THE NAIADES (MOLLUSCA, PELECYPODA, UNIONACEA) OF FISHERY BAY, SOUTH BASS ISLAND, LAKE ERIE

PART I. INTRODUCTION, HISTORY, FAUNAL ORIGINS, AND PHYSIOGRAPHY

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INTRODUCTION

This study of the naiad fauna of Fishery Bay at South Bass Island in the western basin of Lake Erie was initiated in the fall of 1953 as one phase of a comprehensive study of the entire bay area. The present report deals with the Unionidae of Fishery Bay. Collections and observations of the major faunal and floral groups represented were made during the following two years in each habitat area within the bay as well as in several other bays and the open lake in the surrounding region. Subsequent collections of naiades were made in the fall of 1956 and again in the summer of 1957, but most of the material upon which this report is based was obtained during the two-year period beginning in the fall of 1953. Since 1955 the collection itself has been enriched by the addition of many specimens from numerous localities other than Fishery Bay. The largest accession (1953) was that of the K. G. Wood collection from the western basin of Lake Erie. These specimens from the lake, along with other collections, many from central Ohio streams, have been valuable as reference material with which to compare the bay forms.

The objectives of this study are to determine (1) what species of naiades inhabit the bay, (2) in which of the bay habitats the various species live, (3) the variability of each species within a single habitat area and, in cases of greater distribution, from one habitat area to another, (4) the growth rate and longevity of each species in the study area, (5) some of the conditions (physical, chemical, and biological) under which this fauna lives, and (6) the probable origin of the various species which at present comprise the naiad population of the bay.

All the species collected, regardless of the number of specimens taken, are included in this study. It is believed that the knowledge gained from a few specimens carefully studied is far better than the only alternative of no knowledge at all.

ACKNOWLEDGMENTS

This study was made under the supervision of Dr. Thomas H. Langlois to whom I owe a debt of gratitude for numerous suggestions and constructive criticisms. I have also been fortunate in having the use of the extensive library and collections of the Division of Mollusks of the University of Michigan Museum of Zoology and I wish to thank Dr. Henry van der Schalie for this privilege and many others receoved during the course of this study. I greatly appreciate the valuable suggestions given by Dr. Aurèle La Rocque, Dr. Ralph Dexter, Dr. H. Ray Eggleston, and Mr. Clarence Clark, each of whom gave freely of his time and knowledge.

The arduous task of collecting was made less difficult by the assistance of Mr. Paul Webster, master of the Stone Laboratory research vessel BIOLAB, and Mr. Ernest Miller, Superintendent of the Ohio State Fish Hatchery at Put-in-Bay, Ohio.

To these and to others who contributed in one way or another to the fund of information upon which this study is based I wish to express my sincere appreciation.

A HISTORY OF THE STUDY OF THE NAIADES OF LAKE ERIE

The naiad fauna of the Mississippi Basin (van der Schalie, 1950: 451) of North America has been of interest to students of conchology and malacology since its discovery in the early eighteen hundreds. In examining the early literature in this field one finds such names as Say, Lamarck, Rafinesque, DeKay, and Kirtland, familiar in many fields of zoology as well as Lea, Barnes, Conrad, Hildreth, and Swainson, best known perhaps to students of the mollusks. These men were primarily concerned with seeking out and describing the many "new species" of mussels which inhabited the vast drainage basin west of the Appalachians. Their zeal in this undertaking led them (as it did others in other fields) to describe as species many of the ecological variants and aberrant forms which came their way. In those species exhibiting sexual dimorphism, the male and female were frequently described as two distinct species (Kirtland, 1834: 117). These practices led to considerable confusion in the taxonomic nomenclature of the group. Although this problem has been solved in most instances by relegating to synonymy those names which proved to be redescriptions, there yet remains the problem of properly treating morphological-geographical and morphological-ecological clines. These difficulties could hardly have been foreseen by early workers especially in view of their "type" concept of the species. In view of the complexity and the extent of the fauna as we know it today, it is to their credit that they accomplished the truly remarkable job they did. Their work has also made the modern student of the naiades acutely aware of the nature and degree (if not the explanation) of the variations that exist in this complex group.

The first published record of naiades in Lake Erie is apparently that of the original descriptions of Unio alatus and Unio plicatus by Thomas Say (1817). An interesting problem of authorship arose here because the type specimens were collected in Lake Erie by Lesueur and given to Say, along with the suggested trivial name plicatus for the non-alate individual (Simpson, 1900: 767). Say figured the specimen in the article on conchology in Nicholson's Encyclopedia (of Arts and Sciences) (1817) as a variety of Unio crassus (Lea, 1870: 30). Barnes later (1823: 120) recognized the variety as a species, gave it a verbal description and listed Lesueur as author -- as had Say. This is, as far as I can learn, the only instance where the type of a species was collected and named by one individual, figured by a second, verbally described by a third, and published by a fourth. Since Say's figure constitutes a valid description he is today credited with the authorship. The fact that Barnes had actually redescribed a different form (U. peruviana Lam.) under the name of U. plicatus Lesueur led to even further confusion which persisted until untangled by Utterback (1816: 116) and Ortmann (1919: 27) nearly a century later. Ligumia nasuta and Strophitus undulatus, both common species in Lake Erie, were also described by Say in this same publication but were not listed from the Lake.

Lamarck (1819: 74, 532) described U. rectus, U. clavus, and a "variety of U. crassidens" from Lake Erie. The following year Rafinesque (1820) described 68 species of naiades from the Ohio River and/or its tributaries. Eleven of these species were eventually recorded from Lake Erie. Although several additional forms have been described from Lake Erie since the time of Say and Lamarck, only the species mentioned above, i. e., Amblema plicata (Say), Proptera alata (Say), Ligumia recta (Lamarck), and Pleurobema clava (Lamarck), have been established as valid species. The other forms, to be reviewed in the following account of the species, have been recognized as questionable subspecies or ecological variants of previously described forms (van der Schalie, 1941: 246). It is interesting to note that P. clava is known from Lake Erie only from its original description. This fact suggests an error in the type locality and its correctness has been rightly questioned by La Rocque (1953: 97). There remains, however, in view of evidence to be presented below the possibility that this, as well as several other questioned records (Goodrich and van der Schalie, 1932: 12), may well be correct.

The naiad literature of the middle and late nineteenth century was primarily descriptive (Lea, 1828, 1829, 1831, 1834, etc., to 1874) (Conrad, 1834, 1836, 1841, 1842, etc., to 1868) (Say, 1817, 1818, 1829, etc., to 1834) (Rafinesque, 1818, 1819, 1820, 1831, 1832) (Barnes, 1823, 1828) (Swainson, 1822, 1820-1833, 1835, 1840) (Green, 1827, 1830, 1832) (Lamarck, 1791-1832, 1799, 1801, 1805, etc., to 1830) with a generous sprinkling of locality lists (DeKay, 1843) (Dewey, 1856) (Hubbard, 18__) (Whiteaves, 1861) (Lewis, 1874) (Walton, 1891) (Smith, 1894) and personal collection check lists (Ravenel, 1834) (Jay, 1852).

These were followed, near the turn of the century, by several attempts to deal with the origin and distribution of the many forms described. Some of the earliest contributions to these problems in the Lake Erie area are those of Bell (1861: 45-46) and Whiteaves (1861). Bell recorded the discovery of several species of fossil or subfossil "uniones" from what he interpreted to be an ancient Niagara River bed at Niagara Falls, Ontario. Whiteaves dealt with the more general topic of the biogeography of lower Canada. Walker (1889) reported the discovery of the Atlantic Drainage naiad Elliptio complanatus (Dillwyn, 1817) in Michigan and later (1891) specifically noted its occurrence in northern Michigan. This instance of discontinuous distribution, coupled with that which existed in the Grand River of Lake Michigan, when added to Walker's interest in historical geology, may well have been the problem-challenge combination which was responsible for Walker's later contributions along this line. In his paper on the molluscan fauna of Michigan (Walker, 1894: 13) he observed that the Lake Michigan tributaries had species which "belong mostly to the Strepomatidae and Unionidae, the characteristic families of the Mississippi Valley fauna" and notes that "If this is found to be true, it would be in accord with the theory of the geologists, that, toward the end of the glacial period the great lakes had their outlet to the south into the Mississippi Valley, and tend to show that during that period these forms made their way north into Lake Michigan, and thence into its tributaries ...." While there is no evidence (other than the suggestion above) of knowledge of the Maumee-Wabash connection in this paper, Walker later (1898: 12) includes the Des Plaines-Illinois and the Saginaw-Grand outlets in addition to the Maumee-Wabash route in explaining the origin of the Michigan naiades. The postglacial migration routes from the east, the Trent and Nipissing Outlets, are later dealt with in conjunction with a consideration of the faunal history of the naiades of the entire Great Lakes Basin as it exists today (Walker, 1913).

Ortmann (1912, 1913, 1919, 1924) succeeded Walker as the principal North American student of naiad zoogeography, and it is chiefly through his studies (1924: 113) that the post-glacial valley of the Lake Erie Basin suggested by Walker (1913: 16) was verified. Van der Schalie (1938: 10) demonstrated that the discontinuous distribution of particular elements of the naiad fauna of the Clinton, Rouge, Huron, Raisin and Maumee Rivers of Lake Erie also reflected its origin in the manner postulated by Walker and Ortmann.

In addition to taxonomic and zoogeographic works, some of which are listed above, the Lake Erie naiades have more recently been utilized in studies of nacreous and epidermal variation (Grier, 1920), morphological variation (Grier, 1920), erosion and thickness (Grier, 1920), sexual dimorphism (Grier, 1920), and growth rate (Grier, 1922). Wood (1953) made a study of the habitat distribution of the benthic invertebrates of the western basin of Lake Erie including the naiades in his work. It was found that the bivalves made up 78.3 percent (by weight) of the benthic fauna -- even with the weight of the shells deducted. The results of these studies are referred to in appropriate places in the following text.

The only previous study known which refers specifically to the naiad fauna of Fishery Bay is that of Brown, Clark, and Gleissner (1938). These workers found that the Fishery Bay naiades were larger at any given age than Pelee Island specimens of the same species but were smaller than corresponding forms collected at East Harbor on the mainland shore. This fact was correlated with the degree of exposure of these habitats to wave action, the degree of stunting being directly related to the amount of exposure. The thoroughness of their sampling is reflected in the fact that they collected 24 of the 27 species now known to inhabit the bay. Of the three species herein added to the list, two are apparently restricted to the pond (not sampled in their study) and the third is represented in the collection by only three Fishery Bay specimens.

THE ECOLOGICAL, ZOOGEOGRAPHICAL, TAXONOMIC PROBLEM

The naiad fauna of Lake Erie is unusual in several ways. Most, if not all, of the species found there are markedly smaller than their counterparts found in the streams tributary to the lake. This so-called dwarfed, stunted or depauperate fauna is so striking that the majority of the species recorded from the lake have, at one time or another, been described as species or subspecies distinct from those which inhabit streams (Lea, 1840, 1857, 1862) (Conrad, 1834) (Simpson, 1900) (Grier, 1918) (Baker, 1922, 1927, 1928). In view of the paucity of information concerning variation and distribution available to workers such as Lea, Conrad, and Simpson, it is apparent that they were simply describing newly discovered forms as new taxonomic entities.

As the geographic distribution of the naiades became better known it was found that most lake habitats produced stunted forms while most streams did not. It became obvious that these lake forms today have a discontinuous distribution. The possibility that all lakes (and ponds) having such a fauna were once interconnected in a manner permitting migration seems highly unlikely. While the evidence just cited is highly speculative, that obtained by Brown et al. (1938) was not. These workers found that the degree of stunting within the lake was predictable and varied with habitat. This evidence strongly indicates, and van der Schalie (1941), along with most other contemporary students, concludes that naiad lake forms are ecoforms and should not be recognized as subspecies.

He suggests:

> If for any reason whatsoever one wishes to designate a form it would be more sensible to do so as follows: Lampsilis siliquoidea form rosacea. A rule of this sort would eliminate the misleading emphasis which is placed on forms when they are written as a subspecific or even a specific name.

I would add only one modification to the above suggestion and that is to use the term ecoform preceding the trinomen if it has been established that the form is due principally to the action of the environment on the individual. In this manner the term "form" could still be used in the general sense of "a group having a different structure," be it due primarily to environment or heredity.

Baker, Grier, and others apparently were aware of the ecological nature of these lake-dwelling naiades but nevertheless were of the opinion that they should be designated by a trinomial. Baker (1928: 40) states:

> In the matter of varietal names, the writer believes that any form which can be distinguished from another should bear a name. Names are but handles to use in descriptive work and the trinomial system lends itself clearly to the designation of varieties. These varieties may be geographical or ecological.

Ortmann (1919: 81) was more conservative in his use of trinomials and, while using the names supplied by others, did not, at least as far as Lake Erie is concerned, coin any new names himself. This was fortunate in view of the fact that Ortmann was familiar with the lake fauna and could easily have followed the precedent of Baker and Grier thus burdening the synonymy with many more names.

Most of the evidence supports the generally accepted inference that the Lake Erie naiades are ecoforms of species also found in the streams and, AS SUCH, should not be accorded either specific or subspecific status. The problem then becomes one of determining to which stream species these lake ecoforms should be assigned. It has seemed natural to associate each with its most closely related form living in the adjacent lake tributaries. Fusconaia flava parvula (Grier, 1918) of the lake thus became the ecoform of Fusconaia flava (Raf., 1820) of the tributaries and Pleurobema cordatum pauperculum (Simpson, 1900) became the ecoform of Pleurobema cordatum coccineum (Conrad, 1836), a stream subspecies also found in the lake tributaries. This policy has been generally followed by workers in this field for the past thirty years.

There is found among stream forms a problem of variability similar to that of the lake forms. The term similar is important here because, although the problem involves variability usually related to habitat and deals with many of the same species or species complexes which are present in Lake Erie, the degree of variability occurring within a drainage basin such as the Ohio River is markedly greater than that observed in the same form within the lake. While the dwarfed forms in Lake Erie seemed to constitute a single taxonomic unit (for each species represented) within the lake environs, the stream forms were described under as many as five different names. In most cases each described entity was definable and distinguishable from the others and inhabited streams of a particular size. The accumulation of additional specimens during the first quarter of the present century revealed that species within each complex were, or seemed to be, connected by a series of intermediate forms. In passing from a headwaters tributary down to the lower Ohio or Mississippi River one might witness an apparent gradual transition from one species to another. This clinal distribution is particularly striking in, but not limited to, the subfamily Unioninae (Ortmann, 1920: 311) and is represented in this group by the following complexes (see p. 7).

There are a number of other complexes such as the Lampsilis ovata Complex and the Dysnomia torulosa Complex, both in the Lampsilinae. Several of the forms listed above have been long relegated to the

FUSCONAIA FLAVA COMPLEX

HEADWATERS	form flava Rafinesque, 1820
Compressed,	
Elongate,	form rubiginosa Lea, 1829
Low umbones,	
Non-sulcate	
	form trigona Lea, 1831
LARGE RIVER	
Obese,	
Short,	form undata Barnes, 1823
High umbones,	
Sulcate	form wagneri Baker, 1928

PLEUROBEMA CORDATUM COMPLEX

HEADWATERS	form coccineum Conrad, 1836
Compressed,	
Elongate,	
Low umbones,	form cordatum Rafinesque, 1820
Non-sulcate	
	form catillus Conrad, 1836
LARGE RIVER	
Obese,	form plenum Lea, 1840
Short,	
High umbones,	
Sulcate	form pyramidatum Lea, 1834

AMBLEMA PLICATA COMPLEX

HEADWATERS	form costata Rafinesque, 1820
Compressed,	
Fluted wing,	
Low umbones	
	form rariplicata Lamarck, 1819
LARGE RIVER	
Obese,	
Non-fluted wing	
High umbones	form peruviana Lamarck, 1819

synonymy of other members of their species complex. They are used here because measurements given in the original descriptions or taken from the original plates establish them as intermediates between recognized forms. It should be kept in mind that each complex represents a series of anatomically different forms, each of which is related to a somewhat different habitat, and is more or less connected by intermediates. The problem of variation of stream dwelling members of species complexes is treated here because it has a direct bearing upon the nature and identity of several of the naiades of Lake Erie.

There are at least three possible explanations of the observed facts concerning the relationships between the apparently intergrading members of each of the several systematic complexes. They are:

(1) Each form within a complex may be genetically essentially the same as the others and none reproductively isolated from the others. If this be true, the obvious differences in anatomy would be a result of the effects of the different environments. In this case we might expect as many different forms as there are different environments which influence growth form. The result would be a highly variable (polymorphic) species. The variability of the species would, within the limits set by genetic composition, be determined by the range of environments in which it lives and the extent to which these environments affect the growth form.

(2) Each form within a complex may be reproductively isolated from the other forms. These several forms then constitute sibling species (Mayr *et al.*, 1942). If this were the case, it is apparent that the varieties of each such species overlap those of at least one of the others. This would render the identification of some intermediate individuals an extremely difficult and perhaps, at times, impossible task. The impossibility of the identification of these sibling species would not, however, alter the fact of their existence. In the absence of morphological, physiological or other intrinsic differences between forms it would seem that tests of reproductive isolation alone would verify or disprove this theory.

(3) Each form within a complex may be only partially isolated (reproductively) from the others. The differences between these forms would then be attributable in part to a difference in genetic composition and in part to environmental differences. Cases of several defined forms having few intermediates may represent nearly isolated groups (gene pools) between which the gene exchange has all but ceased. Such populations have been termed sympatric subspecies, although this expression has lost favor in recent years.

In the absence of any direct means of measuring the degree of reproductive isolation that may exist between naiad populations or population segments in nature, the evidence needed to determine the relationship of these forms must be sought elsewhere.

While the nineteenth century student of the naiades had only morphology to guide him in learning the relationships of the forms with which he dealt, the modern student is somewhat more fortunate -- not only in having a much better knowledge of the variability of these faunal elements but, more especially, of the distribution patterns of these variations. A knowledge of the type and degree of variation and geographic distribution, viewed in the light of our understanding of population genetics, gives us a much clearer insight into evolution on the species and subspecies levels. This is precisely the knowledge and understanding required to deal with taxonomy in a realistic manner and to avoid decisions based on hunch, guess, and subjective whim which have given the science of classification a bad name in some quarters in the past. While it is not assumed that a knowledge of these things will solve all systematic problems, it seems that little real progress can be made without them.

METHODS AND MATERIALS

Physiography

The map of the bay area (Pl. I, Fig. 3) was constructed from data obtained by triangulation with a surveyor's transit. Depth contours of the pond and inner bay were made from soundings taken through the ice using either a graduated lead line or an oak sounding rod. Depths in the outer bay are based upon those taken by the U.S. Lake Survey (1936) modified to compensate for the increase in lake level (2.10 ft.) which occurred during the twenty year period between 1936 and 1956 (James L. Verber, personal communication). The docks and sea walls were measured with a surveyor's tape and points determined by triangulation were checked by tape where possible. A grid of squares one hundred feet on a side was then superimposed over the finished chart, thus permitting the fixing of any collection site (using coordinates) to the area encompassed by each square. This technique proved satisfactory except in places where habitats changed sharply. In these situations a note concerning the habitat in addition to the appropriate coordinates proved adequate. The sediment terminology used

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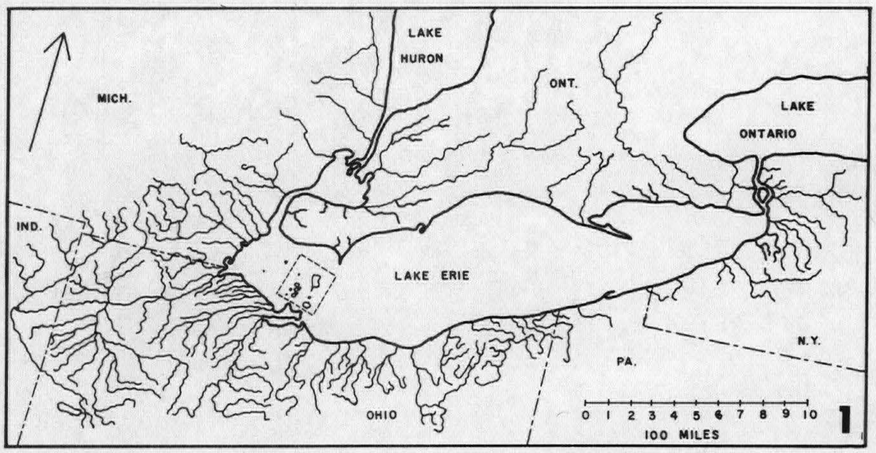
DESCRIPTION OF PLATE I, OPPOSITE PAGE

Fig. 1 Lake Erie and its Tributary Streams

Fig. 2 The Bass Islands of Lake Erie.

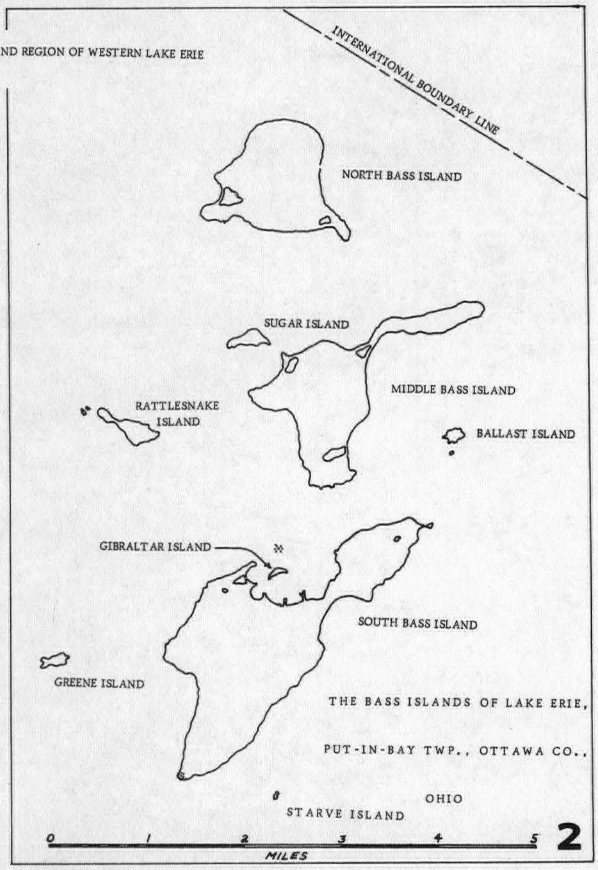
Fig. 3 Fishery Bay of Lake Erie, South Bass Island, Put-in-Bay Township, Ottawa County, Ohio.

PLATE I



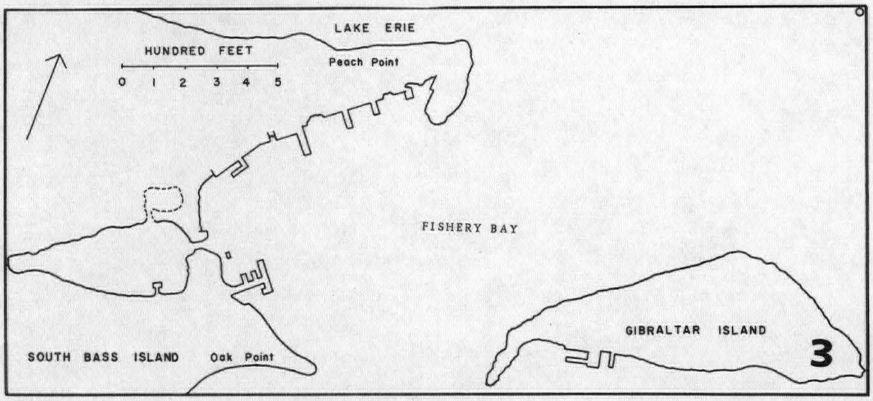
1

THE ISLAND REGION OF WESTERN LAKE ERIE



THE BASS ISLANDS OF LAKE ERIE,
PUT-IN-BAY TWP., OTTAWA CO.,
OHIO

2



3

here is essentially that of Wentworth's Classification (Welch, 1948: 353) with sediment sizes grouped as indicated by the brackets below.

Particle Diameter	Particle Name	Group Name
256 -	Boulder)	Rocks
65 - 255	Cobble)	
4 - 64	Pebble)	Gravel
2.0 - 3.9	Granule)	
1.0 - 1.9	Very-coarse sand)	
0.5 - 0.9	Coarse sand)	Sand
0.25 - 0.49	Medium sand)	
0.125 - 0.249	Fine sand)	
0.062 - 0.124	Very fine sand)	
0.004 - 0.061	Silt	Silt
0.000 - 0.0039	Clay	Clay

The expression "rubble" is here used to refer to an ill-sorted mixture of coarse gravel and rocks, either angular and/or water worn.

Collection of Specimens

Attempts to collect naiades were made by every means that seemed likely to prove fruitful. Efforts at quantitative sampling using an Ekman Dredge were abandoned after several days' labor produced only two specimens. The "noodling" or "polliwogging" technique of passing the fingers lightly over the bottom in waters up to neck deep was also unproductive. This method is many times very successful in streams where the water is so turbid with plankton or silt that the bottom cannot be seen. Dredging, a successful procedure if an otter trawl is used in the deep lake muck, was only moderately successful when smaller, two to four foot (width) dredges were used in the bay. This, however, was the only way, except by diving, that depths over ten feet could be sampled and, even then, the rocky bottoms at those depths were all but impossible to work. Skin diving in boulder strewn areas, following dredging, established the inefficiency of the operation of dredges over such a bottom -- a large number of specimens were taken where the dredge had taken few or none at all. A shovel and floating sieve arrangement produced a few juveniles in shallow areas but worked no better than a dredge and required considerably more labor. The water was seldom clear enough for diving, but this seemed to be the only feasible method of taking specimens from the deeper rocky bottoms. Full advantage was taken of each of several rare periods of warm clear water. The best collecting was accomplished during and just following prolonged strong blows from the southwest. The net effect of such a blow is a surge of water to the east lowering the water level in the island region as much as seven feet (Langlois, 1952: 6). Such a phenomenon is known as a seiche. The naiades may then be hand picked from exposed substrates that are usually three to five feet under water. The only disadvantage is that these blows usually came in late November or March when the water temperature is below 7° C. (45° F.) and most of the mussels are "dug in" beneath the sand and gravel and difficult to see. Barnes (1823: 114) also noted this winter burying behavior and subsequent exposure above bottom in summer. An unusual opportunity came on September 21, 1954, when a wind generated seiche of the type described lowered the water level at least five feet for a period of several hours. The naiades were for the most part in their summer positions, protruding above the bottom or actively moving about. Six hundred sixty naiades, the largest single collection made in the entire course of the study, were taken in approximately four hours.

Collection of Data from Specimens

All specimens collected were taken alive to the laboratory where individuals over ten grams were weighed to the nearest gram on a Hanson Dietetic Scale. This scale has a capacity of 500 grams and is calibrated in one gram graduations. The smaller specimens were weighed to the nearest tenth of a gram using an Ohaus beam balance having a scale calibrated from zero to ten grams, in one-tenth gram steps. Care was taken to remove the excess water from each specimen by placing them ventral margin down on a towel until the valves opened slightly allowing the excess water to drain. The shells were again weighed after the soft parts were removed in order to determine the percentage of shell weight for each individual. The gills were examined for glochidia, and the foot-gill sinus and pericardial cavity were posted for parasitic or commensal symbionts such as flukes, mites, and leeches.

In addition to the weight noted above, the specimens from several of the 1956 collections were weighed while suspended in water so that the specific gravity might be calculated.

Measurements of length, height, and width of each specimen were also made and recorded. It was thought best to follow themethods of measurement used by previous authors so that the bay forms could be compared with those from other localities and, in cases of uncertain identity, with the dimensions and proportions of the types. An examination of the terms and methods used in early descriptive work revealed some gross differences among investigators. Many authors neglected to describe the nature of their lengths, widths, heights, diameters, breadth, and axes. According to Barnes (1823: 112) Lamarck considered "the beaks as the base, ..." and was not alone in terming that side of the beaks having the ligament as anterior. This explanation helps greatly in understanding Lamarck's descriptions. Barnes quotes Say who encourages a reversal of the terms anterior and posterior in order to conform to the definitions of Cuvier and to have the mouth at the anterior end as it "ought always to be considered." In spite of the logical plea of Say, Barnes and others (e.g. Hildreth, 1828) followed Lamarck's usage of anterior and posterior, though Barnes does consider the beaks to be dorsal. In order to avoid deciphering these older descriptions on the occasion of each reference a table of terms was constructed for ease of interpretation. The decision to use the terminology of Call (1900) and McMichael and Hiscock (1958) was made in view of the facts that they are in common usage today by most malacologists and easily understood by workers in related fields. Definitions of the dimensions measured are given below since a word such as "length" may have several meanings:

(1) length parallel to the ventral margin
(2) length parallel to the dorsal margin
(3) length parallel to the hinge line
(4) length parallel to the umbonal slope

The dimensions taken in this study are defined below.

LENGTH is the maximum antero-posterior dimension of the shell. It has been found to be roughly parallel to the hinge line in all the species here studied.

HEIGHT is the maximum dorso-ventral dimension of the shell measured at right angles to the length. This dimension does not include the ligament, umbones nor the wing in the alate species, Proptera alata (Say) and Leptodea fragilis (Rafinesque). The so-called wing or post dorsal ridge of the other species dealt with here is included. It is believed best not to include the structures listed above because in many (if not most) instances they are eroded, broken, or both. This measurement usually can be made best from the inside of the valve. In the cases of P. alata and L. fragilis the height is measured as described above except that the umbonal slope is considered the dorsal limit. The high point of the umbonal slope in both species is almost always just a short distance posterior to the beaks proper and approximates the level of the lateral tooth in the right valve or the lateral tooth sulcus in the left valve.

WIDTH is the maximum transverse dimension of the shell with both valves in normal position and includes sculpturing, when present.

The measurements of length and height were madewith the use of a clam board, constructed for this purpose, with a Glogau vernier caliper, or with a pair of needle-point dividers and a linear metric rule. The clam board was outfitted with a metric grid and with two metric scales placed at right angles

TABLE 1. INTERPRETATION OF TERMS USED BY NAIADOLOGISTS IN DESCRIPTIVE STUDIES

Modern Term	Say 1817[a]	Lamarck 1819[b]	Rafinesque 1820[c]	Barnes 1823	Lea 1828	Hildreth 1828	Conrad 1836	DeKay 1843
Length	no measurements given	breadth	breadth	breadth	breadth	breadth	no measurements given	transverse axis
Height	no measurements given	length	length	length	length	length	no measurements given	vertical axis
Width	no measurements given	-	diameter	diameter	diameter	diameter	no measurements given	diameter
Anterior	anterior[b]	posterior	anterior	posterior	anterior	posterior	anterior	anterior
Posterior	posterior[b]	anterior	posterior	anterior	posterior	anterior	posterior	posterior
Dorsal	-	base or back	dorsal or hinge (margin)	dorsal	dorsal	dorsal (margin)	ligament (margin)	hinge or dorsal (margin)
Ventral	basal[b] (edge)	upper (margin)	basal (margin)	basal	basal	basal (margin)	basal (margin)	lower (margin)

Modern Term	Baker 1898	Call 1900	Simpson 1914	Utterback 1915	Ortmann 1919	Baker 1928	Clench and Turner 1956	McMichael and Hiscock 1958
Length	length	length	length	length	length	length	length	length
Height	height	height	height	height	height	height	height	height
Width	breadth	width[d]	diameter	diameter	diameter	diameter	breadth	width
Anterior	anterior	anterior	anterior (before)	anterior	anterior	anterior	anterior	anterior
Posterior	posterior	posterior	posterior (behind)	posterior	posterior	posterior	posterior	posterior
Dorsal	dorsal	dorsal	dorsal (line)	dorsal	dorsal or upper	dorsal	dorsal	dorsal
Ventral	ventral	ventral	basal (line)	ventral	ventral or lower	ventral	ventral	ventral

[a] Say reverses the position taken here and uses Lamarck's reverse terminology in his American Conchology (1830: pl. 22).

[b] From translated quotes of Barnes (1823) or from quotes of Call (1900).

[c] From translation of Poulson (1832).

[d] Occasionally uses breadth or diameter.

I interpret the "axis" dimension of Rafinesque to be the length of a line passing from the dorsal to the ventral margins at right angles to the length (breadth of Rafinesque) at a point midway between the anterior and posterior extremities.

and meeting at the lower left corner. A transparent hairline T square was used to eliminate parallax error. This method was most convenient, the calipers most precise, and the dividers most rapid. All measurements of length and height were taken at, or rounded off to, the nearest millimeter. The width in every case was taken with the vernier caliper and each figure was rounded off to the nearest millimeter with the exception of those less than ten millimeters, and these were taken to the nearest tenth of a millimeter. The flexible periostracum, extending beyond the anterior, ventral, and posterior shell margins in all but the smallest specimens, was such that consistent readings of an accuracy greater than the nearest whole millimeter were impossible for any but width measurements.

Data for the age-length graphs were obtained by measuring each annulus possible on every specimen. Length only was measured for each year; thus, each specimen yielded as many items of length data as it was years old. This was accomplished using needlepoint dividers and a metric scale calibrated in millimeters. If the specimen being measured had been collected during the winter months of November, December, January, February, or March the margin of the shell was considered to be the last annulus. Shell margin measurements of individuals taken during the growing months from April to October were not used in the growth study. Lake Erie naiades are well known for the regularity and distinctness of their annuli or annual growth rings (Ortmann, 1919: 22) (Grier, 1920: 154; 1922: 132). These rings, much like those found in tree borings, on fish scales, vertebral sections, etc., are produced by changes in growth rate. The well-defined and regular nature of the annuli of Lake Erie naiades may be a result of the greater stability of the lake when compared to stream conditions. This is suggested by Grier (1922: 132) and he gives evidence which supports this inference. While the annuli of lake-dwelling naiades may be more easily read than those of the same species in most streams, there are still difficulties to be overcome and pitfalls to be avoided. Lake Erie naiades are not exempt from false annuli which may be produced at any time during the growing season when the mantle margin is withdrawn to the extent of breaking contact with the edge of the shell where new periostracum and prismatic layer are being deposited (Coker et al., 1921: 131). A seiche which exposed the mussel to the air for several hours might produce a false annulus. Fortunately most, if not all, false annuli present on Lake Erie specimens may be recognized by a combination of the following characters:

(1) The make-up of the material of which the false annulus is composed (i.e., color, texture) is usually quite different from the true annulus and may be quite different for some species. False annuli are almost without exception much thinner.

(2) False annuli are generally incomplete, not extending from anterior to posterior dorsal margin in the unbroken, uniform manner of a true annulus.

(3) False annuli are not flanked by the type of periostracum associated with the cessation and resumption of growth as is the true annulus. The color (and perhaps the thickness) of the periostracum changes as winter approaches in many species. The reverse color change is observed in the spring. Individuals with shell rays frequently lay down unrayed periostracum in late fall and early spring. This produces interrupted rays on the disc and the true annuli pass over the surface of the shell between the interruptions while the false annulus passes through them.

(4) The true annuli of any particular species from any particular habitat have a relatively uniform spacing or periodicity which is the same from specimen to specimen of the same age or between individuals of different ages if the comparison is made between those annuli which represent the same ages. This periodicity changes in the naiad, indicating a rapid growth rate as a juvenile, a moderate to slow growth rate as a sexually active mature adult, and the development of a very slow rate at the outset of senility when reproductive activity begins to decrease. Once the worker learns the periodicity pattern of a species

for a particular habitat he can easily identify an annulus out of position, and he may suspect any such annulus of being false. If the annulus on either side of the one in question is "in place" and satisfies the predicted sequence, and if some or all of the above conditions -- (1), (2), (3) -- are found to prevail, the annulus is pronounced false and is neither counted nor measured.

It should be noted that the above observations concerning false annuli were not made at the beginning, but were developed during the course of this study. It should not be concluded that the criteria used in this study to identify false annuli will be effective everywhere. In even a few of the Lake Erie shells there remains some doubt concerning the validity of a few of the annuli. These instances -- fortunately rare -- were confined to either very old specimens where the annuli were so close together they almost overlapped or to a few young specimens which apparently passed through a winter marked by an atypical annulus. Since the position of this annulus was, in each of the several cases, well marked by the usual color change which accompanies the winter rest period, the annulus was counted and measured even though it was atypical.

A light was used in the manner suggested by Chamberlain (1931; 715) to aid reading the thin to moderately thick shells, when such a technique proved advantageous. This was of particular value in specimens where the annulus on the surface was partially worn away. The transmitted light made even these lines stand out in bold relief.

A number of individuals had eroded umbones with the resultant loss of one or more annuli in a region where the use of transmitted light was not possible due to the thickness of the shell. This was especially true of older specimens from the soft bottoms in deep water. At first it was thought that these individuals would have to be passed over, and that, as a result, it would be impossible to study growth rate during senility or to make any estimates of longevity in some species. It was found, however, by knowing the general periodicity (of the annuli) of the species and by noting the spacing represented by the remaining annuli on the specimens in question, the probable number of missing annuli could be estimated. This procedure was followed and lengths were taken in the usual manner from all specimens having three or fewer annuli missing. Where the eroded zone involved an estimated four or more annuli the shell was passed over and no growth data were taken. By proceeding in this manner it was found that successive annuli outside the eroded zone fell into the respective length ranges of the age groups to which they had been assigned. Some time later an eroded specimen was studied which had the "missing" annuli of the eroded area boldly represented by well-defined curved ridges in the exposed nacreous material of the shell. A close inspection of the eroded shells previously studied revealed in almost every instance the number of estimated missing annuli represented by fine curved lines or grooves at or very near to the position expected on the basis of periodicity.

Treatment of Data

An extensive search of the literature was required to bring together the background of information necessary to treat each of the species or complexes in the proper perspective. The Unionacea of the North American Great Lakes have never been monographed. The same is true for Lake Erie, as such, and waters of the State of Ohio. Fortunately there exist such comprehensive works for Indiana (Call, 1900), Pennsylvania (Ortmann, 1911 and 1919), Missouri (Utterback, 1915-1916), and Wisconsin (Baker, 1928). These studies and other papers of greater and lesser scope were freely used in developing a knowledge of North American Naiades in general and those of the upper Mississippi and Great Lakes drainages in particular. It is believed that such a background is necessary for an understanding and appreciation of the origin, distribution, and present relationships of the Lake Erie naiad fauna. Items such as synonymies, nature and location of types, previous records, and descriptions have been included in this study of the Unionidae. The following discussion concerns the treatment of data beneath each species heading.

SCIENTIFIC NAMES. A complete scientific name, if it is to be an effective reference, should be followed by author and date. Some writers, in referring to the later use by one author of a certain scientific name coined earlier by another writer, omit the name of the describer but follow the trivial name with the name and date of the user referred to. This practice is quite common in early literature. The confusion arising by such a procedure can be avoided and the reader directed to the referred instance(s) of usage by adding the author, date, and a period to the Latin name, and following this by any number of desired references to the usage of this particular combination. In this manner, Fusconaia undata rubiginosa (Lea, 1829). Ortmann (1913: 291) means that the form rubiginosa, described by Lea in 1829, was referred to as a subspecies of Fusconaia undata by Ortmann in 1913. This policy has been followed in this paper.

SYNONYMY. The Descriptive Catalog of the Naiades (Simpson, 1914) contains what is probably the most complete grouping of naiad synonymies in existence and has been used as the principal reference in constructing the synonymies listed here. An attempt was made in this study to include in the synonymy every name under which the species has been known. In each case an effort was made to cite the earliest reference but no others. The result is a "name synonymy" rather than a "bibliographic synonymy," and is reasonably complete down to the year 1960.

TYPE LOCALITY. The type locality was determined by reference to the original description or, that being unavailable, by reference to a subsequent author's citation.

TYPE SPECIMENS. None of the holotypes of any of the species studied has been examined. All references to the nature of type material in existence, and its location, have been obtained from the literature. The only exceptions to the above are the cases of Amblema plicata (Say), Proptera alata (Say), and Ligumia recta (Lamarck). The Lake Erie specimens of these species are topotypes.

LAKE ERIE RECORDS. Only published records are included in the following lists. Although it is certain that these lists for Lake Erie could be supplemented by a study of museum material there seems little possibility of adding to the knowledge of the Fishery Bay fauna through such an undertaking.

SHELL CHARACTERISTICS. It is surprising in view of the fact that so many lake ecoforms have been given specific or subspecific rank, that there are so few comprehensive descriptions of these unusual naiades in the literature. Most of the descriptions refer only to the few characters necessary to separate the lake from the stream forms (Grier, 1918). Since no new taxonomic forms are described herein, all descriptions pertain to the collected material of a species as a unit, and represent a composite of a particular form in a particular habitat rather than an individual. Measurements and the proportions calculated from them are treated in like manner to show the range of variability and to permit comparison of at least some characteristics with non-lake material on a quantitative basis.

Two proportions were calculated from the raw data of length, height, and width. These were computed for each shell so that these specimens might be compared with others on bases other than size alone. This seemed particularly important in view of the stunted nature of the ecoforms.

The first proportion was found by dividing shell height by length. This expression of relative height was multiplied by a factor of 100 and termed the height index. It can be seen that a round shell or a square shell having its length equal to its height would have a height index of 100. A shell twice as long as high would have a height index of 50, its height being 50 per cent of its length.

The second proportion was found by dividing the shell width by length. This expression of relative width was multiplied by a factor of 100 and termed the width index. A specimen having a width index of 100 would be as wide as long while an index of 25 would indicate a width of only 25 percent of the length. These were chosen because the two variables most frequently mentioned as changing in a predictable manner from the headwaters in a downstream direction are relative width and relative height. Ortmann's conclusions (1920: 310) follow:

> 1. the more obese (swollen) form is found farther down in the large rivers, and passes gradually, in the upstream direction, into a less obese (compressed) form in the headwaters;
>
> 2. with the decrease in obesity often an increase in size (length) is correlated;
>
> 3. a few shells which have, in the larger rivers, a peculiar sculpture of large tubercles, lose these tubercles in the headwaters.

Ortmann presented a wealth of data in support of these conclusions. They have held up so well that today they are referred to as Ortmann's Laws. The laws are found to be particularly true for the so-called primitive genera -- Fusconaia, Amblema, Quadrula, and Pleurobema in the Unioninae and Dromas and Obovaria in the Lampsilinae (Ortmann, 1920: 311).

Two tables were utilized for each species in presenting the results of this limited quantitative treatment. The first table presents the means and extremes of the measurements made and indices calculated. The range was added as a matter of convenience. It was observed that proportions sometimes changed with size and a second table was provided in which the specimens were treated in length groups. A ten millimeter interval was chosen for ease in handling data. This technique proved valuable in groups in which the sample size was relatively large (50 specimens or more) but left much to be desired in those groups represented by a small series. This was particularly true in the Unioninae. Fortunately, material from other localities in western Lake Erie was on hand and used to supplement the bay specimens in the general treatment. Only certain species in the subfamily Lampsilinae exhibit sexual dimorphism in the shell and in these species only the data are broken down into the categories of juveniles, females, and males.

PLATES. Each species is illustrated by a plate of a typical or near-typical Fishery Bay specimen. Only one specimen was used as a model for each figure. The few instances where specimens from outside the bay are used are so noted. Each drawing was made using a 1:1 scale and was neither enlarged nor reduced. These plates are not free-hand drawings.

The following procedure was used in constructing all plates.

(1) The valve was centered on the paper and the outline traced lightly with a pencil. Small marks were then made about the margin noting such fixed points as end of ligament, highest point of beak, and intersection of rays with shell margin. The shell was then removed to one side and the exact process repeated on scratch paper.

(2) A system of polar coordinates was laid out on the drawing with a straight edge using the high point of the beak as the origin from which six to eight straight lines pass out to the traced margin. Distances from the origin along the lines mentioned were taken from the shell with dividers and transferred to the drawing. In this manner the precise position of each annular ring and ray was determined and penciled in.

(3) Once the shell outline, growth lines, and rays were positioned they were inked in using India ink and a crow-quill pen.

(4) Following the gross inking, fine ink lines were added between those already drawn to show contours and sculpturing.

HABITAT DISTRIBUTION. Notes were taken at the time of each collection concerning the location of the collecting site and, when possible, the associated fauna and flora. The collection site data were later used to determine depth and nature of substrate. Each specimen taken is represented on the distribution map as a spot and the map may be compared to those showing nature of substrate and depth contour lines to note nature of distribution with respect to these factors. The same base map is used in each case for each comparison.

GROWTH AND LONGEVITY. The published studies dealing with the use of growth rings in the determination of the age of fresh water mussels date back to the work of von Hessling (1859). He was unable to confirm the annual nature of these rings but he aroused the interest of Hazay (1881) who established the existence of a single growing period each year and verified the intervening rings as being of an annual nature. Israel (1911) concluded, after a study of mussel shell margins collected at various seasons of the year, that there was no winter rest period and that more than one ring may be formed in a single year. These results quite understandably cast doubt upon the validity of the growth ring technique of aging. Lefevre and Curtis (1912), in the first North American work in this field, were aware of Israel's conclusions and expressed their own doubt in the following manner:

> Assuming that these rings, when clearly seen, do represent years, it would seem that the shell grows very rapidly during the first few years of the mussel's life and after that much more slowly. To judge from the lines alone, we should say that many of the large Quadrula shells had reached one-half their size in ten or a dozen years and then taken forty or fifty for the remainder, so closely set are their later rings of growth; and that shells of these species can not reach the most desirable commercial size in a less period than twenty or thirty years.

These speculations, based on uncertain information eventually proved to be true; but, uncertainty and the exercise of perhaps justifiable caution prevented their general acceptance for almost twenty years. Grave doubts of their validity still exist in the minds of some (Shuster, 1957: 5). If the value of this technique had been recognized the fresh water pearl button industry might have been saved. In the twenty years following the paper by Lefevre and Curtis the commercially valuable naiad populations of the Mississippi and Ohio basins were all but extirpated by the clammers. It is questionable in view of the inroads of pollution and dam building (and despite the aid of too late protective laws) whether the naiades will ever return to their former abundance. These same workers (Lefevre and Curtis, 1912: 180) planted cages of mussels in the Mississippi River during a period of two winters. One cage was recovered by Coker. Lefevre and Curtis quote his observations:

> Furthermore, the added area of shell is divided by a conspicuous dark ring and a less distinct ring which, one is tempted to assume, represent the periods of cessation of growth during the two winters. If such an interpretation is made, the growth was accomplished chiefly during 1908 and 1909, while during the present year (1910), the mussel having reached adult size, the growth has been considerably less.

These observations and those cited above are so characteristic of these forms that it is difficult to understand why they were not immediately followed up.

Isely (1914) concluded that the "arrested growth rings" were sufficiently regular and definite to be used as age indicators but declined to use them in his own work. The nature of the annulus and its mode of origin were investigated by Coker <u>et al</u>. (1921: 129). It was found that, although annuli were laid down over winter, a disturbance such as the act of measuring a specimen during the growing season might also produce a ring. The winter annuli were noted as being darker than the false annuli.

The first growth study of lake dwelling naiades was made by Grier (1922) using Lake Erie specimens from Presque Isle Bay, Pennsylvania; Cedar Point, Ohio; and La Plaisance Bay, Michigan. Grier reasoned that, since environmental conditions were fairly uniform in Lake Erie, fairly uniform naiad growth would result and that "the number of rings of growth on the shell could be reasonably conceived to represent the number of years the animal has lived." He measured a number of shell dimensions and recorded the age of each specimen. In the absence of any statement to the contrary I assume that all annuli upon any one specimen were counted in arriving at the estimated age. The data are presented in tabular form (Tables 2, 3)

TABLE 2. AGE AND GROWTH DATA OF LAKE ERIE NAIADES[a]

		Mean length in Millimeters																		
Annulus number		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII	XIX
Fusconaia	N	0	1	3	4	4	4	4	4	4	2	2	2	-						
flava	L	-	17	31	31	33	48	49	55	54	52	51	60							
Amblema	N	0	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	-		
plicata	L	-	21	25	35	42	53	61	62	66	72	56	72	76	87	87	86	-		
Pleurobema	N	-	0	0	0	0	0	0	2	2	2	2	2	-						
cordatum	L	-	-	-	-	-	-	-	58	61	67	67	69	-						
Elliptio	N	0	1	1	2	2	2	0	4	4	4	4	4	-						
dilatatus	L	-	21	26	47	51	45	-	71	71	77	80	80	-						
Lampsilis	N	0	0	0	0	0	1	2	2	2	3	3	3	3	3	3	3	2	2	1
siliquoidea	L	-	-	-	-	-	51	56	54	57	69	73	79	55	82	74	75	85	78	85
Lampsilis	N	0	0	0	2	0	0	2	2	4	4	4	4	4	4	4	4	1	0	1
ventricosa	L	-	-	-	19	-	-	63	52	60	65	67	80	72	79	81	87	96	-	98

N = number of specimens; L = mean length in mm. [a] Recalculated from Grier (1922).

TABLE 3. AGE AND GROWTH DATA OF LAKE ERIE NAIADES[a]

		Mean Length in Millimeters																					
Annulus Number		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII	XIX	XX	XXI	XXII
Anodonta	N	0	0	0	1	1	3	3	3	3	-												
grandis	L	-	-	-	53	75	92	87	84	86	-												
Anodontoides	N	0	0	2	2	3	3	3	3	1	-												
ferussacianus	L	-	-	48	53	61	67	69	72	77	-												
Lasmigona	N	0	0	0	0	0	2	2	2	2	2	-											
costata	L	-	-	-	-	-	74	75	84	83	85	-											
Leptodea	N	0	0	1	2	2	4	4	4	4	0	0	4	-									
fragilis	L	-	-	44	55	98	90	92	89	85	-	-	129	-									
Proptera	N	0	1	1	0	1	1	1	1	2	2	0	1	1	2	2	1	0	0	0	1	0	1
alata	L	-	13	14	-	13	33	26	48	49	66	-	90	86	67	110	96	-	-	-	104	-	101
Ligumia	N	-	0	0	0	0	0	0	0	1	2	2	2	1	1	2	2	1	1	-			
recta	L	-	-	-	-	-	-	-	-	61	95	89	89	109	116	90	111	95	104	-			

N = number of specimens; L = mean length in mm.; [a] Recalculated from Grier (1922).

with the mean length of each age group represented as a percentage of the length at two years. Twelve species are dealt with and the sample size of any one year group varies from zero to a maximum of four. It was noted that none of the shells studied had reached extreme old age, although ages as great as nineteen years were reported for two species, Lampsilis ventricosa (Barnes) and Lampsilis siliquoidea (Barnes), and a maximum of 22 years was listed for a specimen of Proptera alata (Say). While graphs of growth (length vs. age) were not constructed, the data necessary for the plotting of such curves were calculated from Grier's tables and are presented here for comparison with the results of the present study.

Grier's comparisons of growth rate demonstrated that the hard shell forms were slow growing (6.8 mm./yr.), the thin shell forms rapid growing (9 mm./yr.) while the intermediate Lampsiline species had an intermediate rate (8.2 mm./yr.). In comparing the lake dwelling forms with those of the streams studied by Coker *et al.* (1921) he noted, as had those investigators, that the most rapid growth occurs early in life while the growth process slows down considerably with age.

An improved technique for age-growth studies was introduced by Chamberlain (1931) in a thorough study of four species of naiades. Every true annulus on each specimen was counted and measured with the result that each individual yielded a datum for every year of age. Although this procedure is far more laborious and time consuming, it has the added advantage of having each length measurement made on the shell where the margin has been at the end of the growth period of that particular year. Mean lengths are calculated for each annulus of each species and these are plotted against age (determined by the annular ring method) on graphs. These graphs are, as far as I have been able to learn, the first such representation of the relationship of age and growth in fresh water mussels. Chamberlain's mean length data have been rounded off to the nearest millimeter and reorganized in tabular form for purposes of comparison with the results of other workers (Tables 4, 5). The methods

TABLE 4. AGE AND GROWTH DATA OF NAIADES[a]

			Mean Length in Millimeters														
Annulus number			I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV
Lampsilis	M	N	100	100	100	97	57	20	9	-							
anodontoides		L	16	55	82	96	104	113	119	-							
(from Iowa)	F	N	100	100	100	100	92	33	10	3	-						
		L	16	52	85	100	108	115	119	123	-						
Lampsilis	M	N	50	50	40	24	7	4	4	2	-						
anodontoides		L	28	67	89	103	115	121	122	133	-						
(from Arkansas)	F	N	50	50	49	33	29	4	-								
		L	34	69	91	104	110	114	-								
Lampsilis	M	N	56	56	49	35	6	2	-								
anodontoides		L	46	80	101	112	120	133	-								
(from Texas)	F	N	26	26	18	5	1	1	-								
		L	48	83	102	121	130	136	-								

N = number of specimens; L = mean length in mm.; M = male; F = female.

[a] Modified from Chamberlain (1931)

TABLE 5. AGE AND GROWTH DATA OF NAIADES[a]

			Mean Length in Millimeters														
Annulus number			I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV
Lampsilis siliquoidea (Lake Pepin, Minn.-Wis.)	M	N	200	200	200	200	196	185	132	85	46	25	8	3	1	-	
		L	20	40	56	68	77	83	87	91	93	94	93	97	106	-	
	F	N	200	200	200	200	192	139	86	30	17	7	1	-			
		L	20	43	57	66	72	76	79	80	81	85	86	--			
Lampsilis siliquoidea (Cross Lake, Minn.)	M	N	100	100	100	100	100	97	85	60	33	10	4	1	-		
		L	23	39	51	62	71	77	82	87	90	93	97	98	-		
	F	N	100	100	100	100	100	100	73	32	12	2	-				
		L	20	34	49	60	67	72	76	79	84	86	-				
Tritogonia verrucosa (Iowa)	M and F	N	16	16	16	16	16	16	16	16	2	1	1	-			
		L	15	34	44	54	60	66	73	78	96	110	114	-			
Unio popei (Texas)	M and F	N	7	7	7	5	2	1	-								
		L	34	66	84	96	108	118	-								

N = number of specimens; L = mean length in mm.; M = males; F = females.

[a] Modified from Chamberlain (1931).

used by Chamberlain in obtaining data from specimens, calculating means, and presenting the results in tabular and graphic form, in all essential points, are followed in the present study. The effects of diverse environments on the growth rate of a single species was revealed in Chamberlain's work on the yellow sand shell, Lampsilis anodontoides (Lea). Male specimens from the Mississippi River at Fairport, Iowa, averaged 16 mm. in length at the end of the first year, while those from White River, Arkansas averaged 28 mm. and specimens from the Rio Grande Valley, Texas had attained a mean length of 46 mm. during the same period. A higher average temperature coupled with a longer growing season seem to be two likely factors capable of producing this effect.

Brown *et al.* (1938) utilized Grier's method of obtaining data from specimens in their study of the relationship of growth and habitat. Their age-growth data are presented here (Tables 7-9) in the same manner as those of Chamberlain. One of their principal contributions was an insight into the age-growth relationships of several species never before investigated in this respect, e. g., Ptychobranchus fasciolaris (Raf.) and Ligumia nasuta (Say).

TABLE 6. AGE AND GROWTH DATA OF LAKE ERIE NAIADES[a]

		Mean Length in Millimeters																	
Annulus number		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII
Elliptio	N	1	1	1	2	4	5	4	7	6	3	6	3	-					
dilatatus	L	20	27	39	45	51	55	61	69	71	75	73	77	-					
(Fishery Bay)																			
Elliptio																			
dilatatus	N	0	1	1	1	1	1	0	3	6	5	2	8	2	3	1	2	-	
(Pelee Island)	L	-	28	33	39	45	57	-	53	58	57	56	61	64	66	63	65	-	
Ptychobranchus	N	0	1	2	7	0	3	2	1	2	3	3	2	3	2	3	0	0	1
fasciolaris	L	-	33	34	37	-	45	47	48	50	53	63	62	60	57	67	-	-	67
(Fishery Bay)																			
Ptychobranchus	N	0	I	1	2	1	2	0	1	2	0	2	-						
fasciolaris		-	31	30	39	48	47	-	51	55	-	56	-						
(Pelee Island)																			

N = Number of specimens; L = Mean length in mm.; [a] Modified from Brown et al. (1938).

TABLE 7. AGE AND GROWTH DATA OF LAKE ERIE NAIADES[a]

		Mean Length in Millimeters																	
Annulus number		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII
Ligumia nasuta	N	2	0	5	7	8	2	4	1	-									
(East Harbor)	L	41	-	66	72	85	101	88	96	-									
Ligumia nasuta	N	0	0	1	0	0	1	0	1	1	0	0	0	0	1	-			
(Fishery Bay)	L	-	-	54	-	-	80	-	65	78	-	-	-	-	76	-			
Ligumia nasuta	N	0	1	0	0	1	-												
(Pelee Island)	L	-	39	-	-	60	-												
Ligumia recta	N	2	0	5	7	8	2	4	1	-									
(East Harbor)	L	41	-	66	72	85	101	88	96	-									
Ligumia recta	N	0	0	1	0	0	1	0	1	1	0	0	0	0	1	-			
(Fishery Bay)	L	-	-	54	-	-	80	-	65	78	-	-	-	-	76	-			
Ligumia recta	N	0	1	0	0	1	-												
(Pelee Island)	L	-	39	-	-	60	-												

N = Number of specimens; L = Mean length in mm.; [a] Modified from Brown et al. (1938).

TABLE 8. AGE AND GROWTH DATA OF LAKE ERIE NAIADES[a]

		Mean Length in Millimeters																	
Annulus number		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII
Proptera alata	N	0	2	2	4	11	15	14	11	5	2	1	2	0	1	-			
(East Harbor)	L	-	61	72	85	92	96	111	115	119	117	130	113	-	92	-			
Proptera alata	N	0	0	4	2	5	6	2	2	-									
(Fishery Bay)	L	-	-	73	69	87	98	103	99	-									
Proptera alata	N	0	4	11	17	11	2	0	0	1	-								
(Pelee Island)	L	-	39	50	64	71	75	-	-	84	-								
Leptodea fragilis	N	0	1	6	11	11	6	2	-										
(East Harbor)	L	-	77	105	113	119	122	130	-										
Leptodea fragilis	N	4	1	5	5	1	1	0	0	0	0	0	1	-					
(Fishery Bay)	L	30	53	68	88	98	103	-	-	-	-	-	111	-					
Leptodea fragilis	N	0	3	4	9	3	3	1	2	2	-								
(Pelee Island)	L	-	42	59	74	82	86	91	100	101	-								

N = Number of specimens; L = Mean length in mm.; [a] Modified from Brown et al. (1938).

TABLE 9. AGE AND GROWTH DATA OF LAKE ERIE NAIADES[a]

		Mean Length in Millimeters																	
Annulus number		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII
Lampsilis	N	0	0	2	8	19	51	27	12	7	3	2	-						
siliquoidea	L	-	-	64	81	85	86	91	91	97	85	103	-						
(East Harbor)																			
Lampsilis	N	0	0	10	15	9	12	13	8	4	2	4	4	2	0	1	-		
siliquoidea	L	-	-	56	58	61	70	68	70	81	83	76	77	91	-	90	-		
(Fishery Bay)																			
Lampsilis	N	1	4	4	12	15	11	6	6	1	2	-							
siliquoidea	L	20	40	47	57	59	61	66	65	68	72	-							
(Pelee Island)																			
Lampsilis ovata	N	0	0	1	0	1	2	2	1	1	-								
ventricosa	L	-	-	70	-	69	86	95	100	107	-								
(East Harbor)																			
Lampsilis ovata	N	0	1	2	0	0	0	1	1	0	1	2	2	4	0	0	0	0	1
ventricosa	L	-	55	62	-	-	-	85	82	-	87	97	85	95	-	-	-	-	96
(Fishery Bay)																			
Lampsilis ovata	N	2	5	7	10	10	10	14	17	17	14	8	1	3	2	3	-		
ventricosa	L	38	52	61	65	68	72	73	76	78	82	85	76	82	82	88	-		
(Pelee Island)																			

N = Number of specimens; L = Mean length in mm.; [a] Modified from Brown et al. (1938).

THE PHYSIOGRAPHY OF FISHERY BAY

General Characteristics

Fishery Bay is one of a number of harbor-like inlets found in the Bass Island region of Lake Erie. It is located on the north shore of the larger of two joined land masses which form South Bass Island. This body of water has been referred to in the literature as part of Put-in-Bay proper, as Fish Hatchery Bay, or as Hatchery Bay. The principal harbor area at South Bass Island, if priority be our guide, should be called Put-in-Bay Harbor since references in the older literature are usually to the entire bay area as such and seldom to any particular subdivision. The Put-in-Bay Harbor has at least three rather natural subdivisions: Put-in-Bay proper, Squaw (Square) Bay, and Fishery Bay. Fishery Bay is the most nearly isolated of the three areas (Pl. II, Fig. 4) being connected to Put-in-Bay and Squaw Bay across Alligator Bar on the southeast and open to the lake itself at the deeper northeast end. It is bounded on the northwest by Peach Point and the submerged Peach Point Reef while its southeast limits are marked by Oak Point, Alligator Bar, and Gibraltar Island (Pl. II, Fig. 5). During strong prolonged southwest blows the lake level may drop three to seven feet resulting in the emergence of the underwater extension of Alligator Bar and the resultant near separation of Fishery Bay from Put-in-Bay. The only water connection across the Bar at such times is that in a dredged cut having a normal depth of about seven to eight feet. It is at such times that naiad collecting is at its best since it is about the only time that specimens may be handpicked -- each from its respective habitat niche. The only unfortunate aspect is that seiches of a five to seven foot magnitude come but once or twice a year, typically in November and/or March and, with rare exception, are accompanied by some of the harshest weather of the Island Region.

The general shape of the bay is roughly that of an elongate isosceles triangle with the base being its communication with the open lake and its apex the innermost extremity of Terwillegar's Pond. The major axis of the bay corresponds to the altitude of such a triangle and passes from the apex at the southwest end of Terwillegar's Pond to a point midway between the can buoy marking the submerged end of the Peach Point Reef and the northeast extremity of Gibraltar Island. The length of the bay, measured along the axis described, is 2,925 feet -- just over half a mile. The greatest width of the bay, which constitutes the base of the triangle, is found at its connection with the lake and measures 1,217 feet -- just under a quarter of a mile.

For purposes of this study the bay was divided into three more or less natural areas. These subdivisions are referred to here as the outer Bay, inner Bay, and Terwillegar's Pond. Each of these areas constitutes a somewhat different composite of habitat types which combined represents almost every type of bay habitat found in the Island Region.

TERWILLEGAR'S POND. The innermost extremity of the bay, known as Terwillegar's

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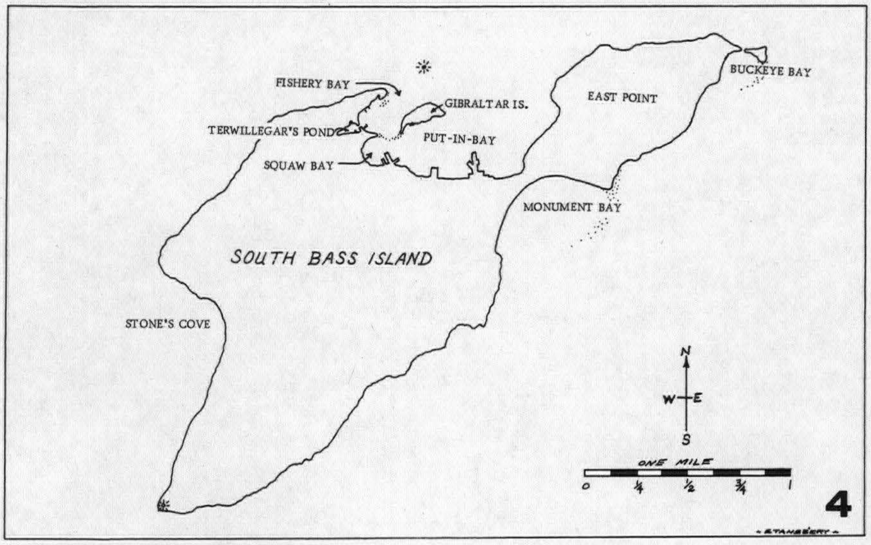
DESCRIPTION OF PLATE II, OPPOSITE PAGE

Fig. 4 The Bay Areas of South Bass Island.

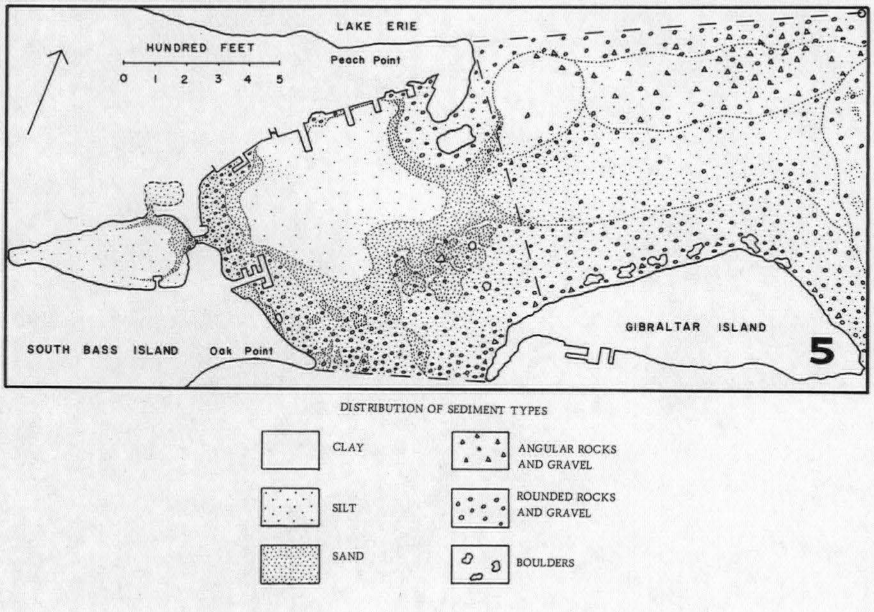
Fig. 5 Fishery Bay of Lake Erie, Substrate Sediments.

Fig. 6 Fishery Bay of Lake Erie, Depth Contours.

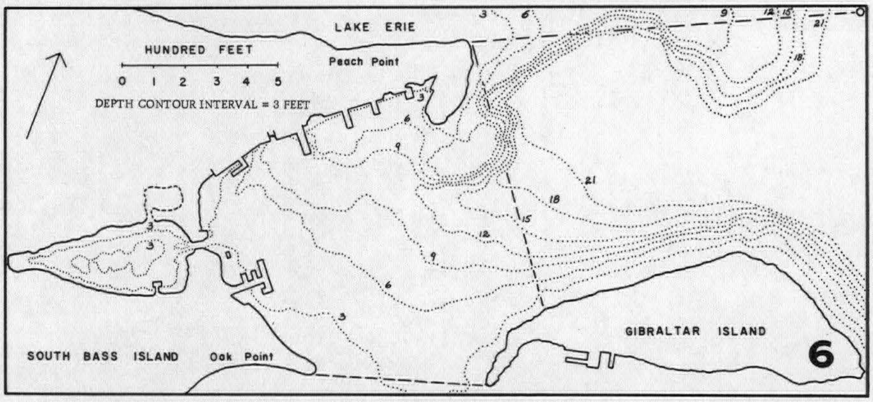
PLATE 2


FISHERY BAY
GIBRALTAR IS.
EAST POINT
BUCKEYE BAY
TERWILLEGAR'S POND
PUT-IN-BAY
SQUAW BAY
MONUMENT BAY
SOUTH BASS ISLAND
STONE'S COVE
N
W
E
S
ONE MILE
0
1/4
1/2
3/4
1
STANSBERY

4


LAKE ERIE
HUNDRED FEET
0 1 2 3 4 5
Peach Point
GIBRALTAR ISLAND
SOUTH BASS ISLAND
Oak Point
DISTRIBUTION OF SEDIMENT TYPES
CLAY
SILT
SAND
ANGULAR ROCKS AND GRAVEL
ROUNDED ROCKS AND GRAVEL
BOULDERS

5


LAKE ERIE
HUNDRED FEET
0 1 2 3 4 5
Peach Point
DEPTH CONTOUR INTERVAL = 3 FEET
3
6
9
12
15
18
21
GIBRALTAR ISLAND
SOUTH BASS ISLAND
Oak Point

6

Pond and hereafter referred to as the pond, is separated from the inner bay by a causeway. A cut through this causeway allows water to flow in and out of this semi-impounded area in a seiche-like manner. The direction of flow is usually reversed every six or seven minutes, although it is known to vary from one to almost fifteen minutes (Krecker, 1928: 5). This apparently continuous surging action of the water through the cut has several effects which have a direct bearing upon this study. This cut is, first of all, primarily responsible for the pond remaining a functional part of the bay rather than developing a true pond flora and fauna and passing through the familiar serial stages to extinction. Descriptions of the pond as it existed half a century ago have led me to believe that this area is becoming less pond-like with the passage of time. Several possible causes for this reversal of natural processes have come to my attention. The pond has been dredged on at least one (and possibly two) occasions with many tons of sediments being used to create "new land" in the corners of the pond and along the causeway. At a later date (1942) nearly all woody vegetation was removed from the shores. While this latter action undoubtedly served to increase the rate of shore erosion it has done little to increase the rate of along-shore sedimentation. It may be that the increase in lake level has produced stronger "seiche" currents which have served to keep the original dredged channel around the center of the pond (Pl. II, fig. 6) relatively clear of sediment deposition. The water action through the cut has been of such a nature as to perpetuate its existence. This is demonstrated by the fact that the greatest pond depth is just inside the bridge which spans the cut and that the bottom beneath and for some distance (15-20 feet) on either side of the bridge is of a firm non-shifting coarse gravel grading away into finer sediments in either direction.

This cut has made possible the exchange of naiads, fish, crayfish, and other strictly aquatic fauna between the pond and the inner bay. In spite of such opportunity of access, however, the pond has maintained a predominantly pond naiad fauna.

The pond is the smallest subdivision of the bay, having a total area of 2.4 acres, or 9,780 square meters. Expressed as a percentage of the total study area this figure is 5.5 per cent. The greatest length of the pond is measured along the major axis of the bay previously mentioned and is about 630 feet. The greatest width measured at right angles to the above mentioned axis at a level just inside the pond dock (Pl. II, fig. 6) is approximately 250 feet. In early January of 1954 the pond was sounded through the ice using a graduated white oak sounding rod. One hundred seventeen soundings were taken at spaced intervals (20 ft.) along a series of 16 transverse lines thus covering all of the pond except a small unfrozen area just inside the bridge. Later soundings from a boat established this latter area to have a depth of at least ten feet. These data were then used to plot contour lines of the pond bottom using a three-foot interval. It can be seen (Pl. II, fig. 6) that these contour lines delineate three regions which together make up most of the pond area. The periphery of the pond extends from the eroding soil shores down over a silt or sandy silt substrate to a depth of about three feet. This shallow zone (10-30 ft.) almost completely surrounds the pond and, during the time of the study, was occasionally characterized by emergent rooted aquatic plants: *Sagittaria latifolia*, *Scirpus americanus*, and *Pontederia cordata*. These beds of vegetation were interspersed with stretches of eroding shore line. This shore zone grades into the channel zone, which has a depth of three to five feet. This zone in turn surrounds an elevated shallow area in the center of the pond. The channel is characterized not only by its greater depth but by its relatively coarse substrate of sandy gravel which becomes progressively finer as one moves toward the shore, toward the pond center, or away from the causeway cut up the channel toward the tip of the pond. Emergent aquatic plants are entirely absent from this zone which is characterized instead by a luxuriant growth of the submergent rooted aquatic Eel Grass (*Vallisneria* americana) in those regions of strongest current. Along the margins of the Vallisneria beds in the finer sediments are a variety of submergent rooted aquatics including Ceratophyllum demersum, Naias flexilis, Potamogeton crispus, Potamogeton Richardsonii, Potamogeton pusillus, Elodea canadensis, Heteranthera dubia, and some Myriophyllum exalbescens. The shallow center area (less than three feet in depth) was composed of the finest (and least compacted) sediments to be found in the pond. This unnatural deposit is due to the dumping of dredgings from the channel -- much of the soil having originally come from the eroding vineyards which drain into the pond. In midsummer this submerged platform supports a dense growth of Myriophyllum exalbescens. This renders a habitat ordinarily difficult to sample even more difficult to work.

Inner Bay

The inner bay is intermediate in both position and size. It has an area of 18.4 acres or 74,600 square meters. The latter figure, expressed as a percentage of the total area, is 42.0 per cent. The inner bay is separated from the pond by the causeway, from the open lake by the Peach Point Peninsula, and from Put-in-Bay proper by the southwestern end of Gibraltar Island and Alligator Bar. The line of demarcation between the inner and outer bays was somewhat arbitrarily determined by extending a line from the tip of Peach Point to the shore of Gibraltal Island -- this line being drawn at right angles to the Gibraltar Island shore. Such a line approximates the division of that portion of the bay (called the inner bay) that is protected by the Peach Point Peninsula from westerly blows from the exposed outer portion of the bay here called the outer bay. It was found that this feature of the physiography, in conjunction with the prevailing climate (and the usual storms), has a marked effect upon the nature of the bottom types and bottom stability in the bay, and hence upon the habitat distribution of the naiad species in this area.

An examination of the chart (Pl. II, fig. 4) shows the inner bay (as defined) to be somewhat squarish in outline and measuring about 1000 feet in length and averaging a little less than 1000 feet in width.

The greatest depth located in the inner bay was just over 18 feet and was found at a point about midway between the tip of the Peach Point Peninsula and Gibraltar Island just inside the line of demarcation between the inner and outer bay (Pl. II, fig. 6). Moving from this point toward Gibraltar Island the water gradually becomes shallow so that the depth becomes less than three feet in approximately four hundred feet traversed. Moving in the opposite direction (i.e., toward Peach Point) the depth decreases rapidly and the three foot contour is passed in less than one hundred feet. The reason for this becomes apparent after one has witnessed a heavy blow from the west. Waves coming across the lake strike the end of Peach Point, roll over the shallowly submerged reef and plunge into the relatively quiet bay on the other side. These waves have scoured a basin about three hundred feet in diameter and 21 to 23 feet

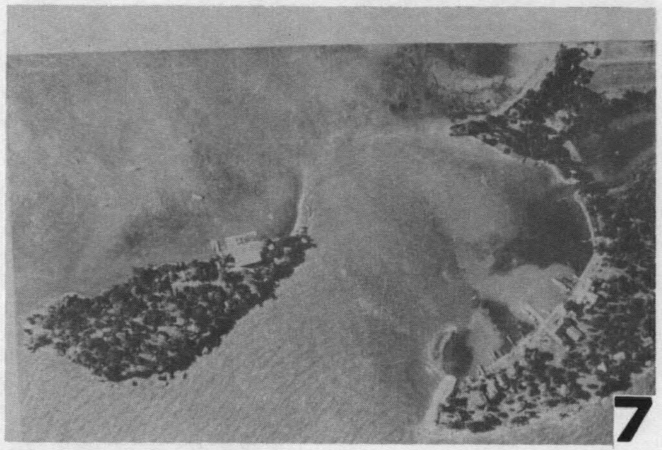
DESCRIPTION OF PLATE III, OPPOSITE PAGE

Fig. 7 Fishery Bay from the Air.

Fig. 8 Fishery Bay from the North.

Fig. 9 Causeway cut during seiche.

Fig. 10 Alligator Bar emerged during seiche.



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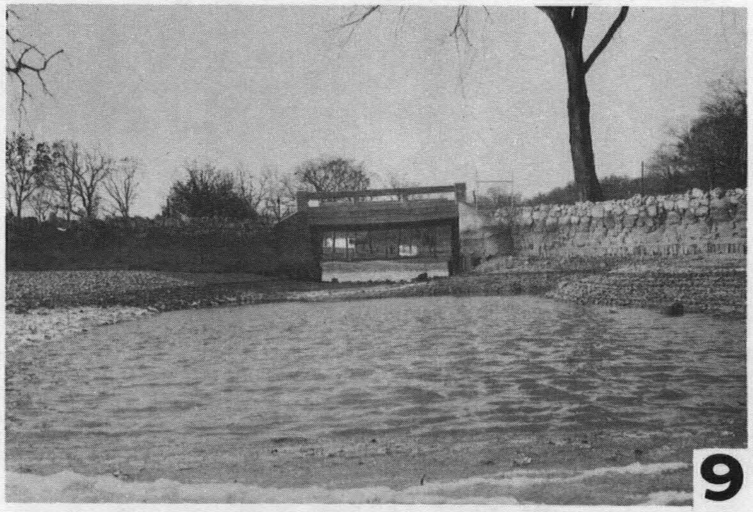

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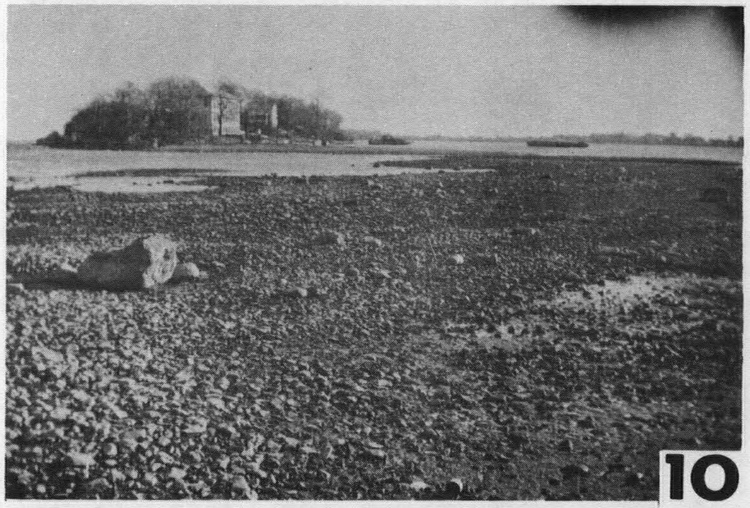

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PLATE 3

deep on the lee side of the base of the reef. Most of the rocks and gravel have been washed out of this submerged plunge pool leaving a hard pan clay bottom. The bulk of the material quarried in this manner has been thrown up into an elongate gravel bar which extends from the inside of the tip of the point back into the inner bay at an oblique angle. A large part of this bar is separated from the point by a shallow channel and, although it is usually submerged beneath six to twelve inches of water, it may be exposed for months at a time during seasonal low lake levels. This sometimes emergent gravel bar has come to be known as "Hartlob's Island." The bar shifts position somewhat with every heavy western blow and only one living naiad was taken from this area during the study. This was an unusually heavy shelled specimen of Anodonta grandis which had become wedged in between several large rocks. In comparing inner bay soundings made in 1954 with those made in the same places by the U. S. Lake Survey in 1936 it was found that the bar had apparently become larger and had moved.

It can be seen that Hartlob's Island in conjunction with the Peach Point Peninsula protects a large part of the inner bay from the action of the prevailing winds. The resultant area of quiet water has probably been one of the major factors producing the silt bottom found there.

The bottom of the inner bay may be divided into three major sediment zones: (1) silt, (2) sand, and (3) sandy gravel strewn with water worn rocks and occasional boulders. Passing from the deep point mentioned and moving toward the end of Oak Point, the depth decreases slowly to less than two feet at the sea wall which surrounds the point. The same would be true in passing to the shore in almost any direction from the 18 foot depth except along the Peach Point dock front where dredging has resulted in depths as great as eight to ten feet in some places. The silt area previously mentioned is surrounded by a belt of rather firm non-shifting sand which grades shoreward through a sandy gravel zone into the rubble area described as (3) above. These last two areas proved to be the most productive in numbers and species of naiades. A deposit of shifting sand along the Oak Point sea wall was searched in vain for naiades with little success. The few specimens found gave the appearance of having been washed into the area from elsewhere.

The submergent rooted vegetation appeared to be related primarily to depth and the nature of the substrate. The substrate in turn seemed dependent upon the prevailing current, nature of storm action, and types of available sediments. The silt bottom area was characterized each summer by a luxuriant growth of Myriophyllum exalbescens which occasionally reached the surface from depths of eight to ten feet. Sandy areas were generally clear of rooted aquatics while the sandy gravel bottoms were very productive. These latter substrates in shallow water supported a variety of Potamogeton species, Naias flexilis, Ceratophyllum demersum, and occasionally Elodea canadensis and Heteranthera dubia. Depths less than five feet exhibited particularly good growths of these aquatics. In depths over five feet these rough bottom areas frequently had extensive patches of Vallisneria americana, the common eel grass. These patches were sometimes dense enough to prevent dredging work. It was not uncommon to pull up a fouled dredge from 18 feet of water and find it loaded with Vallisneria even though no trace of the plants could be seen from the surface. It would seem that eel grass is able to persist under a lower light intensity than the other rooted aquatics of the bay area.

Outer Bay

The outer bay is bounded on the one side by the rugged cliff-shore of Gibraltar Island and on the other side by a somewhat less effective barrier, the submerged Peach Point Reef. The inner margin of this part of the bay communicates broadly with the inner bay while the outer end is continuous with the open lake.

The outer bay is the largest subdivision of the Fishery Bay and has a total area of 23.0 acres, or 93,300 square meters. Although this subdivision constitutes 52.5 per cent of the total study area, far less than 50 per cent of the total effort involved was expended upon it. The depth, turbidity of the water, and nature of the substrate rendered collecting an all but impossible task by either dredging or diving.

The length measured along the major axis is just over 1,100 feet while the width varies from about 700 feet at the narrowest point to just over 1,200 feet at the widest point -- the communication with the lake. With the exception of the clay-bottomed submerged plunge pool previously mentioned the bottom consists of three elongate zones (Pl. II, fig. 4). Each is of a somewhat different composition. These zones parallel each other and the longitudinal axis of the bay. The deepest part of the outer bay lies just inside the reef and varies from 21 to over 23 feet in depth. The bottom here consists mainly of angular fragments of dolomite of various sizes in a matrix of gravelly mud or silt. This rather unusual combination of sediments is apparently the result of the loosened fragments of dolomite on the top of the reef being tumbled into the depths by storms and subsequently being inundated with silt dropping out of suspension during the relatively lengthy stretches of calm.

As one moves away from the base of the reef toward Gibraltar Island the current along the bottom increases somewhat and the angular fragments give way to a water worn sandy gravel. Although the central zone has a distinctly different substrate the difference in depth between it and the zone just described is slight, being on the order of one to two feet. The only submergent aquatic plants collected in the outer bay were taken either from this zone or the adjacent portions of the next and consisted of Vallisneria americana in every case. It occurs in patches at depths at least as great as 18 feet. These patches are interspersed with areas which are apparently devoid of all rooted aquatics. As Gibraltar Island is approached from the bay the water becomes rapidly shallow and the sediments coarser. At the foot of the cliff are found huge blocks of dolomite which have dropped into the bay after being undercut by wave action at the water line. The bottom between and beyond these larger blocks consists almost entirely of rounded rocks of dolomite with an occasional freshly dropped angular piece. No naiades or naiad shells were ever collected here.

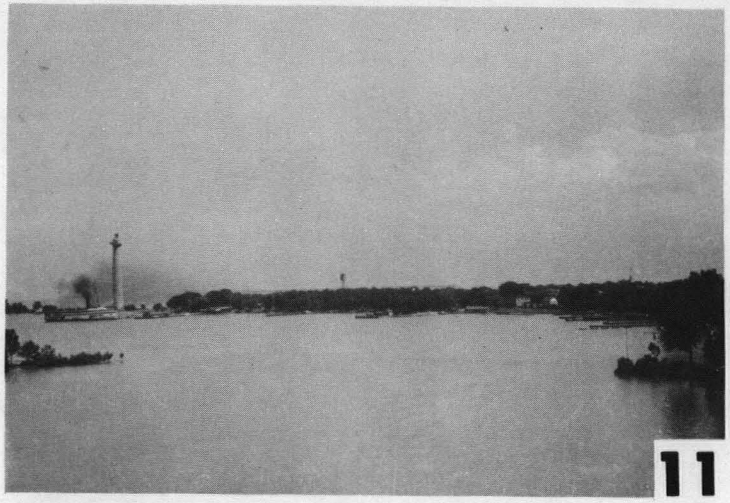
DESCRIPTION OF PLATE IV, OPPOSITE PAGE

Fig. 11 Alligator Bar -- normal water level.

Fig. 12 Alligator Bar -- emerged during seiche.

Fig. 13 Terwilligar's Pond -- normal water level.

Fig. 14 Terwilligar's Pond during seiche.



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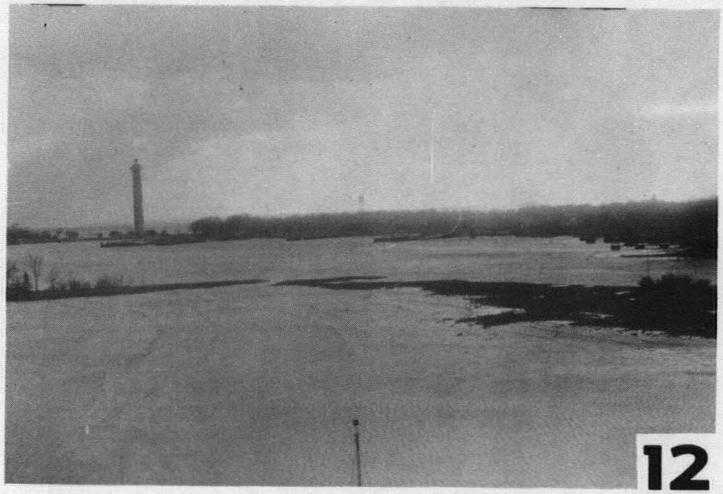

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PLATE 4

THE ORIGIN OF THE LAKE ERIE NAIAD FAUNA

It has been said that through a study of the past we can best interpret the present and better predict the future. Bell (1861), Whiteaves (1861, 1863), and Walker (1895: 13; 1898: 12; 1900, 1913) followed this principle in utilizing the historical physiography of the Great Lakes region in explaining the origin of the naiad fauna found there. Ortmann (1912, 1913, 1919, 1924) was also aware of the value of correlating changes in drainage systems with faunal distribution patterns. In this manner he was able to account for the discontinuous distribution of several species which are found in most of the Lake Erie tributaries but not in the lake itself. This work and Walker's earlier studies in the field of naiad zoogeography have more recently been confirmed by van der Schalie (1938, 1941, 1945). This last worker has also succeeded in using unusual distribution patterns to decipher former drainage patterns whose existence was not evident on the basis of physiographic evidence alone (van der Schalie, 1945). It is of interest to note that geologists (Gilfillan, 1959: 19) only recently have confirmed the existence of a low post-glacial stage of Lake Erie which Ortmann (1924: 113) predicted on the basis of naiad zoogeography thirty-five years ago. Other predictions, some listed below, still await confirmatory evidence from other fields.

The origin of the Lake Erie naiad fauna has, for the most part, been carefully mapped out by the workers mentioned. The movement of the present lake fauna into the drainage system it now occupies is intimately related to and dependent upon the nature of the retreat of the Wisconsin Glacier.

It is generally agreed that the pre-glacial fauna of the Great Lakes region was extirpated with the advance of the Wisconsin ice sheet. Adams (1902: 308) simply states, "The original plant and animal population of the northeastern United States was cleared away by the advance of the glacial ice ..." Walker (1913: 58) is more emphatic in concluding "That the original pre-glacial fauna of the present St. Lawrence system was absolutely exterminated during the glacial period, ..." It follows that any fauna in that region today is properly termed re-entrant and, if an aquatic form is in question, that it moved into the glaciated area by means of a suitable drainage system which was continuous from a non-glaciated preserve at some time since the retreat of the Wisconsin ice. The mode of retreat of the ice from the Great Lakes area was originally worked out by a number of geologists (e. g., Newberry, Winchell, Dryer, Hubbard, Wright, etc.) participating in state survey work during the last quarter of the last century. Their work was brought together, organized, supplemented, and expanded by Leverett and Taylor (1915) in their monumental work -- The Pleistocene of Indiana and Michigan and the History of the Great Lakes. This series of events has recently been reworked in view of the evidence accumulated during nearly half a century of subsequent work and published in book form as the Geology of the Great Lakes (Hough, 1958). A review of this literature reveals that the naiad zoogeography of the Great Lakes can be explained best in a series of four to six chronological steps each of which is in accordance with the known facts of glacial geology. A set of four maps have been drawn to aid in such a presentation and while these maps are in part original, the information upon which they are based comes almost entirely from the above publications. (See Plate V).

The retreat of the Erie lobe of the ice sheet resulted in outwash streams which flowed out and away from the glacier so long as the ice margin extended south of the Ohio divide. When the ice had retreated to the north of the divide meltwater lakes formed along its margin and these eventually flowed over the lowest part of the terminal moraine which contained them. In the case of the Erie lobe the meltwater lake has been named Lake Maumee, the moraine was the Fort Wayne Moraine, and the outlet was at the site of the present city of Fort Wayne. The water leaving Lake Maumee thus flowed across Indiana, joined the Wabash River and continued on to join the lower Ohio River (Pl. V, fig. 15).

While the nature of the Maumee-Wabash Outlet must have been variable, considering fluctuations in the melting rate characteristic of retreating glaciers, it seems certain that it maintained itself as a very large river for considerable periods of time. This is evidenced by the invasion of Lake Maumee from the lower Ohio River by fish species which frequent only such rivers as the Ohio, Mississippi, and the lower reaches of their largest tributaries. These fishes include the Sheepshead, Aplodinotus grunniens Rafinesque; Sturgeon, Acipenser fulvescens Rafinesque; Paddlefish, Polyodon spathula (Walbaum); Spotted Gar, Lepisosteus productus (Cope), Bowfin, Amia calva Linnaeus, Northern Shorthead Redhorse, Moxostoma aureolum (Le Sueur) and the Mooneye, Hiodon tergisus Le Sueur. It is not surprising, then, that a number of large river naiades also made the migration, possibly as glochidia on the gills or fins of the host fish. The Sheepshead, famous as a bottom feeder, acts as host to several naiades including Proptera alata (Say), Leptodea fragilis (Rafinesque), Truncilla donaciformis (Lea), and Leptodea laevissima (Lea) (Howard, 1914: 37). The first three species of this group are common forms in Fishery Bay, as is the Sheepshead, while L. laevissima for some unknown reason is not known from Lake Erie. The results of this study indicate that the large river peruviana Lamarck form of Amblema plicata (Say) and the undata (Barnes) form of Fusconaia flava (Rafinesque) are also part of the present lake fauna.

Records of the Fusconaia subrotunda complex from Lake Erie (Sterki, 1907: 391) (Ortmann, 1909: 203) (Walker, 1913: 22) were later identified (Ortmann, 1919: 11) as the superficially similar Pleurobema cordatum coccineum (Conrad). The fact that the host fish of the F. subrotunda complex, the Skipjack Herring, Pomolobus chrysochloris Rafinesque (Howard, 1914: 19), has never been recorded from Lake Erie supports this conclusion. In view of the fact that the Skipjack is a fish of the swift, clear, deep waters of large rivers (Trautman, 1957: 179), it may have moved into glacial Lake Maumee, perhaps persisted in the Erie River which followed, but did not survive the transition to the relatively slow-moving turbid lake of today.

The opinion of most if not all previous students of Lake Erie naiad geography seems to be that the entire lake fauna was derived from the Mississippi Basin by way of Maumee-Wabash outlet of Lake Maumee. It is my belief that they are correct with the exception of a single species, Ligumia nasuta (Say). This species has never been collected -- alive, subfossil or fossil -- from any stream of the Mississippi drainage although its nearest rela-

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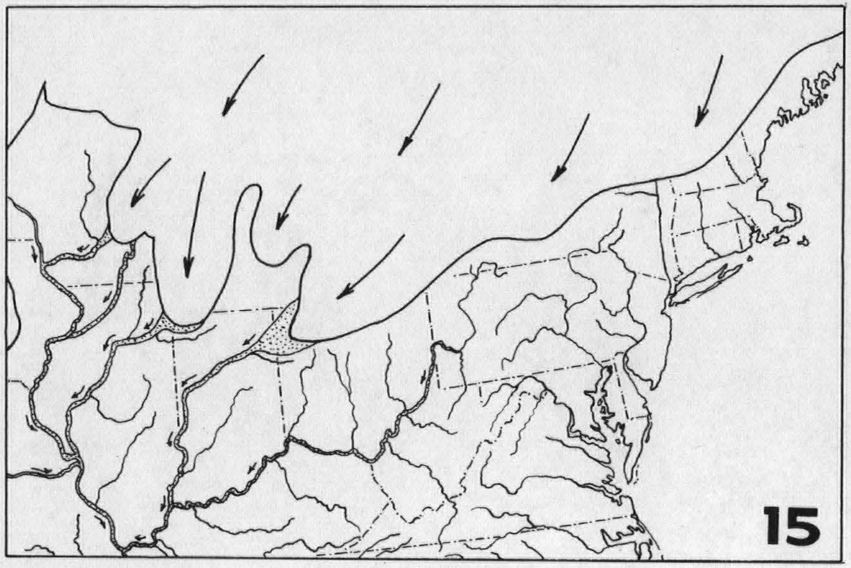
DESCRIPTION OF PLATE V, OPPOSITE PAGE

Fig. 15 Lake Maumee, High Stage.

Fig. 16 The Carey-Port Huron, or Two Creek, or Lake Wayne Stage.

Fig. 17 Kirkfield Stage of Huron and Michigan Basins, Early Erie Stage.

Fig. 18 Distribution of Naiad Faunal Groups in the Northeastern United States.



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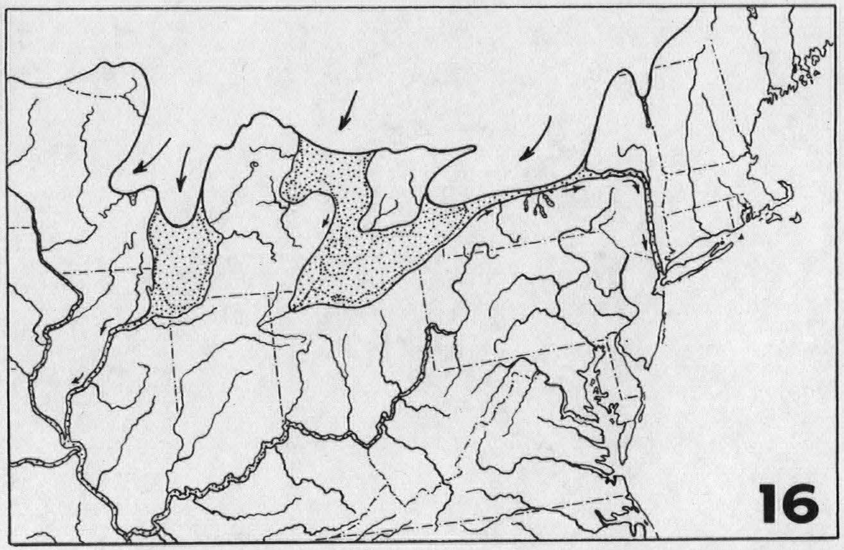

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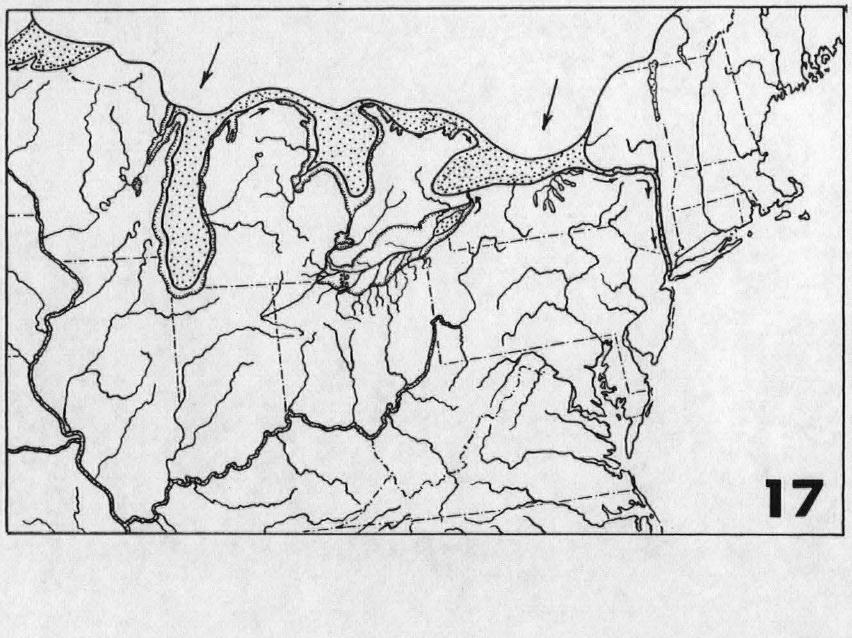

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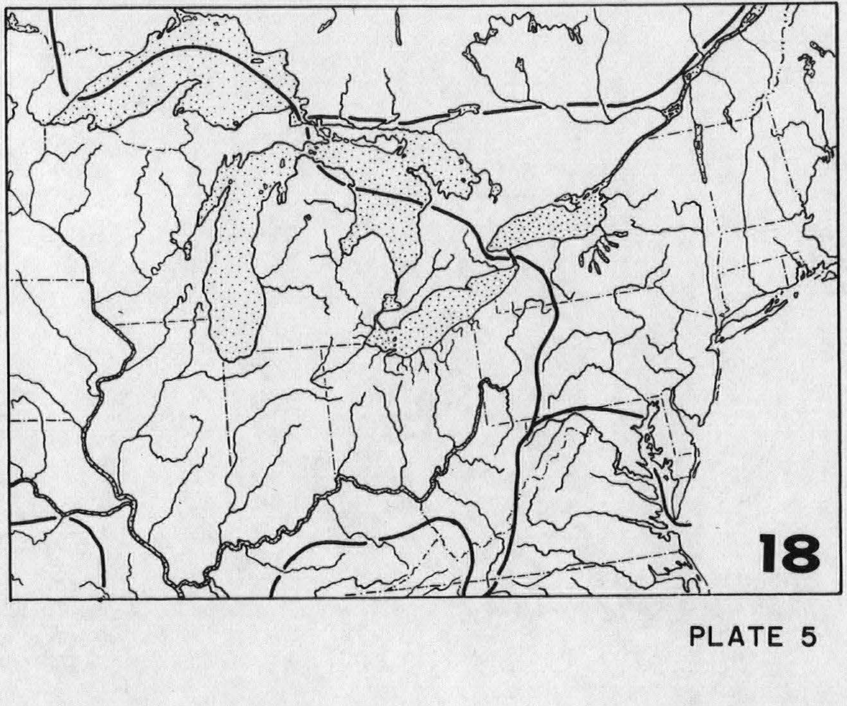

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PLATE 5

tive Ligumia subrostrata (Say) is found only in this system. L. nasuta is found in several Michigan lakes (Goodrich, 1932: 108), Lake Huron, Lake St. Clair, and Lake Erie (Goodrich and van der Schalie, 1932), the lower reaches of several Lake Erie tributaries (van der Schalie, 1938: 64), Lake Ontario and the Erie Canal (Ortmann, 1919: 275-276), New England (Johnson, 1915: 22), and streams flowing into the Atlantic south to North Carolina (Simpson, 1914: 97).

It is further reported from tributaries of a lake in Portage County, Ohio (Dean, 1890: 21), from "Muzzy Pond, near Rootstown, Portage Co.," Ohio (Sterki, 1907: 389) and from the upper Cuyahoga River (Dean, 1890) (Ortmann, 1924: 110). These stream records from Portage County are particularly unusual in view of the fact that this species is found elsewhere in quiet waters and, furthermore, that it is absent from all but the bay-like drowned mouths of the other Lake Erie tributaries. I collected in the upper Cuyahoga in July, 1959, in order to determine if this species still persisted in those waters and, if so, to observe the microhabitat occupied. Several living specimens were taken along with a few empty shells. These few individuals were taken from a firm sandy gravel bottom in a fast current. Except for the strength of the current, the physical habitat seemed not unlike those areas of Alligator Bar where this species is found in Fishery Bay. The host fish is as yet unknown and the presence of this naiad in the upper reaches of a single Lake Erie tributary remains unexplained.

Ortmann (1913: 379) reasoned as follows concerning the origin of the distribution of L. nasuta:

> Its western origin is confirmed by the fact that the only species allied to it, Eurynia subrostrata (Say) is western and is found in the central and western parts of the interior basin in large quiet rivers, ponds and lakes, avoiding rough water and strong current. For this reason, probably, it is not found in the upper Ohio drainage. This species has crossed somewhere in the region from northern Illinois to northern Ohio into the lake drainage, developed there into the species nasuta, which then spread eastward, following the quiet waters of the lakes and those of the canal till it reached the estuary of the Hudson. Thence it had no difficulty to spread farther over the Coastal Plain and reached across New Jersey, the lower Delaware, and even beyond ... We are thus to regard Eurynia nasuta as a quite recent immigrant in the Atlantic drainage, belonging surely to the Postglacial time, and this immigration might have been completed even by the help of modern, artificial canals.

It must be conceded that the above explanation is quite possible but, in view of the available evidence, it seems to be less probable than a second possibility outlined below. A piece of evidence should be added to the above which, although it seems to have little bearing on the problem at present, may be of value to future students. During archaeological excavations at the Fairport Harbor Village site near Painesville, Lake County, Ohio, a number of naiad shells were found (Goslin, 1943: 51). The species L. nasuta was among those yet identifiable, thus placing it in Lake Erie before the canal building era. This would seem to rule out the possibility of a post-glacial east to west migration of the species from the Atlantic coast. Evidence from glacial geology, however, has established an eastward flowing outlet of Lake Erie meltwater at some time (perhaps several times) following earlier outlets to the west (Leverett and Taylor, 1915) (Martin, 1939: 50, 52) (Hough, 1950: fig. 59 and 63). The existence of such a migration route (Pl. V, fig. 17) would provide ready access to Lake Erie of any of the fresh water fishes from the Mohawk or Hudson Rivers in the east. It seems quite possible that the yellow perch, Perca flavescens (Mitchell), may have entered the Great Lakes for the first time by such a route since records (Trautman, 1957: 553) limit its distribution in Ohio during the early eighteen hundreds to Lake Erie and small lakes in the northern part of the state. This original distribution sounds interestingly enough like that of L. nasuta and, in fact, Trautman lists seven collection records of Perca flavescens for the upper Cuyahoga. The distribution of L. nasuta along the Atlantic coast lies entirely within and all but duplicates that of P. flavescens. It would not be surprising to find that a parasite-host relationship exists between these two species in spite of the fact that the evidence is purely circumstantial. The presence of P. flavescens bones in the Fairport Harbor material makes such a possibility seem even more likely. A migration path of the type described would also (1) eliminate the unlikely speciation of this form since the retreat of the Wisconsin, (2) provide a non-glaciated preserve presently occupied by this species in southern Pennsylvania, New Jersey, and other states south to North Carolina, and (3) eliminate the unlikely movement of this freshwater species from stream to stream down the east coast from New York to North Carolina producing the discontinuous distribution found there today. While the available evidence favors this latter theory, it is realized that the question is far from settled and that some evidence to the contrary exists. It is, for example, a curious fact that of all the east coast naiades not found in the Mississippi Basin only L. nasuta is found in Lake Erie.

At a date later than the time of the original Mohawk-Hudson or Susquehanna Outlet dealt with above the ice retreated from the Niagara escarpment and from a large part of the Lake Ontario basin as well. This allowed a much lower outlet of Lake Erie by way of the Niagara River into Lake Iroquois (Pl. V, fig. 17) (a predecessor of Lake Ontario) (Martin, 1939: 56) (Hough, 1958: 293) and a lower outlet of Lake Iroquois which may have followed the Mohawk Valley rather than run parallel to it at a higher elevation somewhat to the south as previously. The Niagara Escarpment was much lower then than now due perhaps to the tremendous weight of the ice sheet. Lake Erie was apparently all but drained and transformed into a valley having only a remnant of its former bulk remaining as a small lake in the eastern basin (Walker, 1913: 15) (Ortmann, 1924: 113) (van der Schalie, 1938: 11). While the geological evidence concerning the lowest level reached is not conclusive, recent finds by Hartley and Verber (Gilfillan, 1959: 19) place the old river channel which occupied this valley at 106 feet below the present lake surface at Vermillion. Such a drop in lake level would effectively drain the western and central basins of the lake as predicted by Ortmann (1924). The river thus formed in the Erie Valley by the confluence of the Maumee, Raisin, Huron, and Clinton Rivers and receiving the Portage, Sandusky, Huron, Vermilion, Cuyahoga, and others as tributaries might well be called the Erie River in contrast with the pre-Wisconsin Erigan River which occupied this same valley.

It seems certain that the Erie River was a stream of major proportions since the large river fauna derived previously from the lower Ohio has persisted in part into the present. The existence of this river enabled several stream species of naiades to move down its length from the Maumee and up into the various tributaries. As the Niagara Escarpment slowly lifted, the lake refilled; thus extinguishing the strictly stream fauna as the valley once again became lake. Three species of naiades are found today in the major lake tributaries and not in the lake itself, thus demonstrating that in some as yet unexplained manner some bodies of fresh water can present an effective barrier to some fresh water animals. One of these naiad species, Actinonaias carinata (Barnes), has been recorded from the Grand River of Ontario, a NORTHERN tributary of the EASTERN basin (Robertson and Blakeslee, 1948: 104). This suggests the past existence of a continuous stream environment of the former Erie River with the Grand River. I doubt the existence of such an extreme low level because of the absence of the other two species, Lampsilis fasciola Rafinesque and Alasmidonta marginata Say, and because the photograph of Robertson and Blakeslee (1948: pl. 12, fig. 7) labeled

"Actinonaias carinata (Binney). Grand River, Ontario." is most certainly a male specimen of the ventricosa form of Lampsilis ovata (Say) -- a common lake species.

The Erie River phase of the retreat of the Wisconsin ice sheet was apparently accompanied by the Trent outlet from the upper Great Lakes by way of the Georgian Bay into Lake Iroquois (Pl. V, fig. 17). This permitted the invasion of the Georgian Bay and upper Lake Huron by several eastern naiad species (i.e., Lampsilis radiata (Gmelin) and Elliptio complanatus (Dillwyn) and resulted in the curious fact that these two species are found on either side of Lake Erie in the St. Lawrence system and yet neither occurs in Lake Erie (Pl. V, fig. 18). Just what factors operate in preventing the movement of these species into southern Lake Huron, through Lake St. Clair, and the Detroit River into Lake Erie are unknown.

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ERRATA

Page 1, line after Fig. 1, add:
2. The Bass Islands of Lake Erie.

Page 2, line after Fig. 16, read:
17 Kirkfield Stage (etc.)

Page 3, left hand column, line 9, for receoved, read received.

Page 4, left hand column, line 9, for 1816, read 1916.

Page 4, right hand column, second line from bottom should read:
knowledge of the Maumee-Wabash connec-

Page 9, table, under "Particle name" 3d to 5th lines, should read Pebble, Granule, Very coarse sand, Coarse sand, and Medium sand.

Page 19, Table 5, under II, 7th line should read 100.

Page 24, left hand column, 3d line from bottom, for Gibraltal, read Gibraltar.

Page 34, right hand column, last reference, authors' names should read:
LEFEVRE, George and CURTIS, Winterton C.

EDITOR'S NOTE. THIS PAPER WILL BE CONTINUED IN A FUTURE NUMBER OF STERKIANA.