11	6	5	7	8	7	10	21	59	58	39	26
WISC.	4	2	3	7	4	2	4	6	7	6	10	7
ILL.	3	2	2		3	2	3	1				1
IND.	3	4	1	1	3	1						2
OHIO	5	3	6	4	2	2		10	9	7	4	7
PENN.			2					1	2	1	1	1
N.Y.	7	5	3	6	5		2	6	7	7	3	7
ME.									2	1	1	
P.Q.					2	2	1	6	21	12	8	3
N.B.									1	1		1
P.E.I.											2	
NFLD.			1	1	1							
N.J.		1				1			1			
MD.		1	1	1						2		
VA.				3					1		1	
W.VA.				1								
N.C.			1									1
S.C.	1											
GA.	2	1				1						1
FLA.	6	4	1	2								

	J	F	M	A	M	J	J	A	S	O	N	D
ALA.	2		2		1							1
KEN.		1										
TENN.	2	1	1		2							2
MISS.	1											
MINN.				1	2	1			1	1	2	1
SO. DAK.				1	1							
TEX.	8	6	5	5	5	2	1				1	3
IOWA						1						
NEBR.					1							
KANS.				2								
MO.	1											
ARK.		1				1						2
LA.	5	5	1	2		1						1
OKLA.				1								
CUBA		3								1		
MEXICO	9	7	6	7	2	1		2	1			1
HONDURAS							1					
NICARAGUA						1						
BAHAMAS						1	1					
TOTALS	82	64	50	64	75	66	64	138	68	147	122	90



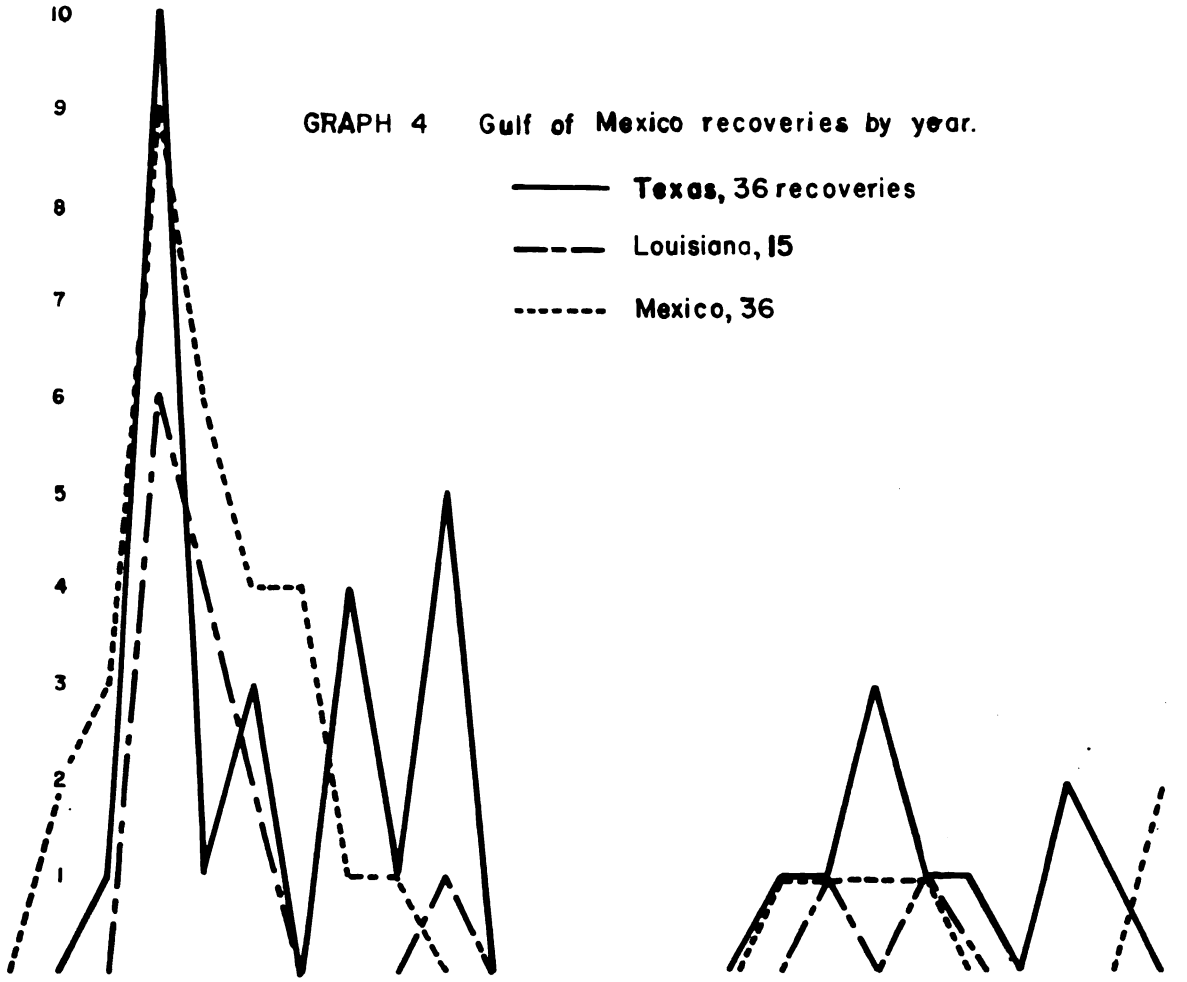
GRAPH 1 ——— no. banded per year, scale on left.

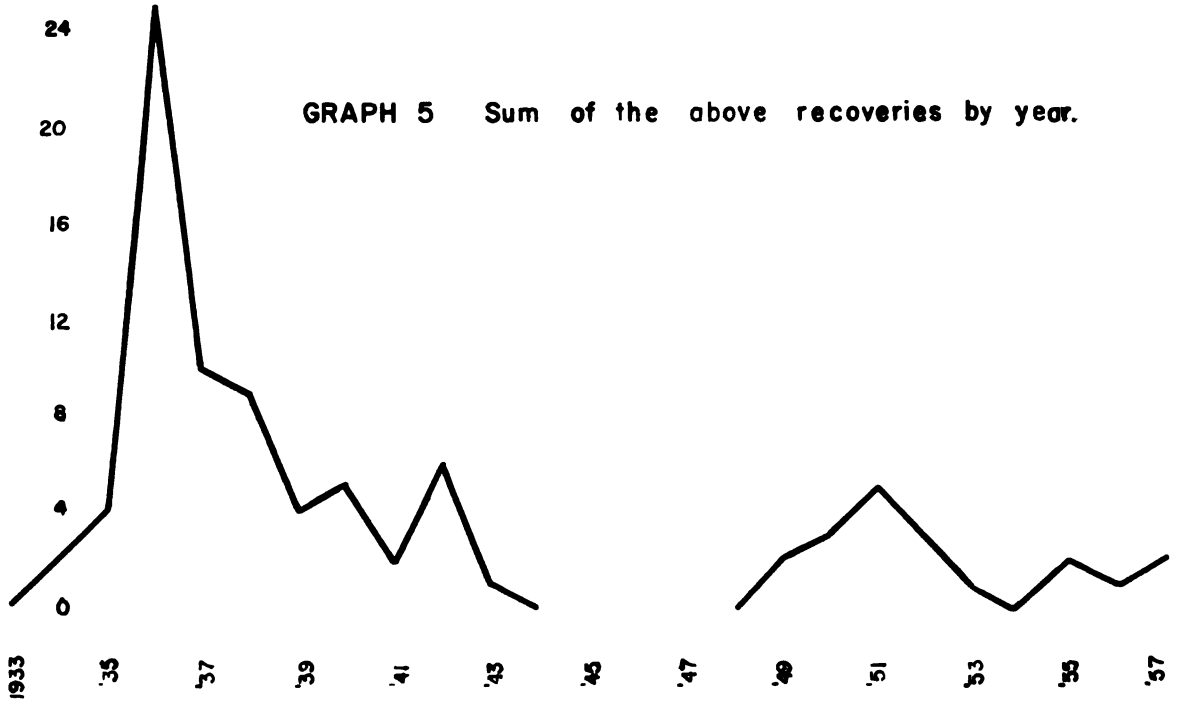
------ no. recovered per year, scale on right.

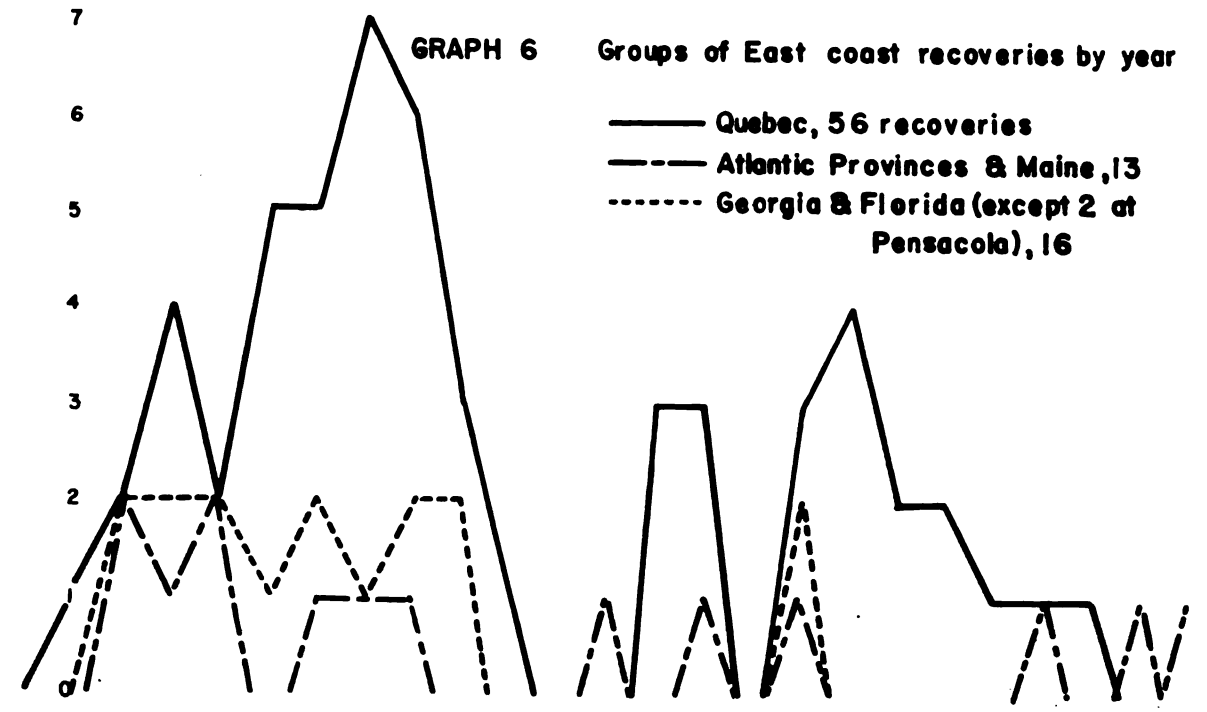


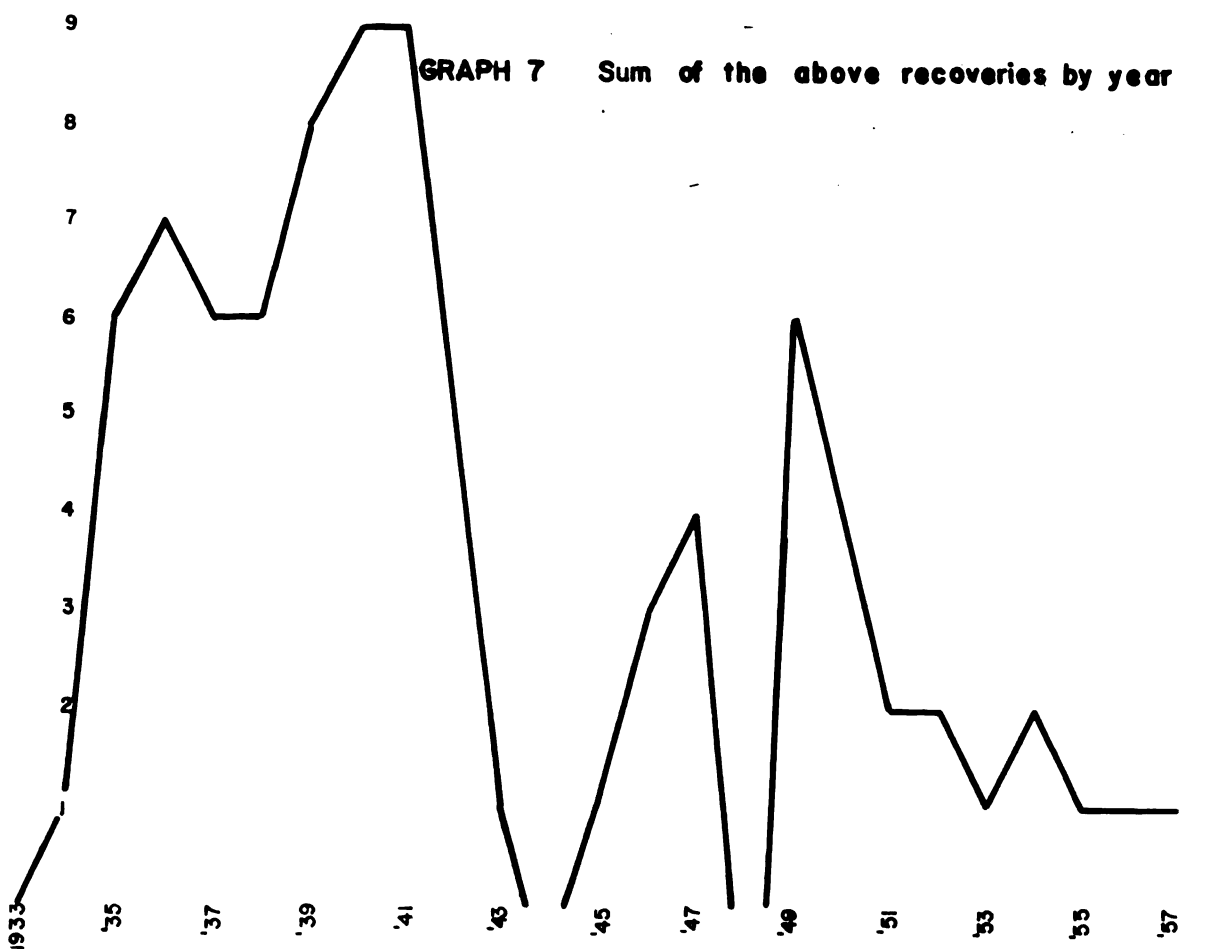
GRAPH 2 Sum of recoveries from Md., Va., W.Va., N.C., S.C., Ga., Fla., Ala., Ken., Tenn., Miss., Kans., Mo., Ark., Okla., La., Tex., by month.

GRAPH 3 Mexican recoveries by month.


10
9
8
7
6
5
4
3
2
1
GRAPH 4 Gulf of Mexico recoveries by year.
Texas, 36 recoveries
Louisiana, 15
Mexico, 36


24
20
16
12
8
4
0
GRAPH 5 Sum of the above recoveries by year.
1933
'35
'37
'39
'41
'43
'45
'47
'49
'51
'53
'55
'57


GRAPH 6
Groups of East coast recoveries by year
Quebec, 56 recoveries
Atlantic Provinces & Maine, 13
Georgia & Florida (except 2 at Pensacola), 16
7
6
5
4
3
2
1
0


GRAPH 7
Sum of the above recoveries by year
9
8
7
6
5
4
3
2
1
1933
'35
'37
'39
'41
'43
'45
'47
'49
'51
'53
'55
'57

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