Population Dynamics, Spatial And Temporal Distributions Of Mysid Crustaceans In A Temperate Marsh Estuary.

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POPULATION DYNAMICS, SPATIAL AND TEMPORAL DISTRIBUTIONS OF MYSID CRUSTACEANS IN A TEMPERATE MARSH ESTUARY

by

Dennis Michael Allen

A Dissertation
Presented to the Graduate Committee
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Dec. 13, 1977

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Accepted, Dec 13, 1977

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the doctoral work of
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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Figure | Page

Figure Page

Population Dynamics, Spatial and Temporal Distributions of Mysid Crustaceans in a Temperate Marsh Estuary

by

Dennis Michael Allen

ABSTRACT

The population dynamics, spatial and temporal distributions of *Neomysis americana*, *Mysidopsis bigelowi*, and *Heteromysis formosa* were investigated in a temperate tidal embayment and the adjacent coastal area at Hereford Inlet, New Jersey. Samples were collected with an epibenthic sled on 80 cruises over a 25 month period. The abundance and population structure of each species was determined at seven stations along the main route of tidal flow from a major marsh creek to several kilometers outside of the inlet.

Neomysis americana occurred in each of the 424 samples, comprised 97% of the mysids collected, and was most abundant from June to October. One overwintering and two short lived summer generations occurred each year. Reproduction was continuous, with much greater activity occurring during the warmest months.

Mysidopsis bigelowi produced three generations per annum in a pattern very similar to that of *N. americana*. Gravid females were collected from April to November.

Heteromysis formosa produced two major generations per year,

the summer stock brooding two or more times.

The swimming behavior of N. americana was investigated in the laboratory. Ordered associations of mysids oriented parallel to each other could only be induced by water movement. The responses were immediate and persistent as long as currents prevailed. In static water, the mysids swam in erratic paths at characteristic speeds.

The dimensions and temporal existences of the induced aggregations were primarily determined by current velocity and secondarily modified by light. Field studies on the effect of tidal currents on the distribution of mysids showed the responses of aggregations in the embayment were similar.

The physical characteristics of the stations determined the overall abundance of N. americana at each site. Resident populations persisted in the upper embayment and offshore, but strong tidal currents restricted the time that aggregations remained in the lower embayment.

Fluctuations in mysid abundance between stations, between cruises, and between seasons demonstrated the dynamic nature of the aggregations in the field. Migrations involving great numbers of individuals occurred during the warmer months as masses penetrated the embayment from offshore areas. The spatial and temporal dimensions of the migrations were highly variable and were often related to temperature regimes.

Mean length and life history information showed that a lag in the growth and reproductive rates occurred in the populations inhabiting the cooler offshore waters during the summer. Upper embayment populations had significantly higher percentages of adults of greater mean lengths than the lower embayment populations.

Mysidopsis bigelowi was generally restricted to the sandy areas in the lower embayment and offshore. The temporal distribution and abundance of the species were closely related to those of *N. americana*.

Heteromysis formosa occurred almost exclusively in the upper embayment. Evidence for its seasonal migration was found.

The ubiquity and abundance of mysids in the study area, and the extent to which they are consumed by predators, define their role as one of the most important components of the trophic structure of the system.

I. INTRODUCTION

A. General

Various names have been used to describe the assemblage of invertebrates which are characteristically associated with the substrate-water boundary zone. The terms epifauna, epibenthos, hyperbenthos, and bottom plankton have been used to describe the diverse group of animals which crawl upon or swim immediately above the bottom. Unlike the benthos, plankton, and nekton, which are comparatively well defined in time and space, the fauna associated with the lowest portion of the water column is extremely variable. This group includes representatives from almost every major invertebrate taxon, but is most often dominated by small pericarid and decapod crustaceans. The temporal and spatial variations in the taxonomic composition of the community are considerable.

The variable nature of this community partially accounts for the lack of information on the life histories, distributions, and abundance of even the most common forms. Despite the ubiquity of small invertebrates associated with the sea floor and their generally well recognized ecological significance, few comprehensive studies of these communities have been undertaken. Bossanyi (1957) discussed early attempts to investigate this fauna and presented the results of a qualitative study he conducted in British waters. Hesthagen (1973) and Boysen (1975) have investigated the "hyperbenthos" in the western Baltic Sea.

Among the most conspicuous members of the near bottom fauna are the mysid crustaceans, or opossum shrimps. Tattersall and Tattersall (1951) present a comprehensive review of the taxonomy and bionomics of the Order Mysidacea. Most of the 450 known species are inhabitants of neritic and estuarine waters. The majority live on or just above the bottom, at least during the daylight hours, and illustrate various degrees of gregariousness. Except for some amphipods and caridean shrimps, mysids often dominate the zone immediately above the bottom.

The role of mysids in temperate coastal systems is generally thought to be significant; however, the lack of quantitative information has discouraged proper assessments. Mysids are omnivores. They utilize filter feeding to procure particulate organic material and phytoplankton, and are predators of small zooplankters. Their trophic role as converters of energy into forms which can be used by higher organisms, especially fishes, coupled with the ubiquity and abundance of mysids in some areas indicates that their significance in the productivity of such ecosystems has been greatly underestimated.

Smith (1879) recognized the importance of mysids in the diet of shad, mackerel, and sea herring in New England. Moore (1947) found mysids comprise the major dietary item of the sand dab _Lophopsetta_ (_Scophthalmus_) in Long Island Sound. Bigelow and Schroeder (1953) found mysids to be the major food for the smelt, sea perch, and yellowtail flounder in the Gulf of Maine. Black (1956) states that many gadids and other cold water fishes in the Bras D'or Lakes in

Nova Scotia feed heavily on mysids. Mysids are important food sources for the striped bass on the west (Heubach, 1969) and east (Shuster, 1959) coasts of the United States. Van Engel and Joseph (1968) found that mysids were an important source of food for juvenile fish populations in the York-Pamunkey River area of Chesapeake Bay, as did Odum and Heald (1972) for the fishes of a Florida mangrove community. A baseline finfish study of the Hereford Inlet area in southern New Jersey conducted coincidentally with this investigation has indicated mysids to be one of the most important foods for the majority of juvenile fishes which inhabit the area (Allen, et. al., 1977).

B. Geographical Distribution

Estimates of the geographical range of *N. americana* in the western North Atlantic Ocean have been extended several times over the past twenty years. Its range is now given as from the Gulf of St. Lawrence to the northern coast of Florida (Williams, Bowman, and Damkaer, 1974). A report by Gonzalez (1974) claims its presence in the South Atlantic in Rio de la Plata, Brazil.

Wigley and Burns (1971) state *N. americana* is the most common shallow water mysid in the Western Atlantic, being most frequently reported from the intertidal zone to 60 m. This mysid has been collected as deep as 232 m, but was found most abundant between 30 and 60 m in samples collected from Nova Scotia to Chesapeake Bay.

Mysidopsis bigelowi occurs along the Atlantic coast from New England to the Gulf coast of Louisiana, from the intertidal zone to 179 m (Wigley and Burns, 1971). *Heteromysis formosa* has been reported from the eastern North Atlantic from France, Norway, and the British Isles as well as from Maine to the Gulf of Mexico in the western North Atlantic. While most records have been from less than 26 m, specimens have been taken in 227 m off of North Carolina (Tattersall and Tattersall, 1951).

C. Objectives

The intent of this study was to investigate the population dynamics, spatial and temporal distributions of three species of mysids within a tidal marsh embayment and the adjacent coastal waters. Since *Neomysis americana* was the most abundant mysid in the Hereford Inlet study area, most of the attention in this investigation was given to the understanding of its life history, behavior, and distribution. *Mysidopsis bigelowi* and *Heteromysis formosa* comprised much smaller percentages of the mysid fauna, but were studied in a similar manner. Quantitative field samples were analyzed to determine the tidal and seasonal abundance and distributions of the populations, and provided materials to elucidate the life history patterns of the species. Laboratory investigations were conducted to facilitate the interpretation of the distribution and life history information obtained in the field.

D. Life History

The life histories of most of the temperate shallow water mysids seem to follow a similar pattern in which an overwintering population reproduces in the spring, giving rise to a summer generation. Depending on the time it takes to reach maturity, the first summer generation (1SG) may produce a second summer generation (2SG) which overwinters with those 1SG mysids which do not mature in the fall. Details of the life histories of less abundant species remain obscure, but probably do not differ significantly from this pattern.

Smith (1879) was the first to describe *N. americana* and to observe breeding during the spring and summer. He suggested that the species may reproduce throughout the year.

Cowles (1930) determined that the population of *N. americana* studied offshore of Chesapeake Bay was endemic and reproduced during the winter. Numbers of brooding females were collected in January, but some breeding was detected during the entire year. Summer samples were dominated by small immature forms.

Fish and Johnson (1937) found that *N. americana* started reproducing later in the spring in the Gulf of Maine than populations observed by Fish (1925) at Woods Hole, MA.

On Georges Bank, the mysids were most abundant in the fall with the lowest numbers occurring in the winter (Whitely, 1948). Breeding was observed only in the spring.

Black (1956) conducted the first thorough study of the life history of *N. americana*. Analyses of samples from the Bras D'or Lakes demonstrated at least two generations occurred per annum, with individuals surviving less than one year. Determinations of growth rates could not be made because of the overlap of the generations. Gravid females were collected almost every month, with peak reproductive activity occurring in the summer and in the spring as the overwintering generation reached maturity.

Hopkins (1965) collected *N. americana* at Indian River Inlet, just south of Delaware Bay, and encountered spawning females every month. Reproductive activity was much greater from the spring to the fall, than during the winter when the samples consisted primarily of large immatures. An overwintering generation and one, or possibly two, summer generations were recognized.

Herman (1962) also found reproduction to be continuous for populations of N. americana in Narragansett Bay. Gravid females were collected every month, with peak numbers occurring in May, June, and October. Immature animals were found to dominate during most of the year, with the exception of mature mysids dominating in May and June and juveniles in July and August. N. americana was least abundant in the spring, before the large overwintering individuals reached maturity, and most abundant during the proliferation of the 1SG and the development of the 2SG.

Wigley and Burns (1971) analyzed samples taken from offshore areas from Nova Scotia to Chesapeake Bay and determined major spawning periods in the spring and late summer/fall for N. americana. Their observations substantiated the conclusions of most of the other investigators and provided further details on the reproduction of the species.

Williams (1972) determined similar patterns of reproduction and growth for N. americana in North Carolina estuaries, which suggested that more than one generation occurred per year. A gradual increase in the numbers of large mysids was observed from late fall to mid May. After this point, the large individuals disappeared rapidly and, by mid June, an abundant new size class of smaller individuals predominated. Reproduction was continuous.

Neomysis integer, an abundant European species which differs more from *N. americana* in behavior than in morphology and life history, has been studied in considerable detail. Vorstman (1951) found that *N. vulgaris* (*N. integer*) produced three generations per year in a lagoon near Amsterdam. An overwintering generation produced young in the spring which matured in the early summer. Some of the 1SG did not mature until the late summer and fall, at which time some of the early born 2SG had begun to mature. The overwintering generation was thus composed of late developing 1SG mysids as well as juvenile and adult 2SG animals.

Kinne (1955) found that *N. vulgaris* (*N. integer*) in the Kiel Canal of Germany developed two major generations, with a 2SG of little numerical importance. Reproduction was suppressed in the late fall and none occurred from November to March. Mauchline (1971b) found a continuous breeding population of *N. integer* in Loch Argyll, Scotland which produced three distinct generations per year. Differences in the timing of life history events, body size, and number of brood per female between the Scottish and German populations were demonstrated.

Whereas the life history of *N. americana* is relatively well known, very little information exists for *Mysidopsis bigelowi*.

Hopkins (1958) collected gravid females in Delaware coastal waters from April to November. Though distinct peaks in the number of brooding females were seen in the spring and fall, reproduction was thought to be continuous at temperatures above 11°C.

Specimens were collected all year, but no gravid females were taken during the winter.

Wigley and Burns (1971) did not find any gravid mysids in their samples, but found numbers of juveniles and immatures from late spring to fall, indicating a long spawning season. Large immatures collected in May were thought to represent the overwintering generation.

Williams (1972) observed a breeding season from April to November for populations of *M. bigelowi* in North Carolina waters.

Despite its wide distribution, *Heteromysis formosa* is not usually collected in numbers sufficient to develop accurate analyses of its population dynamics. Wigley and Burns (1971) concluded from a small collection that spawning occurred from June to September.

E. Distribution

Contagious distributions of organisms in the sea appear to be more prevalent than completely random ones. The patchiness of planktonic organisms has become a widely accepted assumption for investigators working in all sectors of the marine environment. Aggregations with various degrees of coordination are typical of motile nektonic and benthic species. Traditionally, mysids have been considered members of the plankton, but they are strong swimmers which have the ability to seek suitable habitats and remain there. Much of the available information on mysid abundance and distribution has originated from the analysis of incidental catches made with gear designed to sample the plankton. Many of these studies provide inadequate and misleading conclusions about mysid populations. The importance of sampling procedures has been investigated in the present study and will be discussed in the final section.

An understanding of the social behavior and its implications in the microdistribution of the species is essential to the assessment of the abundance and spatial distribution of the mysid populations. Clutter (1967 and 1969) conducted comprehensive field and laboratory studies on the aggregative behavior and distribution of *Metamysidopsis elongata* in California coastal waters.

As a group, mysids illustrate all degrees of gregariousness. Mauchline (1971a) examined the seasonal distribution of 23 species of shallow water mysids to determine the extent to which they aggregate.

Berrill (1968) studied the schooling behavior and antipredatory behavior of 17 species of mysids from various marine habitats. Social organization ranged from extreme solitude to the obligative association of individuals. None of the species on the east coast formed spontaneous schools, but most formed ordered aggregations in response to water turbulence. *Neomysis americana* occurred in a variety of habitats, but formed aggregations only in areas influenced by bottom currents. *Mysidopsis bigelowi* was found to be "as solitary as mysids come" and *Heteromysis formosa* remained cryptic and idle by day, foraging independently by night.

According to many investigators, water movement and light appear to be the most influential factors determining the short term distribution of mysids. Percival (1929) watched swarms of *N. vulgaris* (*N. integer*) swim upstream ahead of the advancing tide in a British estuary. Elmhirst (1932) observed similar tidal responses for the

Scottish mysid Schistomysis spiritus, but noticed that the movements of aggregations into shallow bays were inhibited on bright nights despite the stage of the tide. Laio (cited in Rice, 1961), working on the same species, investigated the pattern of movements of swarms toward the water's edge, and concluded the migrations occurred with the flooding tide at night, but not during the day or during the ebbing tide. Rice (1961) conducted laboratory experiments to determine the interactions between light intensity and hydrostatic pressure on mysids. In agreement with most field observations, he found that the mysids were induced to move upward by low light intensity and increased hydrostatic pressure.

Herman (1963) found that tidal currents affected the vertical migration of N. americana and that the mysids were more abundant on the bottom during the flooding tide at the entrance of Narragansett Bay. Hopkins (1965) observed that tidal movement influenced the abundance of N. americana at night in the surface waters. Turner and Heubach (1966) and Heubach (1969), working in the Sacramento-San Joaquin River Estuary, found variations in the lateral and vertical distributions of N. awatschensis according to tidal velocity and light intensity.

Whereas many investigators consider fluctuations in the tidal direction and current velocity to be major factors influencing changes in mysid abundance and distribution, interrelated factors such as salinity, temperature, turbidity, and dissolved oxygen may be involved. Often, especially in estuaries, these effects cannot be isolated.

Almeida Prado (1973) observed that the movements of mysids between a mangrove embayment and the coastal waters of Brazil were dependent on tidal currents. The horizontal distribution of each species varied according to its tolerance to salinity and dissolved oxygen. Tidal and seasonal fluctuations in tidal amplitude, temperature, and light penetration had significant influences on the occurrence of some species inshore.

Bainbridge (1960) and Hodge (1963) discussed the influence of tidal currents and salinity on mysid distributions in estuaries in Sierra Leone and Australia, respectively.

Ganapati and Shyamasundari (1959-62) determined that seasonal change in the mysid abundance in Lawson's Bay was related to the directions of the coastal currents off the Waltair coast. Mysids were sparse from July to December when a low-salinity, high-temperature, southerly current flowed from the north.

Coastal circulation was also important in Hulburt's study (1957) of the distribution of N. americana in the Delaware River Estuary. He concluded that the abundance of mysids in the bay was partially due to endemism and supplemented by the "entrainment" of animals from the adjacent coastal areas.

F. Seasonal Migrations

Seasonal changes in the water temperature and photoperiod have profound influences on the distribution and abundance of many animal populations. Fluctuations in the seasonal availability of fishes and macroinvertebrates are widely recognized, but little is known about the migrations of small motile invertebrates.

Whereas seasonal variations in the distribution of mysids have been recorded in the literature, few investigators have demonstrated the structures of the migrations or the mechanisms which induce them. Realistic estimations of population sizes for the demonstration of migrations are difficult to obtain because of the great temporal fluctuations of birth and death rates and the problems associated with sampling discontinuous distributions.

Howes (1939) was one of the first to describe the horizontal movements of mysids in an account of the migration of *Praunus flexuosus* from the shallows of a saline lagoon in Essex to the deeper areas during the warmest months.

Holthuis (1954) studied the autumn exodus of *Mesopodopsis slabberi* from the shallows of the Zuidersee. The mysids overwintered in the depths of the adjacent North Sea and returned in the spring. After the damming of the Zuidersee, no further exchanges with the North Sea occurred, and the mysid disappeared from the lagoon. Van der Baan and Holthuis (1971) examined samples collected in the North Sea and presented evidence for the offshore winter occurrence of several species of mysids which inhabit the shallow coastal lagoons during the summer months.

Kinne (1955) found *N. vulgaris* (*N. integer*) migrated from the deeper channels of the Kiel Canal to the shallow flats in the spring as water temperatures approached 8°C. The mysids were abundant near shore all summer and returned to the more thermally stable depths in the fall.

Numerous other European investigators have demonstrated the seasonal migration of shallow water mysids (Zimmer, 1933; Vorstman, 1951; Mauchline, 1967 and 1971 a ; and Hesthagen, 1973). Mysid migrations have also been observed by Tattersall (1938), Ivanov and Vorob'eva (1963), and Zmudzinski (1967).

Changes in the seasonal abundance and distribution of *N. americana* have been reported by most investigators. Black (1956) observed a sudden increase in mysids in the late spring, and suggested migrations from other areas were responsible. Fish (1925), Fish and Johnson (1937), and Whitely (1948) concluded that *N. americana* lived a planktonic existence during the winter. Black (1956) mentioned that the June increase he observed may have been the result of the concentration of mysids which had been dispersed in the water column earlier in the year.

Hulburt (1957) found that the center of abundance of *N. americana* shifted from lower Delaware Bay during the fall and winter to areas further upestuary during the warmer months. Low densities occurred at the mouth of the Bay during all spring and summer cruises.

Herman (1962) demonstrated that populations of *N. americana* did not penetrate deeply into Narragansett Bay during the spring and summer, but remained near the entrances.

Hopkins (1965) reported marked seasonal changes in the abundance of mysids in his samples from Indian River Inlet, but could not attribute these fluctuations to movements of the population.

Williams (1972) found *N. americana* most abundant around the inlets of North Carolina from November to May. Summer densities were more variable. In general, mysid abundance was greater and more uniform in the rivers.

Mysis stenolepis is the only east coast species for which directional seasonal migrations have been documented. Amaratunga and Corey (1975) found mature brooding females migrated from deep over-wintering grounds in Passamaquoddy Bay, New Brunswick to shallow waters in the spring. The males died in the deep water and, after spending the warm months in the shallows, the immatures migrated to the wintering areas in the fall.

No evidence for seasonal migrations of *M. bigelowi* or *H. formosa* has been reported.

II. THE STUDY AREA

The Hereford Inlet study area is situated within the bounds of 38°58' and 39°06' N and 74°44' and 74°48', approximately 16 km from the southern tip of New Jersey. The area includes a tidal embayment flanked on the west by extensive Spartina marshes and shallow waterways and on the east by a barrier island (Fig. 1). Many similar systems occur along the east coast of North America.

The sampling sites were located along the main route of tidal flow (Great Channel) from a major marsh creek approximately 8km from the inlet to an area about 3 km outside of the inlet breakwater. The locations of the stations are indicated in Fig.1, and the physical details of the sampling sites are reconstructed from fathometer charts in Figs. 2, 3, and 4.

Station 1 was situated in the major tidal channel near the entrance to Great Sound. Tows were made in the direction of tidal flow starting from midchannel and terminating on the edge of the surrounding mudflat. The bottom of the channel supported a dense population of the sulfur sponge, Clione celata, and the slope and mudflat had extensive accumulations of detritus and algae. These materials were collected in every tow and occasionally fouled the epibenthic sled.

Station 2 was located in Great Channel near the entrance of a principal marsh creek. The bottom at this station was the most irregular of all of the stations. Sharp rises and trenches characterized the bottom on either side of a 9 m depression at the

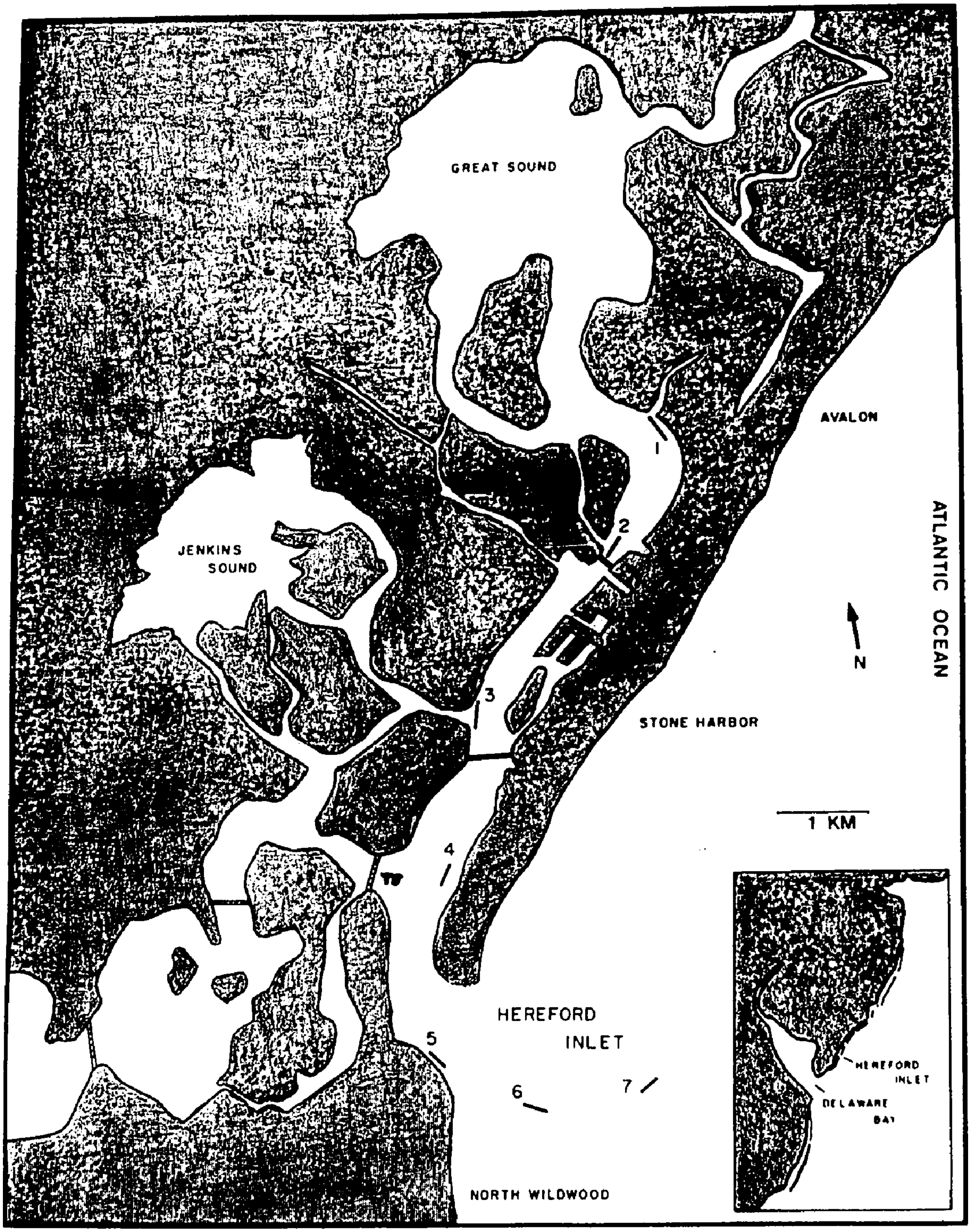

Fig. 1. Locations of sampling sites at Hereford Inlet, New Jersey. Stations 1 and 2 are in the upper embayment and stations 4 and 5 are in the lower embayment. Stations 6 and 7 are offshore.

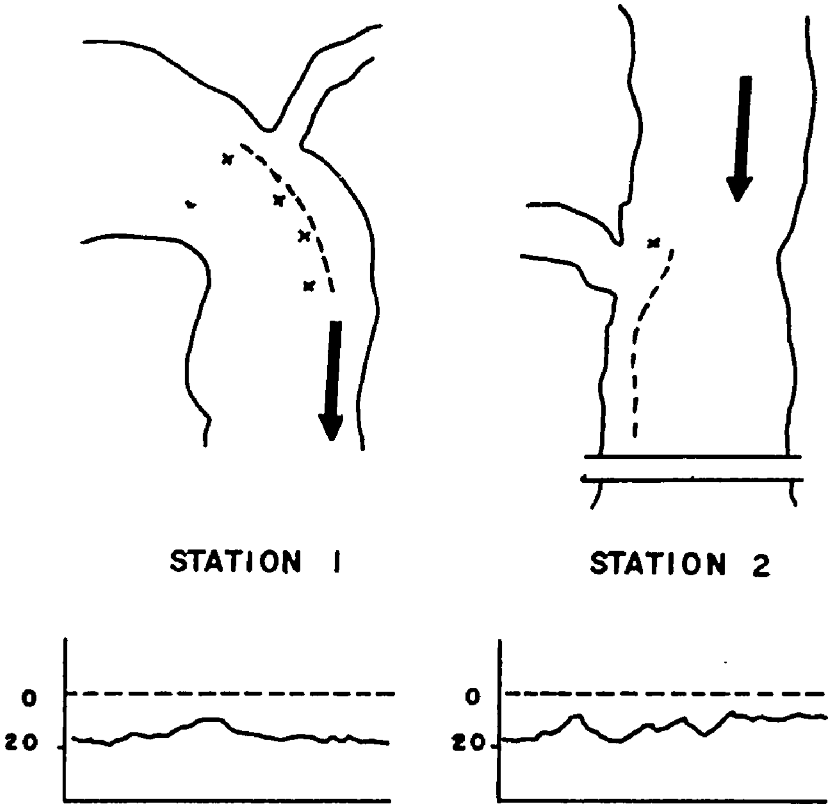

Fig. 2. Physical details of stations 1 and 2. The upper diagram is a view from above. The solid arrow indicates the direction of the ebbing tidal current and the dotted line shows the tow path of the epibenthic sled. The x's indicate locations of Intracoastal Waterway markers. The lower diagram illustrates the bottom topography along the tow path and the depth is indicated in feet.

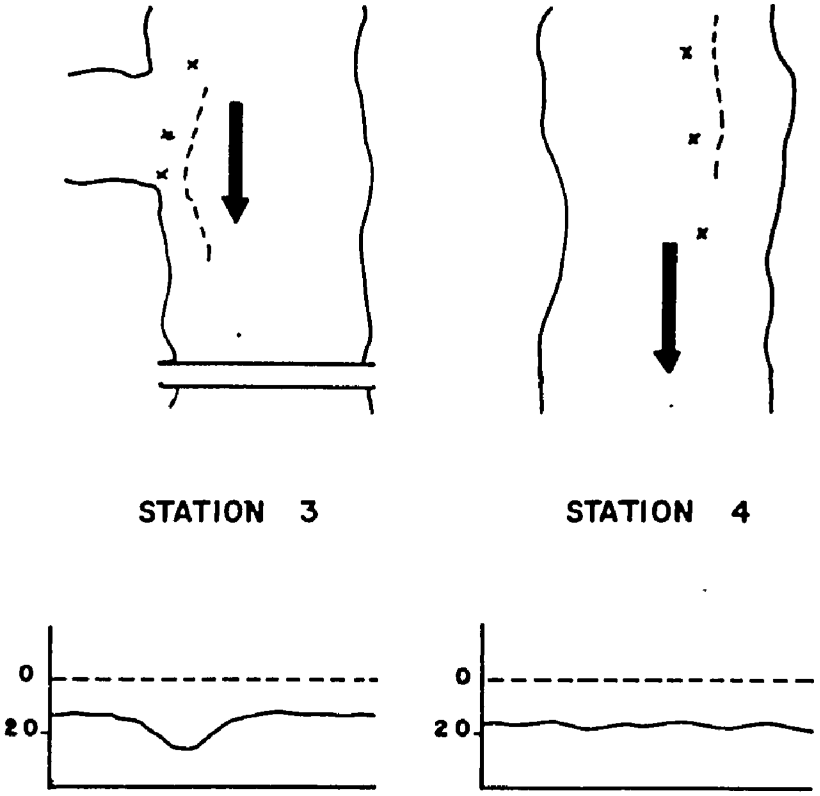

Fig. 3. Physical details of stations 3 and 4. The upper diagram is a view from above. The solid arrow indicates the direction of the ebbing tidal current and the dotted line shows the tow path of the epibenthic sled. The x's indicate locations of navigational markers. The lower diagram illustrates the bottom topography along the tow path and the depth is indicated in feet.

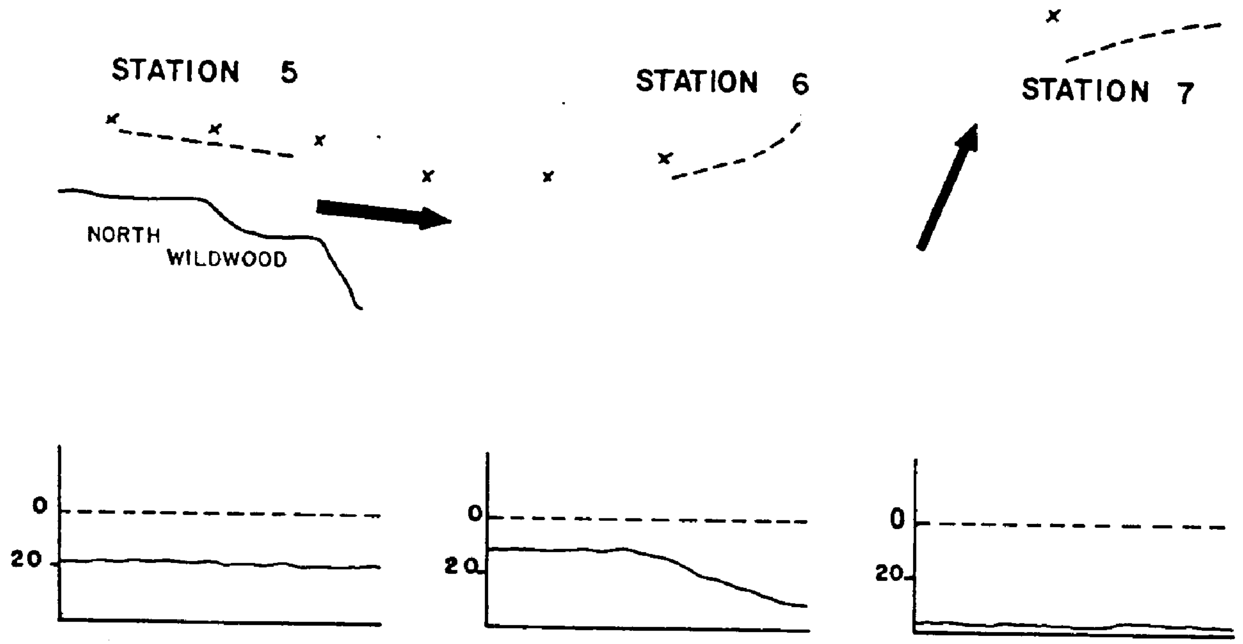

Fig. 4. Physical details of stations 5, 6, and 7. The upper diagram is a view from above. The solid arrows indicate the direction of the ebbing tidal current and the dotted lines show the tow paths of the epibenthic sled. The x's indicate the location of navigational markers. The lower diagrams illustrate the bottom topography along the tow paths and the depths are indicated in feet.

creek mouth. High densities of detritus and macroscopic algae were usually collected.

Station 3 was located at the intersection of Great Channel and a major branch of the waterway which contributed a considerable portion of the tidal volume. The current structure was the most variable at this station. The tows were made across the mouth of Dung Thorofare, where a depression of about 11 m in depth was situated. The rate at which the size and shape of the basin changed indicated that the area was one of the most dynamic in the embayment. The bottom at station 3, like stations 1 and 2, was composed of muddy sand; however, accumulations of debris were not frequently encountered.

Station 4 was located on the slightly deeper side of the wide channel adjacent to the southern end of the barrier island. Station 5 was in the deepest channel (7 m) at the entrance of Hereford Inlet. Shallow sand flats extended from the northern edge of the channel to the southern tip of Stone Harbor. Stations 4 and 5 had similar flat sandy bottoms, which were constantly flushed by unidirectional tidal currents. Maximum tidal current velocities of 85 cm/sec were measured about 15 cm from the bottom, but probably exceeded 1 m/sec several times per month for short periods. Surface currents were considerably greater. The strength of the tidal currents were not as great at stations 1 and 2.

Station 6 was in the navigational channel on the offshore side of the barrier bar across the mouth of Hereford Inlet. The end-points of the tows were on top of the bar (4 m) and at the bottom of the slope on the ocean side (11 m). Bottom water currents on the bar were toward or away from the inlet, while those at the bottom of the slope were in an almost perpendicular direction, toward or away from the entrance of Delaware Bay. The direction of the tow was designed to follow the net direction of both currents (Fig.4).

Station 7 was located offshore on flat sandy bottom approximately 13 m in depth. This area is representative of the bottom from the slope outside of the inlet barrier bar to the next slope, which runs roughly parallel to the coast about 9 km offshore. Some mud-bottomed trenches lie between station 7 and the offshore slope. These sloughs are up to 15 m in depth, less than 0.5 km in width, and stretch parallel to the beach for up to 2 km. The dominating NE-SW coastal currents restrict the extent to which the nearshore and offshore waters mix.

Stations 1 and 2 were collectively referred to as the upper embayment, whereas stations 4 and 5 were called the lower embayment. Stations 6 and 7 were offshore.

The tidal influence extends to the southern portion of Great Sound with an mean amplitude of about 1.4 m. A lag of about 45 minutes occurs between stations 1 and 5, but the timing and amplitude of the tidal peaks may be strongly influenced by meteorological conditions. The ebbing tide from Hereford Inlet cannot be detected near the bottom outside of station 6 where tidal currents toward and away from Delaware Bay move roughly parallel to the coast. The ebbing tide is dispersed in the surface waters while the underlying water mass moves in a northeasterly direction with the ebbing tide from Delaware Bay. There does not appear to be appreciable mixing of the two tidal currents, as evidenced by the formation of a thermocline outside of station 6 during the summer.

Tidal activity and wind were responsible for a complete mixing of the water column in the embayment. No vertical stratification of temperature, salinity, or dissolved oxygen was observed in the shallow inshore area. Lateral temperature gradients were measured in the study area from spring to fall and were considered important in the distribution of the mysid populations. Bottom water temperatures corresponding to the sample collections are presented in Appendix 1.

Temperatures through the winter and early spring were comparable at all stations. Slightly lower temperatures were recorded in the upper embayment, where the sounds and smaller waterways remained frozen for several weeks in February. Differential warming rates of the shallow lagoons occurred in the spring, establishing the most distinct lateral gradients between the inshore stations of the year. Short term changes in air temperature had marked effects on the temperatures of the sounds, resulting in much greater fluctuations at stations 1 and 2. Variations between sampling dates at the other inshore stations were less pronounced. The greatest difference between inshore stations on a single cruise was recorded on April 20, 1976, when the temperatures were 16.3^{o}C and 11.9^{o}C at stations 1 and 5, respectively.

During the summer, the innermost stations were generally warmer than all others. Tidal and diurnal fluctuations were not significant, and little variation between sampling dates occurred. During the early summer, as inshore levels approached 20°C, a distinct thermal discontinuity was established at the inlet. Figure 5 compares the seasonal temperature curves for stations 1 and 7. Coastal currents maintained a relatively stable temperature of 15°C at station 7 until late summer. Though the cool offshore bottom water occasionally penetrated inshore as far as station 4, a sharp differential was usually observed just outside of the seaward extent of the Hereford Inlet tidal current. The thermocline at station 7 persisted until late summer, when its rapid degeneration resulted in equivalent inshore and offshore temperatures. Whereas station 6 usually had temperatures comparable to station 5, the cool coastal current occasionally swung onto the slope depressing the temperature at this station.

There is no significant source of fresh water input into the study area. The strong tidal influence maintains a high and stable salinity the year round. Salinities in the major waterways ranged from 28-32 ppt over the four years measurements were recorded.

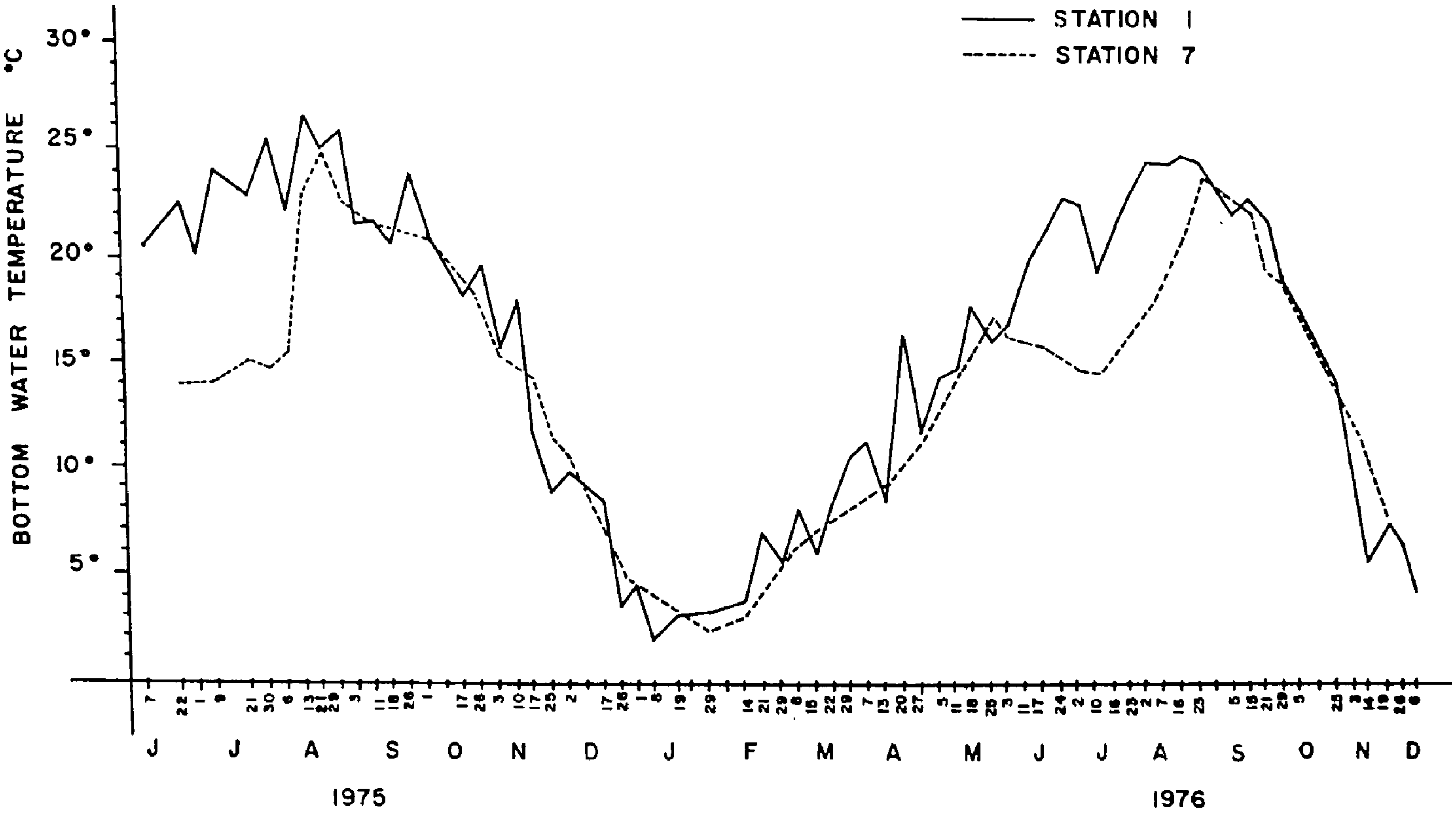

Fig. 5. Bottom water temperatures at stations 1 and 7 on cruises from June 7, 1975 to December 6, 1976. The solid curve is representative of the inshore temperature regime and the dotted line illustrates the seasonal pattern of temperature change in the coastal waters.

III. METHODS

A. Sampling Apparatus and Procedure

The importance of proper sampling equipment and procedures for the determinations of mysid abundance and distribution cannot be overemphasized. The techniques described in this section were developed after preliminary sampling trials demonstrated that great variability in collection efficiency is caused by changes in hydrographic factors. A familiarity with the swimming behavior of the mysids proved essential to the proper design and execution of the sampling program.

An epibenthic sled, towed in the direction of the tide flow, proved to be the most efficient way to collect mysids in the study area. The apparatus is diagramed in Fig. 6. A rectangular 30 cm by 51 cm frame oriented the mouth of the 0.366 mm Nytex net perpendicular to the bottom. The towrope was fastened to the metal framework which extended forward from the lower edge of the vertical face. A depressor plate at the top of the net opening kept the sled tight against the bottom. Materials lying loosely on the bottom were collected, but wide rounded skis prevented the apparatus from digging into the substrate. Attempts to fit the sled with a wheel and metering device were abandoned because of the irregularity of the bottom and amount of fouling debris. No closing devices were used on the sled, since the chances of biasing the samples in the setting and retrieval of the apparatus were negligible. A torpedo type flowmeter (General Oceanics Model 0954) was mounted just inside the mouth of

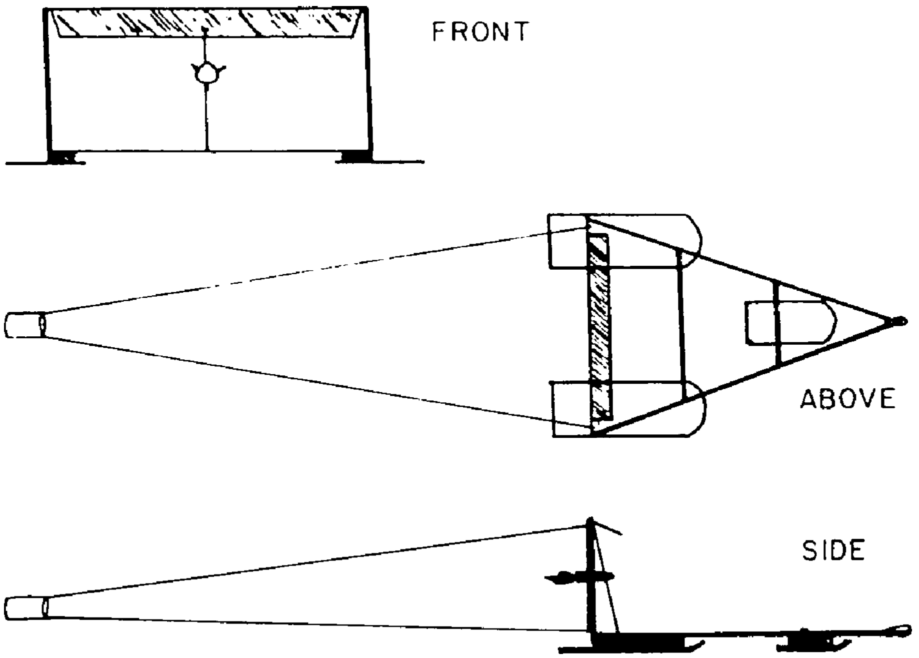

Fig. 6. Design of the epibenthic sled. A plankton net is mounted on a frame so that the mouth is perpendicular to the bottom. A flowmeter is located just inside the mouth and the sample is removed from a jar at the cod end of the net. Skis keep the apparatus from digging into the substrate and a depressor plate keeps the sled in contact with the bottom. The height of the apparatus is 30 cm and the width of the mouth is 51 cm.

the net.

The sled was towed from an 18 foot outboard at speeds sufficient to keep the boat oriented in the direction of the tidal current. At the termination of the tow, the sample was washed into a bucket of seawater and the macroscopic organisms and debris were removed. The sample was drained through a fine mesh net (approx. 0.5 mm) and preserved in a 10% solution of Borax buffered formalin.

Water temperature and salinity were measured with a Beckman RS-5 induction salinometer. Shipboard assessments of the meteorological conditions and sample compositions were recorded. Light intensities on the surface and bottom were measured with a Kahl Scientific Model 268WA310 submarine photometer. Current velocities were measured with a Kahl Scientific Model 4120 current measuring system. Bottom topography was charted on a Raytheon DE-725-B recording fathometer. Preliminary sampling indicated that dissolved oxygen levels were high and stable throughout the study area, thus precluding constant monitoring. Light, current, and dissolved oxygen data were collected only periodically.

In addition to the regular collections, several other short term sampling programs were designed to investigate the effects of tides on the distribution of the mysid populations. These included a series of three 12-hour studies, a six-hour sampling survey, a tag and recapture study, and day-night cruises.

The 12-hour studies involved towing the epibenthic sled with and against the tide at three stations in the embayment. One tow was made in each direction at station 2, followed by two tows at station 3, and then by two tows at station TB. After station TB was sampled, the procedure was started again at station 2. All tows were five minutes long, and temperature and salinity were recorded for each collection. A total of 48 samples were collected from 0600 to 1800 hours. Only the samples from the August 13, 1974 cruise have been completely processed.

On July 28, 1976 a series of nine samples were collected with the ebbing tide at station 5 to determine whether a large aggregation of *N. americana*, centered in that vicinity, changed its position over the ebbing tide. All tows were five minutes long and covered approximately 150 m of bottom.

A tag and recapture study was conducted on August 4, 1976 to determine whether adult mysids could maintain positions against strong tidal currents. Collections amounting to tens of thousands of adult 1SG mysids were maintained for about three hours in large plastic containers filled with a dilute solution of Rose Bengal in sea water. The stained animals were released at the surface inside station 6. All tows were with the flooding tide, starting from the release point, and terminating at station 5.

The nocturnal abundance and distribution of the mysids were investigated on August 23, 1976. The series of stations sampled on a regular basis were sampled in the morning and evening according to the procedures described above.

B. Sample Analysis

The samples were analyzed for the total number of individuals of each species of mysid. Collections which contained volumes of detritus or mysids were split with a cylindrical plexiglass plankton splitter until a workable aliquot was obtained. In most cases, the entire sample was processed. Rose Bengal was occasionally added to facilitate the recognition and counting of juvenile mysids. All sorting and counting was done at 10.5 X with the use of a binocular zoom microscope.

From each sample 150-200 individuals were isolated, measured, and sexed. Individuals were designated as mature or immature males or females according to the presence of primary and secondary sexual characteristics. Immature males had discernible penes between the last pair of thoracic appendages, but lacked the elongated fourth pleopods typical of mature individuals. Immature females did not have oostegites which were sufficiently developed to form a complete brood pouch. Small mysids which did not have any primary features were called juveniles.

Mature females were categorized according to reproductive condition. The eggs and larvae in the marsupium were enumerated, and the developmental stages of the brood were determined. The brood were distinguished as eggs, early eyed larvae, or advanced larvae.

Accurate measurements of the total length of preserved mysids are difficult to make because they are usually curled. Various investigators have used the antennal scale (Herman, 1962), the outer uropod

(Clutter, 1963) or carapace (Amaratunga and Corey, 1975) for estimations of the total body length. In the present investigation, a linear relationship between the length of the outer uropod and the total length was determined. The relationship was constant for mysids of all sizes and sexes, but different for all species. The length of the outer uropod was measured with an ocular micrometer at 45X (± 0.03 mm). Total length was the distance from the tip of the antennal scale to the end of the outer uropod, minus the setae.

The data obtained from the sample analyses were punched on IBM cards and run through the LEAPS (Lehigh Amalgamated Package of Statistics) program in Lehigh University's Control Data Corporation 6400 computer. Various combinations of the data cards were processed to yield comparative statistics on mysid abundance between stations, months, and years. The procedure was also used to analyze the spatial and temporal variations in the population structure of *N. americana*. Since the data base for the life histories of *M. bigelowi* and *H. formosa* was incomplete, only the abundance statistics for these species were determined.

C. Laboratory Experiments

Aspects of the life histories of all three species were investigated in experiments conducted in a running seawater system. Individuals were usually isolated in plastic containers with screened ends. Data on the growth and reproduction of the captive animals was recorded during most seasons.

Behavioral observations were made in a variety of aquaria in both closed recirculating and running seawater systems. Experiments were conducted to determine the swimming behavior of individuals and groups of mysids under a variety of conditions which simulated the dynamic character of the natural habitat.

The social behavior and responses of groups of mysids to water movement were investigated in the laboratory. Most of the observations were made in wide shallow tanks designed to direct currents of variable speeds parallel to the bottom in a circular direction (Fig.7).

A submersible pump fitted with a rheostat generated a current which kept most of the water in the tank in motion. The greatest velocities occurred around the circumference, and the slowest currents occurred near the center. Current speeds were measured with dye markers and a stopwatch. Most experiments were conducted in shaded sunlight, but light intensities and temperatures were occasionally regulated.

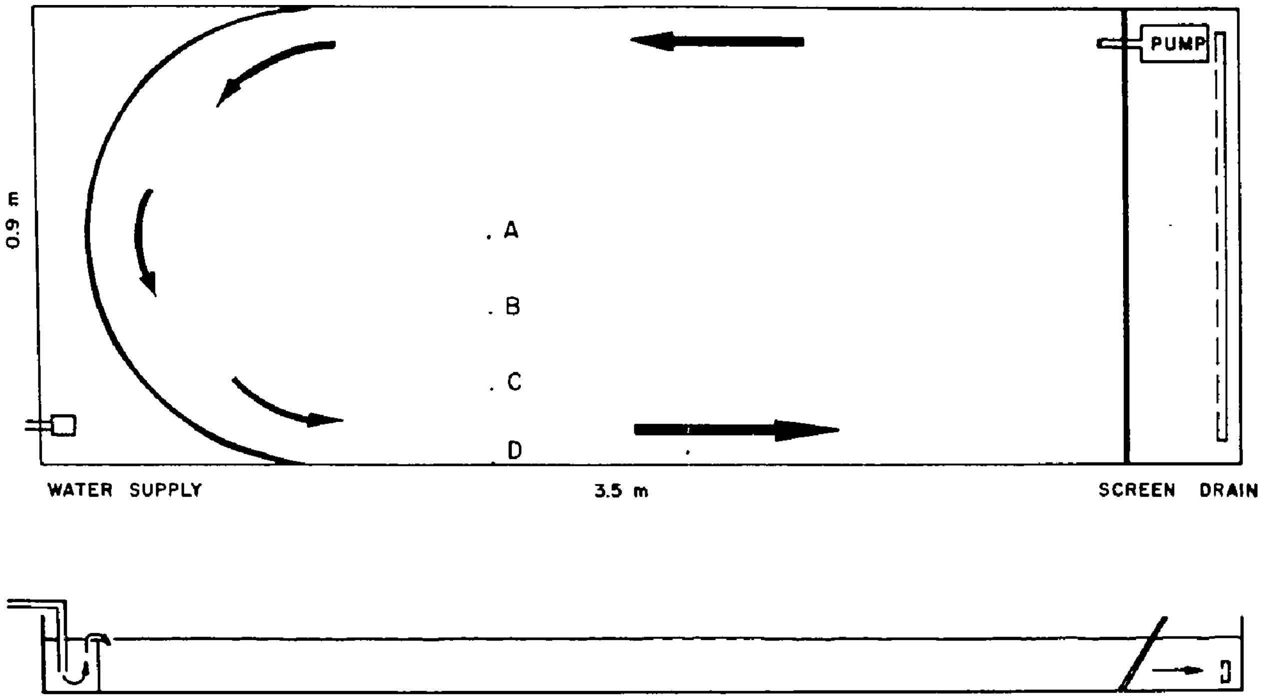

Fig. 7. Diagram of the tank used for the study of responses of mysids to water movement. The upper diagram is a view from above. A submersible pump generates currents in the direction indicated by the solid arrows. The velocities are lowest near point "A" and increase to a maximum at point "D". The lower diagram is a side view showing the input of water from a running seawater system. Equal volumes of water exit from the drain at the opposite end of the tank, maintaining a constant depth of 14 cm in the tank.

IV. RESULTS

A. Life History of *Neomysis americana*

The size, sex, and stage of sexual maturity of approximately 46,000 individuals collected in 254 samples from 44 cruises were determined to establish the life history pattern of *N. americana*.

Juveniles dominated most of the samples collected. Immatures were dominant in January, February, and March, 1976 and in January, 1977 (no samples were taken in February 1977). Mature mysids dominated only in samples collected in March, 1977. The mean percentages of male (immature and mature), female (immature and mature), and juvenile mysids were determined for the samples collected on each cruise. These values are found in Table 1. The mean monthly percentages of the mature (male and female), immature (male and female), and juvenile life stages are plotted in Fig.8. A monthly analysis of the life history patterns observed during 1976 is presented below.

In January,large immatures dominated all samples, although a high percentage of large juveniles were present. These animals represented the main body of the overwintering generation. About 20% of the population was composed of mature mysids which were reproductively active in the late fall before decreasing water temperatures suppressed the spawning activity. Some of these second summer generation (2SG) individuals may have brooded once during the fall, but it is not known whether any survive through the winter to reproduce again in the spring. Less than 1% of the mature females

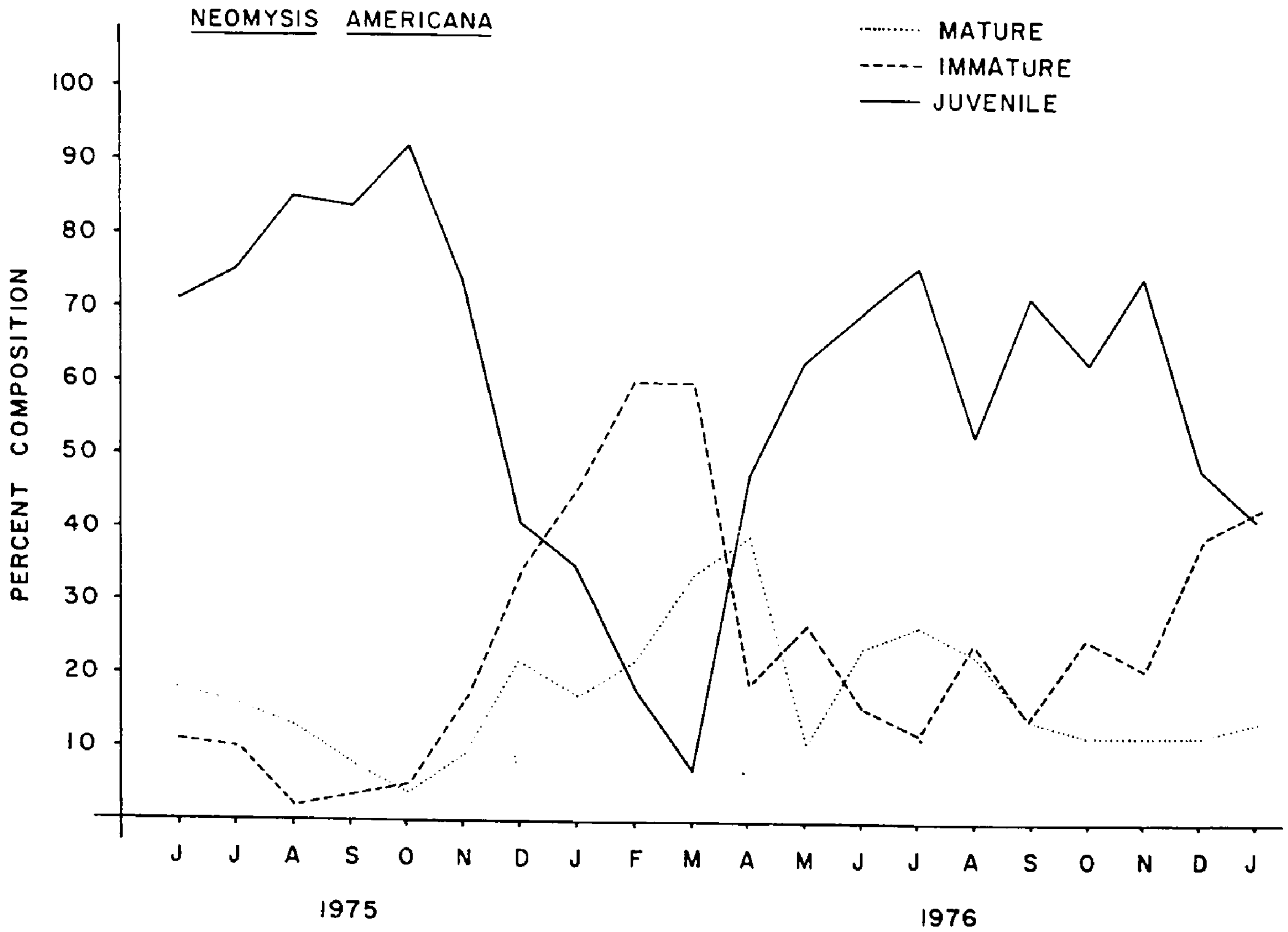

Fig. 8. Mean monthly values of the relative percentages of mature (male and female), immature (male and female), and juvenile N. americana composing the sample populations from June 1975 to January 1977. Approximately 46,000 individuals from 254 samples were processed.

Table I

Average Composition of *N. americana* per Cruise Expressed as Percentages

Date	♂ Mat.	♂ Imm.	♀ Mat.	♀ Imm.	Juv.
6/7/75	6	6	5	4	80
6/22	16	5	10	7	63
7/7	14	2	11	4	70
7/21	4	6	3	9	79
8/6	15	2	6	2	75
8/21	3	1	1	1	96
9/3	11	9	5	7	68
9/18	1	1	1	1	99
10/1	3	3	2	2	91
10/17	1	3	1	2	94
12/2	4	23	3	6	60
12/17	23	26	15	12	22
1/1/76	14	27	4	23	36
1/16	12	18	4	21	46
1/29	12	27	4	33	24
2/14	12	21	5	37	24
2/29	20	22	8	40	11
3/15	23	25	9	40	5
3/29	21	22	16	33	9
4/13	34	11	21	23	11
4/27	3	1	9	2	83
5/11	2	13	1	14	71
5/25	8	14	10	13	56
6/11	7	5	7	5	75
6/24	8	10	6	11	65
7/10	5	7	4	7	80
7/23	12	3	6	7	72
8/7	3	10	2	10	72
8/23	16	13	20	15	36
9/5	3	2	1	2	91
9/21	16	12	9	12	52
10/5	9	13	8	15	55
10/25	3	9	4	12	72
11/3	4	13	2	14	66
11/19	2	9	10	5	83
12/6	9	20	3	19	49
1/6/77	14	15	1	28	41
3/4	29	11	28	17	14
3/21	26	20	14	27	13
5/3	3	5	4	5	83
6/2	2	6	2	5	85
6/14	12	7	12	7	61

collected in January were gravid, and very few recently spawned juveniles were taken.

In February, the percentages of both mature and immature mysids increased. A complementary decrease in the proportion of juveniles resulted as the larger young developed primary sex characters and were assigned to immature categories. Immatures continued to dominate.

March samples indicated the continued dominance of the immature class which constituted almost 60% of the population, the highest percentage of the year. Nearly the entire remaining fraction of the population consisted of mature organisms. Increasing numbers of reproductively active mysids appeared in March, with about 30% of the mature females carrying eggs or brood in the March 29 samples. On March 15, juveniles reached the minimum population level (5%) of the year. An increase in the percentage to 9% on March 29 reflected the low level recruitment by the earliest brood releases of the overwintering generation (WG).

Samples taken on April 13 indicated a marked reduction in the percentage of immatures as the WG was approaching its reproductive peak. About 55% of the population was mature and 70-80% of the mature females were brooding by mid-month. By late April a dramatic change in the composition of the population had occurred. Juveniles dominated all samples with an average of 83%, the greatest proportion of young since the fall. Only 12% of the population was mature and the reduction in numbers indicated that mature individuals had died after their reproductive efforts were completed. While the WG had essentially disappeared by late April, some immature animals originating from low level mid-winter spawning activity persisted.

In early May, there was evidence the first of the WG progeny, now 4-6 weeks old, had developed primary sex features. This accounted for increases in the percentages of immatures in the samples. On May 11, mature forms made up only 3% of the population. These represented reproductively active individuals of winter origin which were much smaller than the April spawners. This tends to indicate that total length does not determine maturity. On May 25, increases in the mature classes were observed as the spring spawn reached maturity. Decreases in the percentages of juveniles reflected the slow rate of recruitment between the peak activity of the WG and the peak spawning period of the first summer generation (1SG) in the early summer.

In June, the population was composed almost exclusively of the 1SG, although all sizes and degrees of maturity were represented. The largest individuals were the first spawned of the WG and the smallest the progeny of the winter born animals. The most conspicuous members of the population were the mature and immature 1SG animals which were 10-12 weeks old. By late June about half of the mature females were brooding and, even though the peak reproductive period of the 1SG had not occurred, a large number of young had been released, signalling the start of the 2SG.

July samples were similar to those in June, with juveniles dominating the population. The peak spawning activity of the 1SG occurred and all stages of development were apparent. Large mature females were carrying their second and third broods by late July and small females, having just reached maturity, had their first broods. The continuous reproduction of the population from early summer made it impossible to trace the development of particular groups through maturity.

The relative percentages of the life stages were similar in August as well. The peak activity of the 1SG was over by mid-month and, by late August, the 1SG began to disappear from the population.

In early September, marked reductions in the number of large 1SG animals had occurred, and juveniles of the 2SG comprised 91% of the population. Though some 1SG adults persisted, most of the larger animals were the first of the early summer spawn (10-12 weeks old) which had reached maturity by mid month.

The 2SG produced young from late September to the end of October. It appeared as though most of the 2SG had not reached maturity by November, when reproductive activity was sharply decreased. Most of the 2SG, then, overwintered as immatures and became sexually mature the next spring.

A schematic representation of the temporal distribution of the generations of N. americana in the Hereford Inlet study area is illustrated in Fig. 9.

The 1SG originated in the early spring and persisted until mid summer, so that a longevity of 3-4 months was likely. The largest

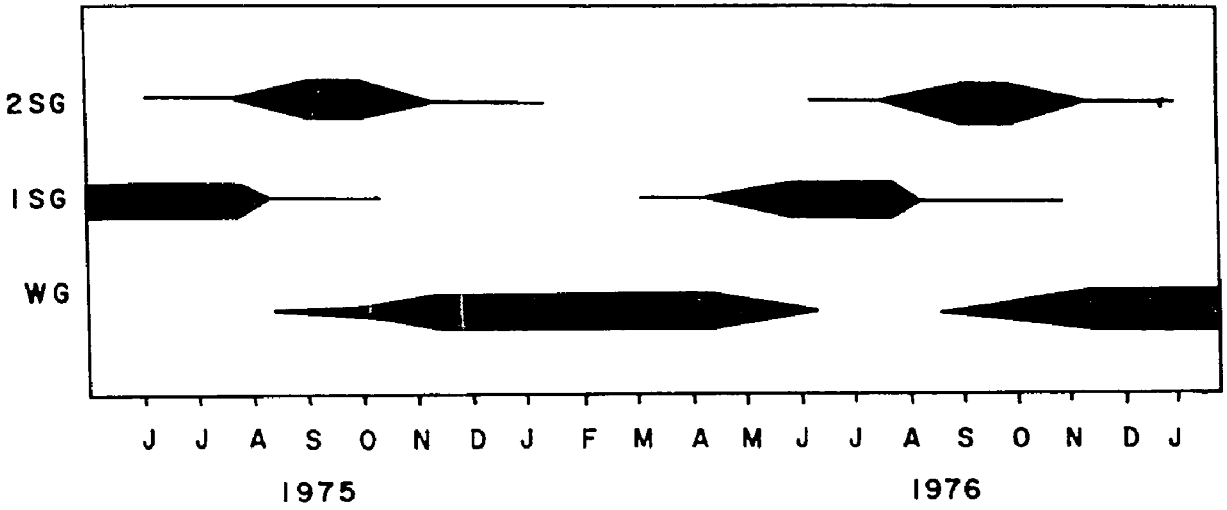

Fig. 9. Schematic diagram of temporal distributions of generations of *N. americana*. The winter generation (WG) spawns in the early spring, giving rise to the *first summer* generation (1SG). The second summer generation (2SG) originates from the reproductive activity of the 1SG. Some of the 2SG matures and dies in the fall and the remainder becomes the WG. Because of the overlap of the generations, the horizintal dimensions of the kites are approximate. The vertical dimensions of the kites schematically represent temporal changes in the abundance of the generations.

of the 2SG present late in the fall were also 3-4 months old before they started disappearing from the samples in early winter. Mysids born in the fall did not reach maturity until the following spring, indicating a longevity of 6-9 months. Individuals could not be maintained in the laboratory for sufficient lengths of time to confirm these estimations from the field sample analyses. Variations in the growth and reproductive rates of laboratory maintained individuals were large and supported observations made on the field populations. Such variability in the population probably accounts for the occasional giants and dwarfs in the life stage categories. Some individuals of the 1SG may overwinter and survive 10-11 months, but it is unlikely any live as long as 12months.

Despite the many sources of variability within the population, the timing of the reproductive peaks was quite stable. The spring spawning peak of the WG occurred during the last part of March in 1975, 1976, and 1977. The abrupt disappearance of the 1SG was observed in late August during all three years.

The size range for all specimens of _N._ _americana_ measured was 1.6-15.2 mm. The mean lengths of the five life stages are shown in Fig. 10. The largest mysids (11-12 mm) occurred in March and April, and the smallest mature animals (7-8 mm) occurred in September and October. These mature 2SG mysids were smaller than the largest immatures (8-9 mm) of the year, which occurred in March and April. The smallest individuals on which primary sex features could be determined were the immature of the 2SG in September and October.

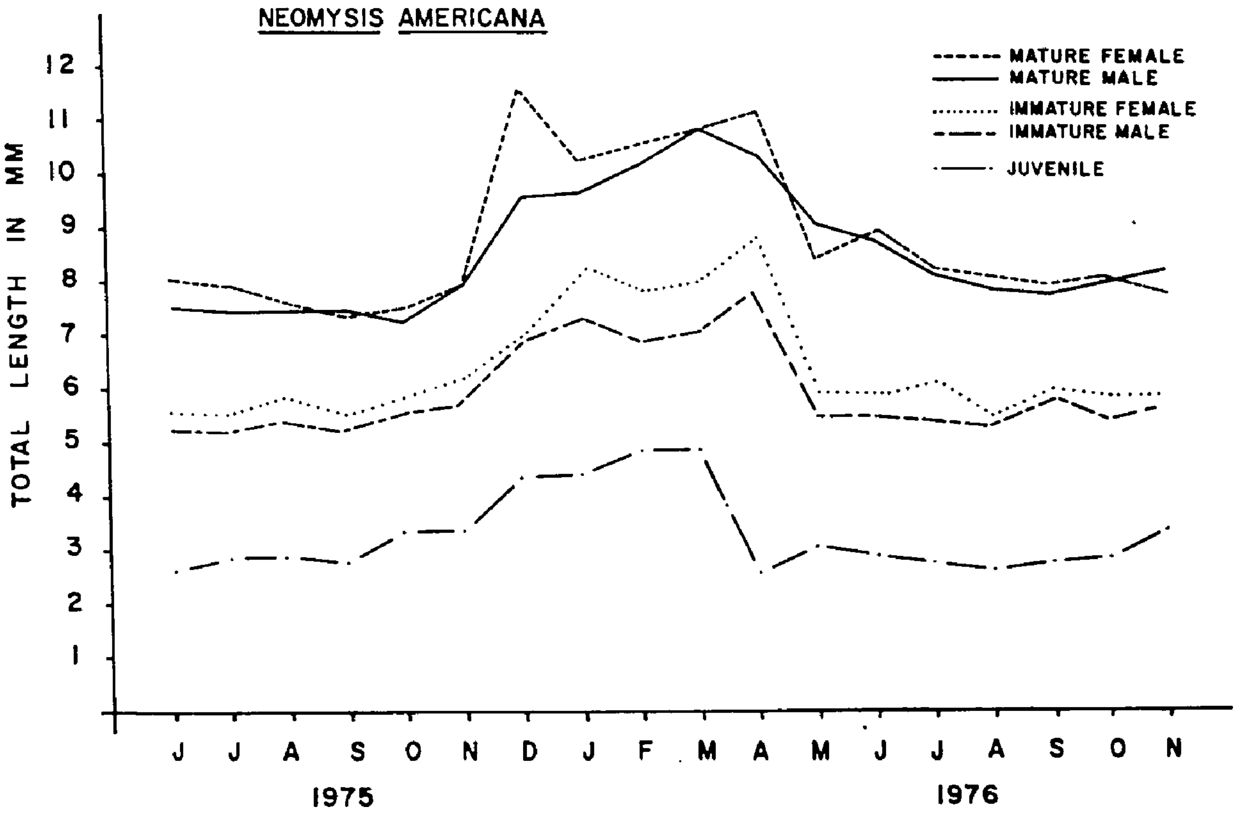

Fig. 10. Mean total lengths of five life stages of _N. americana_ by month from June 1975 to November 1976. Approximately 46,000 individuals from 254 samples were measured.

The largest juveniles (4-5 mm) were collected in February and March. Small juveniles (2-3 mm) often dominated the summer samples. Mature females tended to be larger than their male counterparts during all months.

Attempts to determine growth rates in the laboratory were generally unsuccessful, primarily because mysids could not be maintained for extended periods. For large collections maintained in the running seawater tanks (Fig.7), a 50% mortality was usually observed after 10 days. In isolation, individuals were maintained for several weeks according to the water temperatures. Some WG individuals were kept for as long as 16 weeks, whereas 1SG animals seldom lasted more than 2 weeks at the higher summer temperatures. In general, the large overwintering mysids were hardier than the small summer animals. The cold acclimated generation had a greater tolerance to the thermal, heavy metal, and handling stresses they were exposed to in laboratory experiments.

Limited observations in the laboratory indicated juveniles molted more often than larger individuals,and that there was a great deal of variability in the frequency of molting and the increment of growth between individuals of the same age maintained in identical conditions.

The ratio of females to males was essentially unity, with both sexes accounting for 21% of the total number of individuals measured and sexed. While one sex often dominated in the samples for weeks or months at a time, there was no seasonal pattern. Males often outnumbered females toward the end of a generation, possibly indicating a greater longevity for the males.

Gravid females were collected every month, although only small numbers occurred from December to March. During this period,recently spawned juveniles were also uncommon. Table 2 demonstrates the differences in size and fecundity of the mature females of the three generations. The large spawners brooded more than twice as many eggs and larvae as the 1SG, and three times as many as the 2SG. While the size of the 1SG and 2SG animals was comparable, the 1SG brooded a significantly greater number of young. Brood mortality in the marsupium may be on the order of 10% for all generations. Estimates of fecundity were complicated by the loss of eggs and embryos from the pouches during collection and sample processing. The variation in the numbers of brood carried by females of the same size was also a source of error in the fecundity determinations. The smallest brooding female was collected on September 5, 1976. This individual was 6.2 mm long and was carrying five advanced larvae. The largest brooding female was 14.8 mm and had 61 early eyed larvae. It was collected on April 30, 1976.

In the laboratory, mysids were observed to molt and copulate only in darkness. Within minutes of molting, a sexually mature female was usually approached by a male which assumed a position below the slow swimming female and passed sperm into the empty brood pouch. The female then released the eggs into the pouch. Laboratory observations indicated an incubation period of about 15-25 days with distinct seasonal variations. A terminal molt by the female usually occurred

Table 2

Comparison of Mean Length and Fecundity of Mature Females of Three Generations

Generation	Length in mm	Number of Brood	Stage
WG	11.2	39	eggs
	11.4	35	early eyed larvae
	11.2	35	advanced larvae
1SG	8.3	16	eggs
	8.0	15	early eyed larvae
	8.0	16	advanced larvae
2SG	8.0	11	eggs
	8.3	11	early eyed larvae
	8.0	11	advanced larvae

after the last of the brood was released. On several occasions, females of the 1SG released young, molted, and dropped a new clutch of eggs into the pouch. No males were present in these isolations and the unfertilized eggs degenerated within a few days. Decomposing eggs were occasionally observed in field collected females. Laboratory observations supported field evidence that summer generation females were capable of reproducing more than once. The presence of both large and small egg bearing females in July provided evidence that some of the 1SG which matured in June survived after their first brood releases and were able to reproduce again. It was not possible to determine whether or not individuals could brood more than two times.

B. Behavior of Neomysis americana

Neomysis americana was maintained in both recirculating artificial and running seawater systems for behavioral studies. Although conditions were designed to simulate the natural habitat, only moderate success was achieved in the maintenance techniques. The mysids proved to be extremely delicate, and mortality resulting from the collection and handling procedures were high. The horizontal limitations of the holding tanks coupled with the impracticalities involved with the simultaneous maintenance of sufficient concentrations of filterable particles and high water quality are thought to have influenced the limited success.

The density of mysids in the systems was found to influence both the success of the maintenance procedures and the behavioral responses of the captive aggregations. The numbers of animals which comprised the aggregations, and the difficulties involved with observing their small and almost transparent bodies in turbid water, rendered quantitative observations impractical.

Behavioral observations were further complicated by the high degree of individual variability inherent within the aggregations. The responses were never uniform as a result of the differences in the swimming capabilities of small and large animals and the physiological condition of the individuals. The trends described in this section apply to the responses of the majority of animals from a series of replicate assays.

Neomysis americana was not capable of forming spontaneous aggregations in any of the experimental systems. In static conditions, individual and group swimming appeared random, and no changes in environmental conditions other than water movement could induce ordered aggregations. In the absence of currents, individuals swam almost continuously in erratic paths. There was no indication of any coordination between individuals, so that the net response of the captive population appeared random regardless of the density of animals. Attempts to accurately determine the cruising speeds of individuals of different sizes were discouraged by the rapid turning rates of the animals in spacious tanks and by the aberrant behavior of individuals examined in more confining aquaria. Adult mysids usually swam at 3-4 cm/sec, whereas juveniles moved at somewhat slower rates. There was a great deal of variation between individuals and between speeds and distances of consecutive excursions by any one individual. Cruising speeds were usually slower in the dark.

As water currents were initiated in the systems, juveniles usually responded before adults. The minimum velocity capable of inducing the orientation was on the order of 1 cm/sec. Both oriented into the currents, but the smaller animals were swept away at velocities greater than 20 cm/sec against which the larger mysids could maintain positions. Adults could tolerate currents up to 30 cm/sec for short periods.

Increasing current velocities in the experimental tanks had almost predictable effects on the mysid aggregations. At velocities which ranged from 0-10 cm/sec, the adults and juveniles were homogeneously distributed, holding relatively stable positions into the currents.

As speeds were increased, there was an incomplete separation of the size groups. The larger mysids oriented into currents of 10-20 cm/sec in zones BC and CD (Fig.7) and smaller individuals oriented into currents less than 10 cm/sec toward the center of the tank. The centers of maximum density for the two groups could be shifted between points A and D by changing the rheostat setting. In response, zones of preferred velocities were selected by the animals. A reduction in the overall velocities resulted in the movement of the center of maximum density toward the outside and increases shifted the groups toward the center again. The responses were immediate and could be elicited repeatedly. The preferred velocities were different for each size class and were highly variable according to light, temperature,and physiological condition. Generally, adult summer generation mysids (6-8 mm) showed a preference for speeds of 8-12 cm/sec in shaded sunlight at about 20°C. Juveniles in the same experiments responded preferentially to 5-9 cm/sec.

Collections of mysids were introduced to the systems within minutes of capture, and the responses were monitored as long as sufficient numbers of animals persisted. The responses of the groups usually changed over time. These variations were often density related.

Neither the composition of the sample population,nor the higher mortality rates of the juveniles in captivity,could be controlled and thus constituted significant sources of variability in the experiments. Reductions in the densities of mysids between observations also affected the group responses. Since the animals demonstrated preferences for specific velocities, and those excluded by overcrowding were forced to inhabit other zones, group responses were often difficult to assess.

There was no indication of periodicity in the responses. A series of reversals in the current direction resulted in immediate reversals in the direction of the orientations. Mysids maintained in idle water for 96 hours oriented into currents as soon as they were generated.

Large mysids were generally more responsive to decreases in velocity than juveniles. As currents gradually subsided, juveniles continued to remain relatively stationary and oriented. Adults would drift backward with the current, stop, and reorient, repeating the behavior many times. As current speeds approached zero, the ordered aggregations of large mysids degenerated until a random dispersion resulted.

The distances between individuals oriented parallel to one another remained relatively stable at constant velocities, but were decreased in stronger currents. Light intensities strongly influenced the inter-individual distances.

Within the aggregations, individuals often shifted positions, frequently changing swimming speeds and using currents to move both horizontally and vertically. Large mysids usually remained relatively stable for several minutes in moderate currents before assuming new positions. Juveniles were often more active.

In more than 100 observations, the orientations of groups of mysids in the experimental systems were induced with the generation of water currents and persisted as long as the water continued to circulate. The only exception was observed on June 3, 1977 when a large collection, consisting primarily of adult 1SG mysids, was placed in the tank. The animals remained oriented for 24 hours and dispersed when the flow was stopped. Minutes later, the same current was reestablished and all of the mysids began to swim downstream. The animals continued to swim slightly faster than the 8-15 cm/sec current for about four hours, at which time the current was again stopped. A random distribution ensued and, when the current was regenerated minutes later, the aggregation responded by orienting into the current in the typical manner. No changes in any factors other than water movement could be determined. This unique group response could not be induced again. This response demonstrated an aspect of the social behavior of N. americana which may be operational in the rapid and extensive changes in the distribution of the species in the tidal embayment.

Changes in the vertical conformation of the orienting aggregations were observed, but were difficult to quantify. Experimental tanks of many designs proved to be inadequate because of water turbidity, mysid transparency, and the aberrant behavior elicited by the confinements of the chambers. Vertical displacements of individuals were induced by changes in current velocity and were density dependent. Generally, adult mysids shifted to zones of slower velocity as current speeds in the experimental tanks were increased. In overcrowded situations mysids remaining in high velocity zones responded by moving closer to the bottom. At extreme velocities, individuals used their thoracic appendages to hold themselves in sandy substrates. Such responses usually lasted for less than an hour. The effect of the vertical depression of the aggregations was to decrease the number of individuals per unit surface area. Field studies on the effects of tidal velocity on the distribution of N. americana produced results consistent with these observations.

Field observations of mysid behavior were limited by the infrequent occurrence of the animals in clear shallow water. During March, 1977, N. americana was abundant in shallow troughs and pools on the tidal flats of Delaware Bay at Norbury's Landing. The swimming behavior was very similar to that observed in the laboratory. Nonoriented, actively swimming individuals occurred in the static pools and oriented ordered aggregations occurred where currents prevailed. The larger animals maintained stable positions in stronger currents and swam against weaker ones.

Neomysis americana was observed on several occasions in the shallow areas adjacent to stations 2 and 3 during the spring of 1976 and 1977. A large aggregation was seen swimming just above the bottom from a vantage point on a floating dock in March 1976. Large WG mysids were observed swimming randomly at slack tide in full sunlight, crossing temperature gradients of 4°C or more. On other occasions, mysids were observed swimming actively in shallow intertidal pools which were 4-5°C warmer than the adjacent waterways. Mysids were observed in these situations only during the spring before the WG disappeared. Laboratory studies on the influence of temperature changes on the swimming behavior of mysids were inconclusive, but captive WG animals usually demonstrated a preference for warmer areas in static gradient assays.

Laboratory studies on the effects of light on the responses of mysids in the water current experiments were necessarily qualitative. In general, the mysids demonstrated preferences for the areas of lowest light intensity during the daylight hours. Factors such as density, population composition, physiological condition, and degree of photoacclimation (time and intensity) influenced the group responses. In shaded sunlight, the mysids chose to orient into currents rather than to occupy dark but static areas in the tank. In areas of equal current velocity, highly reflected bottoms were avoided when densities did not inhibit most animals from orienting over darker bottoms. Aggregations oriented over dark bottoms were extremely difficult to observe in the laboratory.

In darkness, _N. americana_ did not form well ordered aggregations into currents similar to those which elicited parallel orientations during the day. Mysid collections maintained in total darkness in the experimental systems were observed immediately after the lights were switched on and found to be loosely oriented into the currents. Most of the dark oriented mysids hovered high in the water column and maintained orientations into the currents which were less precise than those observed in daylight. A greater percentage of animals were drifting with the current than were usually observed during the day. Interindividual distances were significantly greater in the dark and the aggregations were generally less completely organized than in the light. Ordered assemblages which were indistinguishable from those observed in shaded sunlight formed minutes after the darkened systems were illuminated, only to partially disperse when the lights were turned off again. These group responses could be elicited repeatedly.

Vision was thought to be a primary means by which mysids maintained ordered orientations in the experimental systems. In an optomotor apparatus,mysids in still water responded to a pattern of alternating black and white stripes which was rotated around the outside of a circular tank. As the pattern was rotated in one direction, the mysids would respond by swimming actively in the opposite direction at the same speed. A reversal in direction would elicit a reversal in the swimming path, and a change in the speed of rotation would result in an equivalent change in the swimming speed. These observations suggest the responses of the mysids to currents may be partially influenced by the animals' visual detection of materials borne on the current, but further study is needed.

Experiments were conducted during the light period to determine the responses of oriented groups to various disruptive factors. The captive mysids were sensitive to shadows passing over the water's surface and reacted by moving laterally. In zones of moderate velocity, oriented aggregations would respond differently to objects pushed along the bottom according to the directions from which they approached. If the disturbance came from upstream, the response was usually in the form of a slight lateral shift without any significant upstream displacement along the current axis. When confronted from downstream, the avoidance was much more active and resulted in much greater lateral displacement. Disturbances directed from the side resulted in an active effort to swim upstream or drift with the current. The responses in all cases were confined only to that portion of the oriented aggregation which was directly confronted. As soon as the disturbance passed, the mysids reoccupied the same area.

C. Tidal Distribution of *N. americana*

There was no indication that the numbers of mysids collected in the embayment were strongly influenced by the direction of the tide; the animals were not passively transported from one point to another in the study area. In the regular sampling program, *N. americana* occurred in each of the 254 samples collected on 44 cruises with the ebbing tide. It was also found in each of the 170 samples taken in 36 cruises with the flooding tide. The mean numbers of individuals collected per tow were 34,706 and 20,756 for the ebbing and flooding series respectively. A statistical analysis of the abundance of mysids in the samples indicated a great similarity for the two series.

In general, tidal activity did not appear to induce major changes in the abundance or composition of the population at the sampling sites over short periods of time. Samples collected at the same stage of the tide on several consecutive days were usually similar, except for periods when major migrations between the embayment and coastal areas were occurring. Over longer periods of time, great variations in the abundance and composition of the populations at any station could be observed. These spatial and temporal fluctuations in the distribution of the populations will be described in other sections, and were probably related to the mysids' responses to tidal currents.

Laboratory observations demonstrated the immediate and sustained orientational responses of *N. americana* in the presence of currents. It is likely that similar responses are elicited by tidal currents in the embayment.

The influence of tidal activity on the abundance and composition of the populations of N. americana was investigated in a 12-hour sampling study on August 13, 1974. A total of 151,064 individuals were collected in 24 samples in which the epibenthic sled was towed in the same direction the tide was flowing. About one tenth (15,362) as many mysids were taken in the 24 tows against the tidal currents. Figure 11 illustrates the difference in the number of individuals collected with and against the tide. These observations were consistent with laboratory tests in which mysid aggregations oriented into the current were more susceptible to capture with a dip net confronting them head-on than by nets approaching them from downstream.

While the number of individuals collected against the tide was consistent, great fluctuations in the size of the catch occurred in the series of samples collected with the tide. The lowest numbers were taken around slack tide and the greatest numbers occurred with the strongest tidal velocities around mid-tide. In the laboratory, mysids remained in oriented assemblages just above the bottom at slow current velocities and moved closer to the substrate with increased velocities. In standing water the mysids dispersed randomly.

A comparison of the average lengths of the mysids showed that the values for the mature, immature, and juvenile animals were greatest at station 2 and smallest at station TB. No significant changes in the average sizes occurred over the sampling period. The population structure for station 2 was determined for samples taken

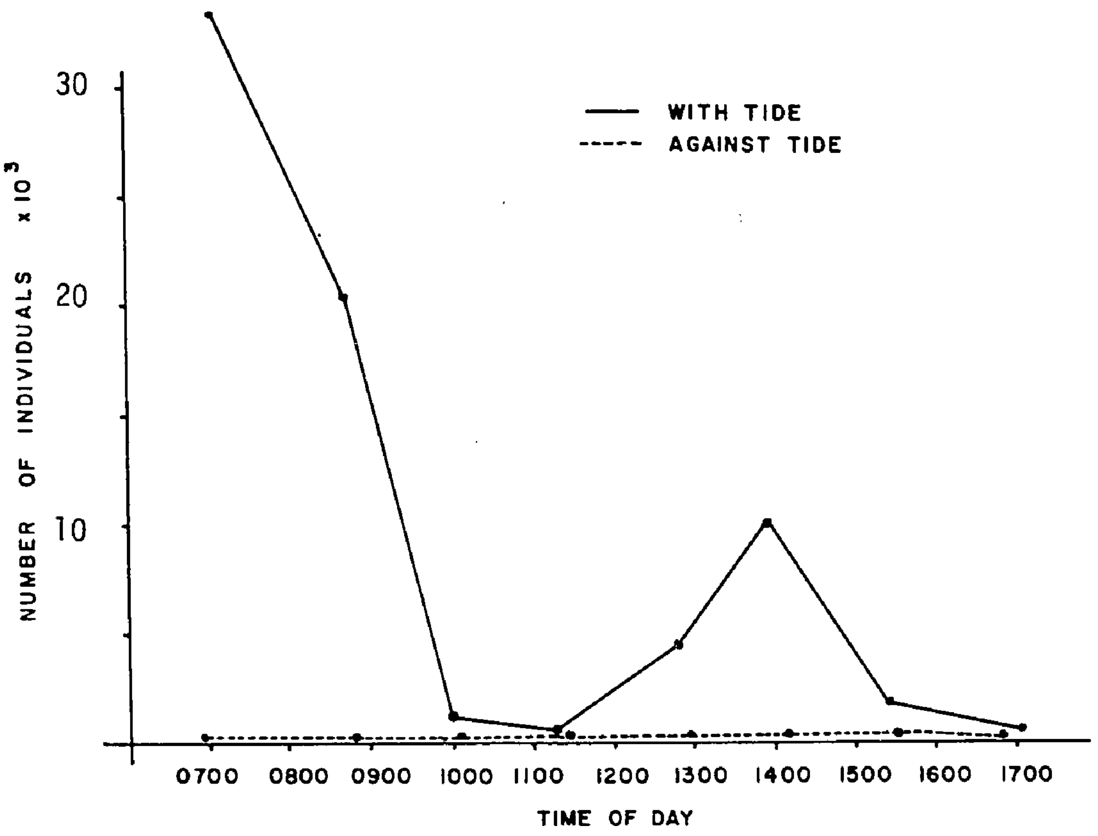

Fig. 11. Abundance of *N. americana* in samples collected "with" and "against" current in 12-hour tidal study at station 2. The study was conducted on August 13, 1974. Flood tide occurred at 1700. The vertical scale indicates numbers of individuals collected per tow.

with the tide and, though the average sizes remained stable, the composition did change over the tidal cycle. The composition is illustrated in Fig.12. The fluctuations in the relative percentages of the three life stages were probably related to behavioral responses of the mysids to current velocity. Changes in the spatial dimensions of the oriented aggregations as a function of current velocity were probably significant in determining the numbers of individuals which could be collected with the sampling apparatus.

In an analysis to determine the similarity between all samples taken with the tide, a significant correlation (r= +0.4210) was found between the number of individuals collected and the percentage of mature animals comprising the samples. Adult mysids constituted a greater percentage of the population in samples collected at the stronger velocities.

In tows made with the tide, a negative correlation existed between the percentage of juveniles and current velocity so that as velocities increased, the proportion of the population composed of juveniles decreased (r= -0.3547). In tows against the tide, increases in the velocity resulted in increases in the percentage of juveniles (r= 0.4484). In general, an increase in the number of individuals collected against the tide resulted in an increase in the percentage of juveniles (r= 0.4415). In the laboratory, juveniles were transported downstream with stronger currents so that lower numbers were captured by dip nets pulled with the current. Mature mysids were much more capable of avoiding nets approaching them from behind than were juveniles.

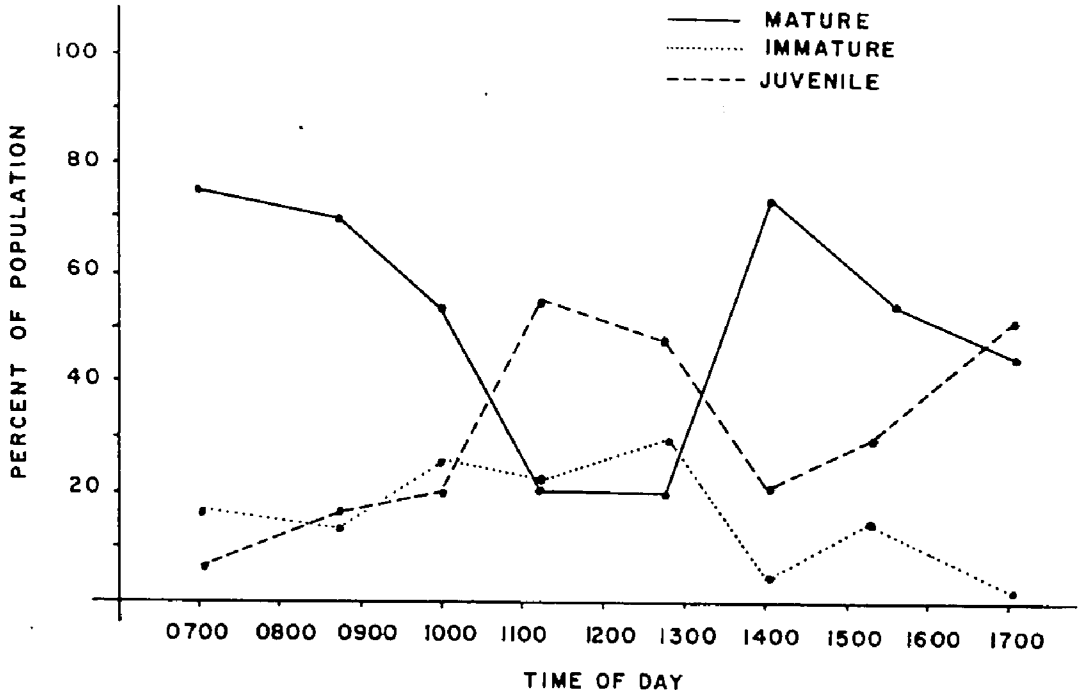

Fig. 12. Mean relative percentages of mature (male and female), immature (male and female) and juvenile N. americana composing populations in samples on August 13, 1974. All samples were collected "with" the tide in the 12 hour tidal study. Ebb tide occurred at 1040 and flood tide occurred at 1700.

The stability of a large aggregation of *N. americana* centered around station 5 on July 28, 1976 was tested in a series of nine tows with the ebbing tide. The aggregation maintained its position over the entire tide. Fluctuations in the numbers of mysids collected at different stages of the tide were observed (Table 3). These variations were similar to those observed in the 12 hour study. The highest numbers were collected at the strongest velocities and the lowest numbers were taken around slack tide. The salinity remained stable, but the temperature increased from 20.1°C just after the flood tide to 24.4°C at ebb tide. These observations demonstrated the ability of aggregations of *N. americana* to maintain positions against the strongest tidal currents in the embayment.

On August 4, 1976 a tag/recapture study was conducted between stations 5 and 6 to determine whether individuals released at the surface in strong flooding currents would swim toward the bottom and remain oriented into the current for any length of time. Stained mysids were released at 1405 hours inside of station 6 and tows with the flooding tide toward station 5 commenced at 1420. On the first tow,one red mysid and some stained detritus were recovered. Five individuals were collected in a tow started at 1440 and three in a tow started at 1520. Despite surface currents of about 120 cm/sec and bottom currents on the order of 50 cm/sec, mysids were collected up to 80 minutes after release. Since the stain had faded beyond detection after about 70 minutes,no further tows were made. This study substantiated conclusions drawn from laboratory experiments and

Table 3

Results of Six Hour Study at Station 5, July 28, 1976

Time	Individuals/Tow	Volume (m^3)	Density	Current Velocity (cm/sec)
1018	76800	27.7	2773	10
1100	84000	30.1	2822	20
1203	201000	31.4	6420	35
1320	304000	40.5	7506	55
1403	233600	45.1	5179	30
1452	272000	48.6	5597	25
1544	122000	31.2	3936	15
1605	149600	35.1	4262	10
1655	84800	36.0	2356	5

the other tidal studies. Mysids are able to maintain positions against strong tidal currents in the embayment. A more detailed understanding of the effects of tidal currents on the distribution of *N. americana* was difficult to obtain because of the numerous sources of error originating from the sampling procedure. The effectiveness of the epibenthic sled was probably strongly influenced by the tidal currents. These variations, coupled with the changes in the responses of the aggregations to different current velocities, compounded the difficulties in the interpretation of data.

D. Nocturnal Distribution of N. americana

Quantitative information on the nocturnal distribution of the mysids was obtained on August 23, 1976 when all seven stations were sampled on a morning and an evening cruise. Table 4 demonstrates the differences in the abundance of the three species on the bottom on the day and night cruises.

Neomysis americana was more abundant in the day collections than those taken at night at six of the seven stations. A comparison of the population structures (average sizes and percent composition) indicated little change had occurred between cruises except at station 1. The number of mysids collected at station 1 was slightly greater at night. Reductions of one to two orders of magnitude were characteristic of the samples collected at night. Subsurface night net collections at stations 1, 3, 5, and 7 contained mysids only during the evening cruise. These determinations of the nocturnal distribution of *N. americana* were consistent with other

Table 4

Numbers of Mysids on Day and Night Cruises, August 23, 1976

Station	1	2	3	4	5	6	7
N. americana							
Day	4210	42800	4326	48880	499392	276224	41024
Night	5744	5078	1818	584	15244	33684	931
M. bigelowi							
Day	6	16	44	188	2208	4288	248
Night	8	2	10	136	316	1344	162
H. formosa							
Day	16	16	4	0	0	0	0
Night	478	6	56	12	24	0	1

field studies and behavioral observations in the laboratory in which oriented mysid aggregations were more vertically dispersed during the dark period.

E. Abundance and Spatial Distribution of *N. americana*

Neomysis americana was by far the most abundant species collected in the Hereford Inlet study area, accounting for 97% of the mysids collected in the investigation. It was taken in each of the 424 quantitative samples and in several hundred supplemental epibenthic sled collections made at a number of localities other than the seven regular stations from May 1974 to November 1977. A total of 12.3 x 10^6 individuals were captured in the biweekly sampling program, and the mean number per sample was 29,113. The range in the number of animals per five minute tow was 1 to 1,337,600. The number of individuals collected per sample appears in Appendix 2. Figure 13 illustrates the numbers collected at the five inshore stations on each cruise and Fig. 14 shows the log plot of the same data.

Densities of mysids collected were determined by dividing the numbers per sample by the volume of water filtered. A highly significant correlation (r= 0.8136) was found between the total number and the calculated density (#/m^3) values for the samples, but the relationship was inconsistent between stations. The correlation coefficients ranged from 0.5419 to 0.9849, with the lowest values occurring for the samples collected at stations 1 and 2. The green alga, *Ulva lactuca*, was most abundant at these upper embayment stations and frequently impaired the movement of the flowmeter propellor during

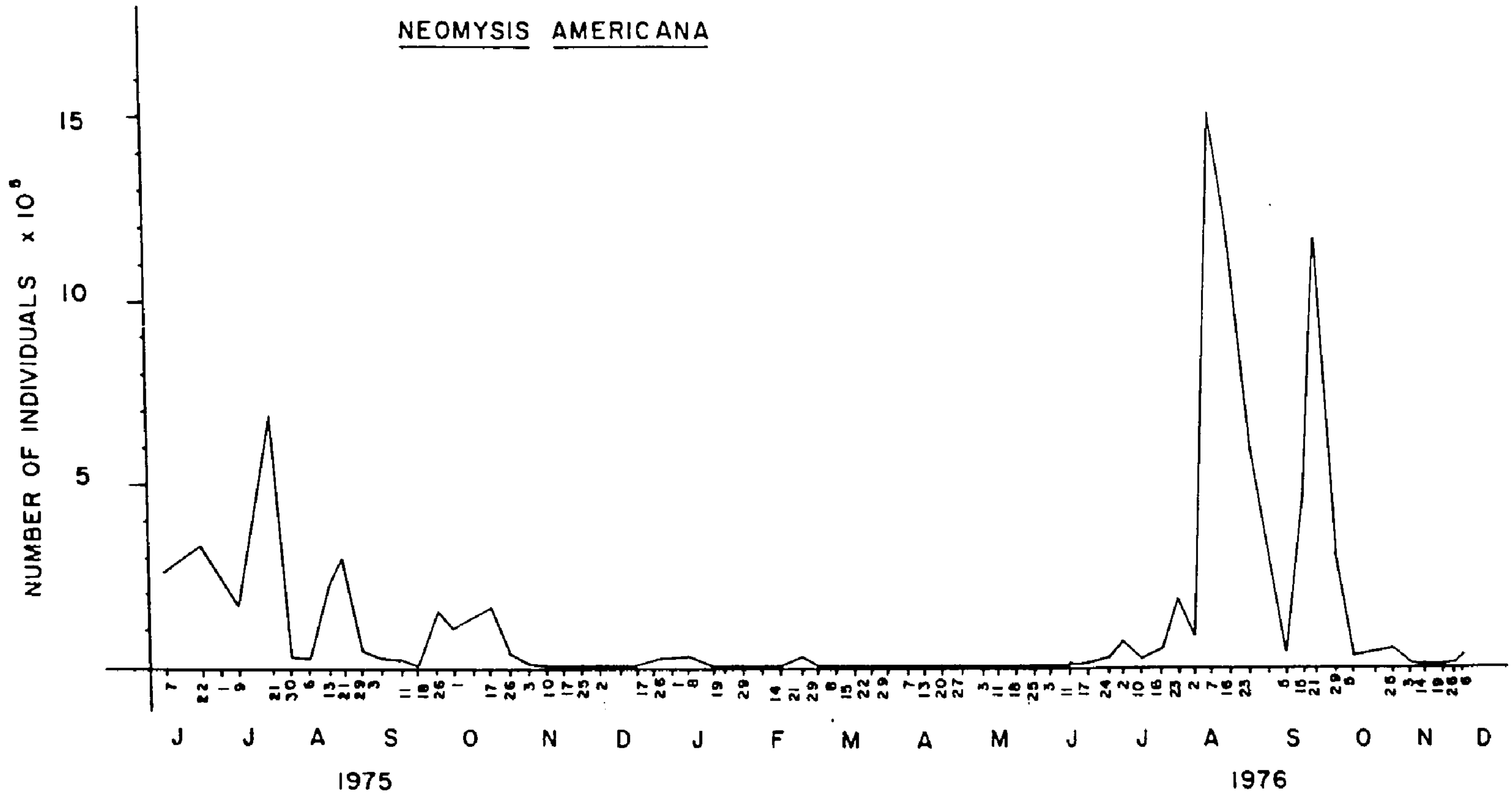

Fig. 13. Total number of individuals of N. americana collected at stations 1-5 on cruises from June 7, 1975 to December 6, 1976. Numbers on the vertical scale are times 100,000.

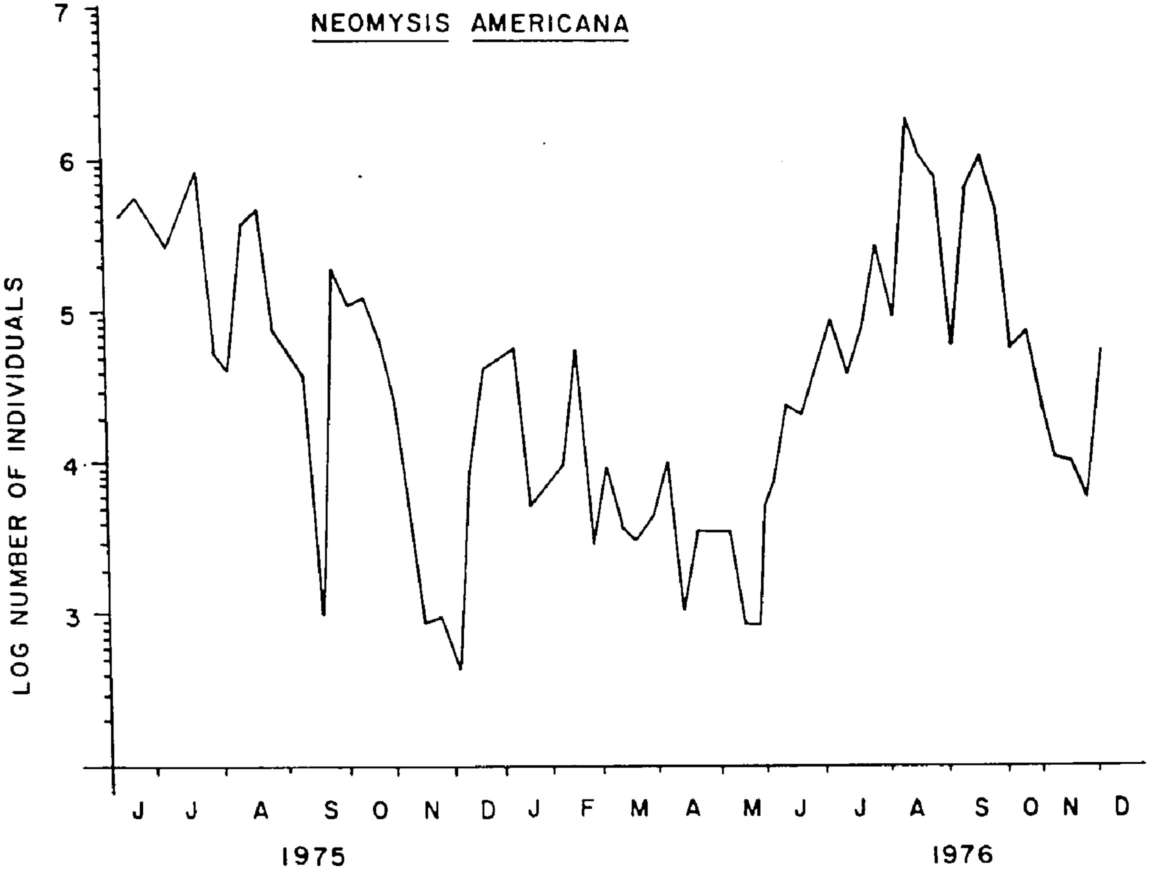

Fig. 14. Log of total number of individuals of N. americana collected at stations 1-5 on cruises from June 7, 1975 to December 6, 1976. Numbers on the vertical scale represent powers of ten.

the sample collections. Since the density values were not always reliable, numbers per tow were used in the analyses of the abundance and distribution of the mysids.

Migrations of aggregations of mysids from the coastal areas were responsible for the periodic repopulation of the inshore waters. Temporal changes in the spatial distribution will be described in the next section.

The physical characteristics of the sampling sites were significant factors in determining the abundance and distribution of _N. americana_ in the study area. Temperature regimes and current patterns were not only primary factors influencing the migrations of the populations into the embayment, but were significant in determining the number of mysids which occurred at a given station, and the amount of time they remained there. Table 5 summarizes the results of the statistical analysis of the abundance of _N. americana_ by station.

Stations 1 and 2 had similar hydrographic properties and supported comparable densities of mysids during all seasons. Because of the irregular bottoms characteristic of the upper embayment, the currents were slower and more varied than those nearer the inlet. These conditions were more amenable to the persistence of aggregations since a variety of microhabitats was available. Higher concentrations of filterable organic particles may have been partially responsible for mean mysid densities which were considerably higher and more stable than those at stations 3 and 4. The abundance at station 1 was more variable than that at station 2 because of its proximity to the

Table 5

Statistical Analysis of Abundance of *N. americana* by Station

Station	1	2	3	4	5	6	7	All
Mean Number	23183	22403	9738	17846	68313	55149	15570	29113
Minimum	24	47	1	16	15	181	1	1
Maximum	418080	374752	125520	281536	1337600	440320	75640	1337600
Standard Deviation	60587	54366	23466	48255	218180	94989	16508	101415
Coefficient of Variation	261	243	241	270	319	172	106	348
Standard Error of the Mean	7241	6592	2802	5767	26458	15616	2382	4925
Number of Samples Collected	70	68	70	70	68	37	48	424

shallow expanses of Great Sound. Short term temperature fluctuations were the greatest in the upper embayment and were closely correlated with changes in mysid abundance between cruises.

At station 3,a turbulent eddy formed at the convergence of a major marsh creek and the main channel. Velocities high enough to keep sand in suspension near the bottom were encountered on most cruises and mysids were not usually abundant here. Station 3 had the lowest overall mean abundance, high numbers occurring only during periods when major movements of animals between the upper and lower embayment were occurring.

Station 4 had a flat sandy bottom which was almost constantly scoured by moderate to strong tidal currents. The abundance of _N. americana_ was usually low, although greater than at station 3. The densities at this station were highest during the warmer months, especially when migrations from the coastal waters were occurring. During these periods, the abundance usually fluctuated in proportion to that at station 5.

Station 5 had the highest mean number of individuals of all of the stations. This area was subject to the strongest tidal currents in the embayment and served as a major avenue of exchange between the inshore and offshore waters. While large collections of mysids were frequently taken at this site,there was little consistency in the abundance and composition from cruise to cruise. Strong tidal currents were not amenable to supporting aggregations for extended periods,and it is likely that the migrating masses passed through the area quickly.

The hydrographic structure of station 6 was more variable than either station 4 or 5. The epibenthic sled was pulled from the top of the barrier bar, where the tidal currents were similar to station 5, diagonally across the slope to the flat coastal shelf. At the bottom of the slope,the tidal currents from Delaware Bay flowed perpendicular to the overlying tidal currents from Hereford Inlet. The zone of intersection near the top of the slope was turbulent and usually accumulated amounts of fine detrital materials. The combined effect of the varied velocities and the abundant food supply probably had much to do with the consistently higher mysid densities at this site.

Station 7 was the most uniform area with respect to all environmental factors and supported moderate but stable numbers of _N. americana_. The composition of the mysid population in this area was generally stable, indicating the existence of a resident population. Summer densities occasionally fluctuated greatly as large masses of mysids arrived from other coastal areas.

An analysis of the population structure of N. americana at each of the seven stations demonstrated the differences in the average length, composition, and reproductive condition of the mysids. Table 6 summarizes this information. Stations 1 and 2 had the greatest mean length values for the mature male and female mysids. In both categories, the mean size became smaller toward station 5. The offshore stations 6 and 7 had mean lengths significantly greater than

Table 6

Mean Composition (%) and Length (mm) of _N._ _americana_ by Station

Station	1	2	3	4	5	6	7
% Mat. Male	11.7	11.5	14.2	7.5	6.2	8.8	12.0
Length	8.4	8.4	7.6	7.6	5.7	7.4	7.8
% Imm. Male	8.9	10.0	10.2	10.8	12.0	10.0	13.5
Length	5.7	5.7	5.5	5.3	5.7	6.1	6.1
% Mat. Female	7.2	6.5	9.1	4.2	3.8	7.5	9.6
Length	7.8	7.4	6.1	5.3	5.3	6.9	7.6
% Gravid	27.4	27.7	25.7	13.9	9.6	28.6	34.7
% Imm. Female	11.6	13.3	13.8	12.2	13.2	12.6	14.5
Length	6.3	6.5	5.9	5.3	5.5	6.9	6.5
% Juvenile	60.8	58.9	53.3	65.3	65.1	61.3	50.7
Length	3.6	3.8	3.4	3.6	3.8	3.6	3.6

stations 4 and 5. The average length for immature females was also greatest at stations 1 and 2, but the trend of decreasing size toward the inlet did not hold for immature males. The average size values for juveniles were similar at all stations.

The highest percentages of juveniles comprising the population occurred at stations 4 and 5. The greatest proportions of mature females and males occurred in the upper embayment, while the percentages of immatures were generally higher offshore at station 7.

The highest percentages of gravid females occurred at stations 6 and 7, but, among the inshore stations, the samples collected at stations 1 and 2 contained higher percentages.

F. Temporal Distribution of *N. americana*

Neomysis americana was not homogeneously distributed in the study area, but occurred in aggregations which were defined in time and space. The dimensions of the aggregations could not be determined, but evidence from the magnitude and rapidity of the fluctuations in abundance at the sampling sites indicated that simultaneous movements of large numbers of animals occurred. Major changes in the abundance of *N. americana* in the upper and lower embayment and offshore were frequently observed during the 25 month period. These temporally defined shifts in the spatial distribution of the aggregations were highly variable. Changes in the abundance of mysids over short periods of time (days) often amounted to three orders of magnitude. Variations between adjacent stations were occasionally as large as four orders of magnitude on a single cruise. Sometimes, the abundance at the station remained stable for several weeks or months and, at other times, significant fluctuations in numbers occurred daily.

Seasonal changes in abundance were more regular, and patterns of movements of aggregations between the embayment and coastal waters could be detected. The ultimate source of the inshore populations of *N. americana* was the coastal area outside of Hereford Inlet. Resident populations of mysids occurred in the upper embayment, but the abundance and structure of the populations in the lower embayment were highly variable. Large numbers of mysids usually migrated into the embayment in the early summer and remained until late fall, when rapidly declining water temperatures resulted in great reductions in numbers. After water temperatures stabilized in the early winter, a migration of mysids from offshore repopulated the embayment.

During some periods, the migrations could be followed as dense aggregations moved from the inlet area to the upper embayment over a period of days or weeks. More often the inshore penetrations were rapid and could only be detected after the fact by comparing the abundance of mysids between cruises.

A summary of the statistical analysis of the abundance of *N. americana* by month is presented in Table 7. The mean number of mysids collected per month remained relatively stable from November to May, with the lowest number occurring in March. The mean number collected in June was about eight times greater than the May value and

Table 7

Statistical Analysis of Abundance of *N. americana* by Month (Jan.-June)

Month	Jan.	Feb.	March	April	May	June
Mean Number	3882	3303	1505	4152	3943	29744
Minimum	7	26	1	16	14	15
Maximum	16864	18484	13381	33642	49008	374752
Standard Deviation	4538	4475	2693	7755	10859	67173
Coefficient of Variation	117	135	179	187	277	226
Standard Error of the Mean	968	1055	449	1653	2089	9227

Table 7 cont.

Statistical Analysis of Abundance of _N. americana_ by Month (July-Dec.)

Month	July	Aug.	Sept.	Oct.	Nov.	Dec.
Mean Number	34660	94348	63735	16707	3176	4564
Minimum	570	39	13	60	8	1
Maximum	546696	1337600	440320	69632	63444	30952
Standard Deviation	82015	232874	106427	17617	8920	7296
Coefficient of Variation	237	247	167	105	281	160
Standard Error of the Mean	345	1036	3235	22	129	189

constituted the greatest difference between two consecutive months. The numbers increased in July and August (maximum) and declined in September (second highest). A substantial decrease in the mean number was found in October.

The description of the spatial and temporal distribution of *N. americana* to follow has been developed from abundance and life history information obtained from the sample analyses, and demonstrates the dynamic nature of the populations. The number of *N. americana* per sample is found in Appendix 2, and the corresponding temperatures are found in Appendix 1.

June 1975

Non-quantitative samples collected during May showed that a sudden increase of great magnitude occurred around the third week of May as a migration of 1SG mysids penetrated the embayment. The first quantitative samples were taken on June 7 and indicated that high numbers of animals were present at all inshore stations. Five minute tows at stations 1 and 2 yielded up to four liters of solidly packed mysids. The population was composed primarily of juveniles of two size classes, the larger ones originating from recent WG spawns and the smaller ones from the more recent reproductive activity of the first mature 1SG animals. Mature mysids of the 1SG and some late developing WG animals dominated at station 4 on June 7 and at stations 2 and 3 on June 22. In samples where mature animals were dominant, lower numbers occurred. Juveniles dominated at all other stations, but immatures of the 1SG often accounted for a high proportion of the samples.

July 1975

High numbers persisted at all stations during July. On July 7, matures dominated at stations 1 and 3 and, although most were small recently mature animals, numbers of overwintering individuals were still present. Juveniles dominated all other stations and comprised 98-99% of the population at stations 4 and 5. Temperatures at offshore station 7 were almost 10°C less than inshore and the samples were almost entirely composed of juveniles.

On July 21, the numbers remained high at all inshore stations, but there was a shift in the center of abundance within the embayment toward the inlet. The number of juveniles in the upper embayment decreased toward the end of the month, while their numbers reached a summer high at station 5. The highest densities of mature 1SG animals were found at station 3. While numbers of immatures occurred in association with the matures, the 1SG had approached its peak reproductive period by late July.

Great reductions in the numbers of mysids occurred on July 30 at all stations, but a decrease of three orders of magnitude was observed as the juveniles disappeared at station 5. The densities at station 7 remained essentially unchanged in the four samples taken in July.

August 1975

Moderate numbers of brooding 1SG mysids occurred at stations 1 and 2, but juveniles dominated all inshore samples on August 6.

A distinct difference in the mean lengths of juveniles collected from the various areas was observed. The young at stations 1, 3, and 4 had mean lengths of about 2.1 mm and represented the most recently spawned contingency of the population. The mean length of the collection at station 2 was 3.2 mm and at station 5 was 3.5 mm. The largest juveniles of the cruise (4.0 mm) were found at station 7 where the water temperature remained about 7°C colder than at station 5. Mature 1SG mysids dominated at station 7.

On August 13, reduced numbers of brooding 1SG mysids occurred at station 7. The percentage of juveniles increased and the average size decreased as the 1SG continued to release more brood during the peak reproductive period. Inshore, the population remained relatively stable except for a very large collection of juveniles taken at station 4. The increased numbers observed on this cruise did not represent a migration from offshore.

Samples taken on August 21 indicated that the 1SG had almost completely disappeared, since the samples were composed almost entirely of juveniles. A large collection of brooding 1SG animals was taken at station 2. Essentially 100% of the mature females were gravid, although juveniles also dominated this sample. Immatures did not occurr in any of the inshore samples except for the few associated with the matures at station 2. The abundance of <u>N. americana</u> inshore was comparable to that on August 12; however, the distribution was more homogeneous.

Samples taken at station 7 on August 21 indicated the 1SG had not yet disappeared. High numbers of immatures and matures remained offshore indicating a delay in the development of the generation in the cooler coastal waters. The offshore waters warmed to inshore levels during the last week in August (Fig.5).

The population dynamics of *N. americana* were extremely complicated during the warmer months because of continuous reproduction and individual variation in growth and sexual development. Females which reached maturity in June spawned two or more times before dying off in mid-summer. Meanwhile, other females originating from the overwintering generation continued to produce young. Water temperature differences were probably responsible for the temporal delay in the development of the 1SG offshore relative to the 1SG which had penetrated the embayment in May and had remained all summer.

September 1975

On September 3, remnants of the 1SG were located at station 1, with lower numbers occurring at stations 3 and 4. Increased percentages of immatures occurred at all inshore stations, signifying that the 2SG was approaching maturity. All stations were dominated by juveniles and a distinct spatial separation of juveniles of different mean lengths was observed. The largest juveniles were found at stations 3 and 5 and the smallest (representing the most recent spawn) were collected at station 1 where the last of the 1SG brooders were located. A large concentration of lingering 1SG animals was found at station 7. The relatively large brooding females in these samples were carrying their second or third broods. These females were significantly larger than those at station 1.

On September 18, the first samples collected since the onset of ten days of severe weather demonstrated that abrupt reductions had occurred at all inshore stations. Supplementary sampling efforts failed to demonstrate any areas within the embayment which supported numbers of mysids. Figure 15 illustrates the changes in abundance in late September. By September 26, a migration from offshore had repopulated the embayment. Temperatures had increased inshore and were slightly higher than those outside of the inlet.

October 1975

On October 1, temperatures remained stable and the highest densities since early June occurred at stations 1 and 2 (Fig.15). The migration which started in late September had continued and reached the upper embayment by this time. The aggregation was primarily composed of large 2SG juveniles. The mean lengths and relative percentages of the five life stages were similar at all stations. Very high densities were also detected at station 5, and one of the largest collections of the investigation was taken at station 6.

On October 17, temperatures decreased in the upper embayment and the center of distribution shifted toward the inlet. Juveniles composed almost 100% of the samples at stations 1 to 4, but station 5 was populated by a large aggregation of adults which had been concentrated in the upper embayment two weeks previously.

The abundance and distribution of mysids at the inshore stations remained stable on October 26. High numbers of immatures and small

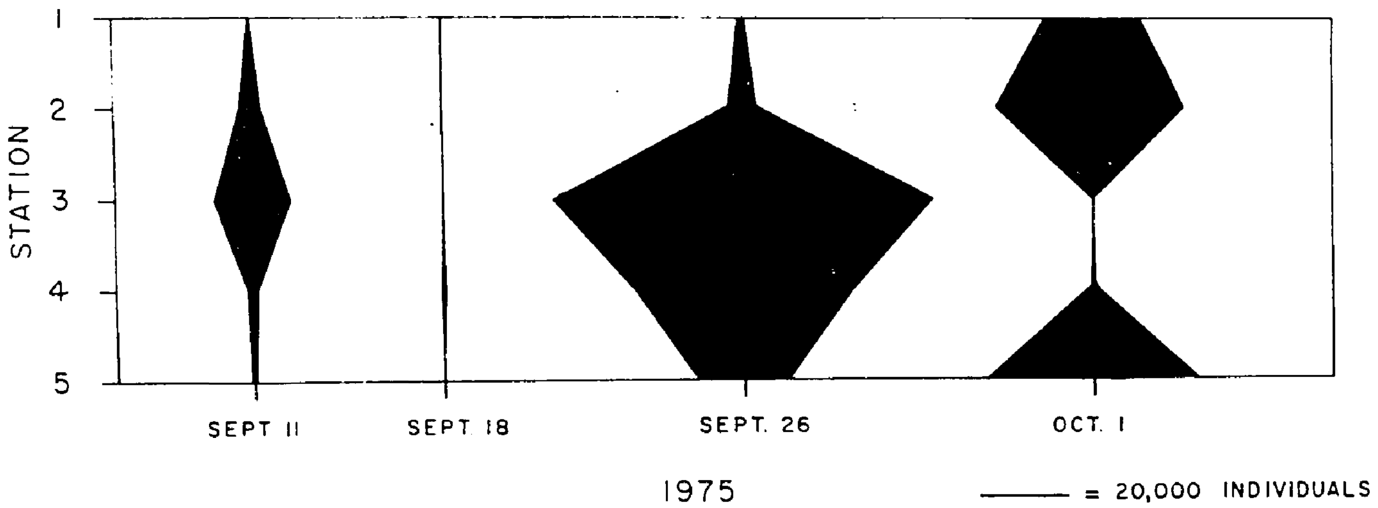

Fig. 15. Spatial and temporal changes in abundance of *N. americana* at stations 1-5 on four cruises in September and October 1975. Details of the migration are found in Section IV F..

matures (representing the 2SG) were located at station 7. The percentage of gravid females in this sample was the highest since the disappearance of the 1SG. The 2SG produced young throughout the month.

November 1975

Reduced but moderate numbers of mysids remained inshore on November 3. Station 5 was still the only inshore station with any number of adult animals. Samples taken at station 7 were very similar to those at station 5.

Densities continued to decrease on November 10 and, on November 17, virtually no mysids were collected at stations 1 to 4. *Neomysis americana* was somewhat more abundant at stations 5 and 6 where juveniles were dominant. High numbers of immature and mature mysids occurred in the vicinity of station 7.

No changes were observed on November 26 and numbers of adult 2SG animals remained at station 6 on November 29. Immatures dominated the samples, and about 75% of the matures were brooding.

December 1975

Extremely low numbers of mysids were collected at the inshore stations on December 2. Extra sampling in the sounds and shallow waterways indicated *N. americana* was not abundant anywhere in the embayment. Large juveniles and immatures dominated the samples, but some brooding 2SG animals representing the last of the fall reproductive activity were present.

On December 17, marked increases were recorded at all inshore stations (Fig.16). The mature mysids which occurred in these samples were conspicuously larger than any collected inshore on December 2. Mature males outnumbered mature females 2:1, and the large females displayed senescent characteristics. Most of these broodless individuals had lost their oostegites. The immatures and large juveniles which dominated the samples comprised the overwintering generation. The lengths and relative percentages of the five life stages collected at the inshore stations were similar to those determined for the offshore population on December 2.

Samples collected on December 26 indicated that the migrating population continued to move toward the upper embayment (Fig.16). High numbers of immatures and large juveniles were collected offshore on December 29.

January 1976

No major changes in abundance, composition, or distribution occurred on January 1 or 8, but reduced numbers on January 16 indicated that most of the largest animals had died. Of the matures remaining, males outnumbered females 6:1.

Densities were low and stable on January 29 as immatures completely dominated the population. Some gravid females were found. Mysids were more abundant at offshore stations 6 and 7 than any of the inshore stations, but the population structure was similar in both areas.

February 1976

Moderate numbers persisted at stations 1 and 2 on February 14,

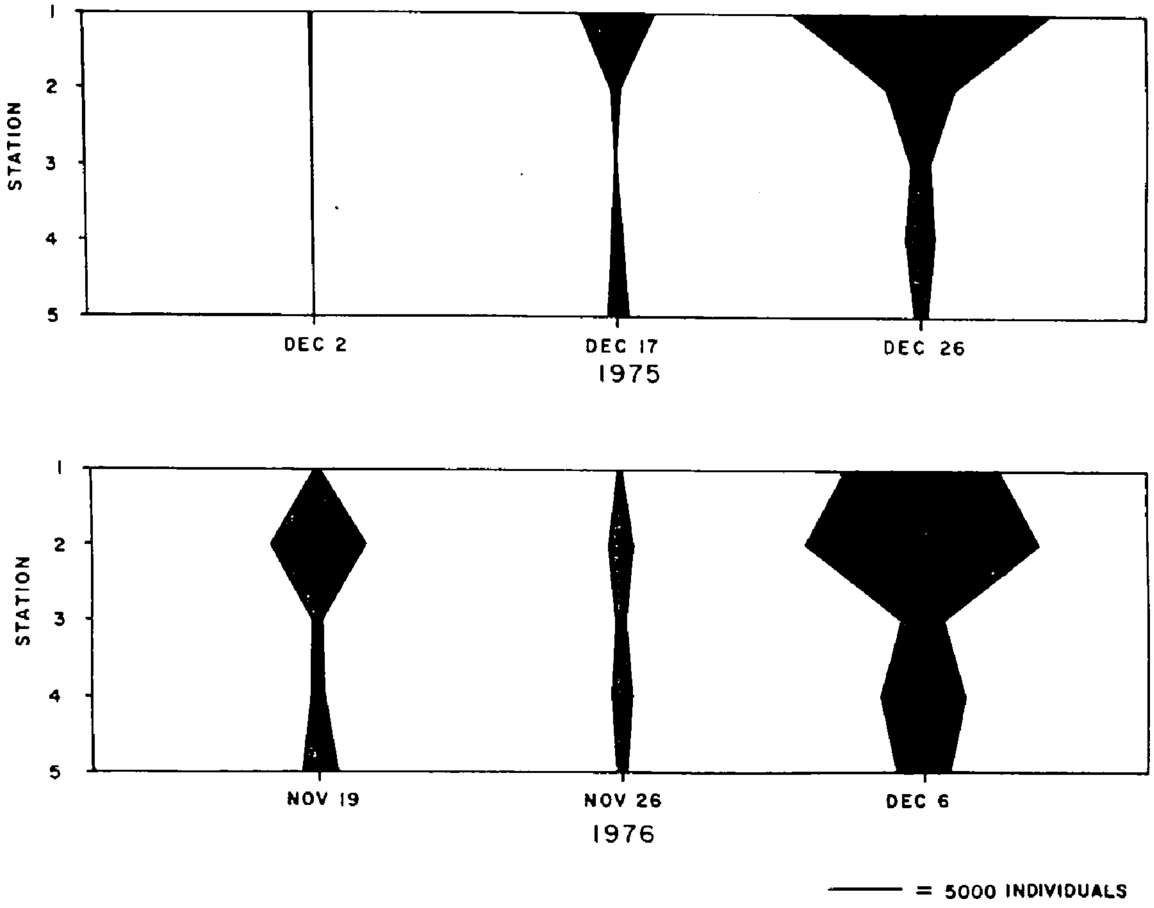

Fig. 16. Spatial and temporal changes in abundance of N. americana at stations 1-5 on cruises in December 1975 (above) and November-December 1976 (below). Details of the migrations are found in section IV F. .

while low numbers occurred at stations 3 to 5. Changes in the population structure were consistent with the developmental pattern of the WG.

On February 21, increases were observed at all of the inshore stations as water temperatures increased for the first time since the fall. This small migration from the coastal area was short-lived, since samples collected on February 29 revealed a population similar to that found earlier in the month.

March 1976

On March 8, slight increases were observed inshore, while high numbers were recorded at station 7. No major differences in the population structure were discernible between the inshore and offshore samples. About one third of the WG was mature and, although few were brooding, many females had oocytes about to be released into the marsupium. The percentages of juveniles were near the annual minimum and reflected the low reproductive rate during the winter months.

Slight density reductions were recorded on the March 15 and March 22 cruises. On March 15, about 30% of the mature females were gravid, signifying the beginning of the overwintering generation's peak reproductive activity. The densities remained low and stable at all inshore stations on March 29. Recently released juveniles were conspicuous in the samples. The largest mature, immature, and juvenile mysids were found at station 1 and the smallest at station 5. Densities were higher at station 6, where about 24% of the population was composed of juveniles. The greatest numbers were collected at station 7, where matures dominated the samples for the first time since the fall. The sizes of the matures and immatures were significantly smaller than those occurring in the upper embayment.

April 1976

The abundance of N. americana had not changed according to samples collected April 7. Densities were decreased on April 13, with low numbers of WG animals occurring at all inshore stations. The mean lengths of the mature and immature mysids were the greatest of the year. Very few juveniles were collected, but more than 80% of the mature females were brooding. Samples collected at station 6 on April 15 had a similar composition, although the numbers were greater. Large numbers of juveniles were collected at station 7 indicating a difference in the timing of the major brood release between the WG populations of the inshore and coastal areas. No significant releases had yet been detected in the embayment. The average lengths of the mature and immature mysids collected inshore were greater than those found offshore.

Temperatures decreased 8^{o}C in a seven day period at station 1, and, while the numbers inshore remained constant on April 20, there was a shift in the center of abundance toward the inlet. Mysids were abundant at stations 6 and 7.

Non-quantitative samples taken on April 27 indicated increases in the numbers of juveniles in the embayment had occurred. Almost no matures and only a few immatures occurred at stations 1, 3, and 4.

Tows at station 3 yielded the greatest numbers of individuals taken in the embayment since October.

On April 30, moderate numbers of juveniles occurred at station 6, whereas higher numbers of matures dominated the station 7 samples. The mean length of the juveniles increased indicating the development of the first born 1SG.

May 1976

On May 5, low densities characterized all of the inshore stations. Samples taken on May 11 produced similar results. The abundant juveniles found after the WG spawning peak were no longer present. Moderately high numbers of juveniles were collected at station 6. Great numbers of juveniles were taken at station 7, in addition to the first large collection of the first WG spawn to develop primary sex characteristics. Some large immatures and matures originating from mid winter reproductive activity were present.

No changes in the inshore abundance were observed on the May 18 cruise.

On May 25, increased numbers of mysids were collected at stations 1 and 2, but virtually none were found at stations 3 to 5. The upper embayment population was primarily composed of late overwintering animals, although some of the oldest 1SG (now immatures) mysids were present. The temperatures at stations 1 and 7 were similar, and there was no indication that any exchange between the populations of mysids in the coastal waters and the embayment had occurred.

June 1976

In early June,offshore densities were higher than those inshore. Small immatures dominated at station 6 and juveniles dominated at station 7. Moderate numbers of brooding individuals from the late overwintering stock were present.

The abundance at stations 1 to 5 had not changed significantly from May 25, but some increases were observed on June 11. Juveniles dominated at all stations, the largest occurring at station 1 where the greatest number of mature mysids in the embayment were collected. The brooding females were primarily lingering WG animals, but the first of the 1SG (now 10-12 weeks old) were also represented. At station 7 the numbers were comparable to station 1, but the population structure differed. Unlike the inshore brooders,the mature females at station 7 were small, recently mature 1SG animals. Almost no WG females occurred offshore.

On June 17, the center of abundance was located near station 3, but the overall inshore abundance had not changed significantly. Samples taken on June 17 at stations 6 and 7 revealed similar numbers and compositions. Samples collected one day later at the same stations indicated a large body of mysids had moved to the area just outside of Hereford Inlet. The abundance had increased by almost three orders of magnitude at both offshore stations. Samples at station 6 were nearly completely dominated by small juveniles and, while juveniles dominated at station 7, almost half of the population was composed of matures and immatures of the 1SG.

On June 24, the inshore densities remained stable and the distribution was centered around station 2. Station 1 was dominated by low numbers of juveniles. Although the young dominated at station 2, matures (80% brooding) and immatures of the 1SG composed the most conspicuous fraction. A segregation of juveniles of different mean lengths was apparent, with the smallest (2.7 mm) occurring at station 1 and the largest (3.6 mm) occurring at station 3. Offshore abundances had decreased markedly since June 18, and the composition had also changed. The population structure at station 6 was similar to the inshore area, but at station 7 moderate numbers of adult 1SG mysids dominated. These changes in abundance and composition occurred over short periods of time and demonstrated the dynamic nature of the offshore population in terms of their spatial distribution.

On June 28, the samples collected at stations 6 and 7 were similar in abundance and composition for the first time since the early spring. A highly active reproducing 1SG was in evidence, and the first of the young 2SG were now a conspicuous part of the population.

July 1976

The numbers of mysids collected at stations 1 to 6 on July 2 were the greatest since the fall of 1975. Water temperatures had dropped at all inshore stations as cool bottom water from outside of the inlet penetrated the embayment at least as far as station 3. Mysids which had been found at stations 4 and 5 the previous week moved toward station 1 as a result of the influx of cool water. Mysids similar to those outside of the inlet in late June were found in the cool water at stations 3, 4, and 5.

On July 6, high numbers of juveniles remained at station 6, while samples at station 7 yielded high numbers of mature and immature 1SG mysids.

On July 10, the temperatures inshore were more homogeneous, but station 1 ($19^{o}C$) was still the lowest it had been since early June. Densities at all stations were reduced and depletions of adult 1SG animals were apparent. Low numbers of matures and immatures were present at station 1, but high numbers were present at stations 5 and 6. Only moderate numbers of juveniles occurred at station 7, where temperatures remained at about $16^{o}C$.

By July 23, the inshore temperatures had reached the levels that prevailed before the influx of coastal water. Juveniles were abundant upestuary. While mature and immature 1SG mysids were collected in moderate numbers at station 3, high numbers of reproductively active 1SG animals remained at stations 5 and 6.

Abnormal fluctuations in water temperature during July obscured the pattern of distribution so that the trends were not as distinct as in previous months and during the summer of 1975. By late July, the inshore population had originated from movements of mysids from coastal waters. This was a somewhat different means of repopulation of the embayment from the previous summer.

August 1976

On August 2, offshore temperatures had warmed to inshore levels

(Fig.5) and the densities and compositions at all stations were relatively stable.

Although juveniles dominated all inshore samples on August 7, the continued presence of high numbers of adult 1SG animals at stations 1 and 2 indicated that the stability of this population had persisted since mid-July. Virtually no mysids were taken at station 3, but very high numbers occurred at stations 4 and 5. The maximum number of mysids collected in a single tow was taken at station 5. This sample was composed of approximately equal numbers of juvenile 2SG and adult 1SG mysids. The mean length of the adults was significantly smaller than that of the adults in the upper embayment, but was similar to that of the offshore animals. A lag in the growth and reproduction of the 1SG in the cooler offshore waters was also seen during the same period in 1975.

The migration penetrated as far as station 3 on August 16, while high densities remained at stations 4 to 7.

While the 1SG population in the upper embayment had already passed its reproductive peak, the very abundant 1SG population which had recently repopulated the embayment was producing young at a rapid rate. The oldest 2SG mysids (8-10 weeks) were now approaching maturity. The 1SG was showing signs of depletion.

Evidence that the major die off of the 1SG had occurred could be seen from samples collected on August 31 at stations 5 to 7, where moderate numbers of juveniles and practically no adults were present.

September 1976

Inshore water temperatures decreased in early September and samples taken on September 5 yielded low numbers of juveniles. Highest numbers were collected at station 5. An aggregation of large late 1SG brooders occurred at station 7 along with the first of the 2SG to reach maturity.

Samples taken on September 15 showed the greatest numbers of mysids at inshore stations since June of 1975. This was an indication of a large migration (Fig.17). Further evidence of the migration could be seen in samples from station 1,where the composition of the population (immature and mature 2SG) was similar to that found at station 6 on September 11.

The migration continued and,on September 21,the maximum numbers recorded at stations 1 and 4 were collected. Liters of mysids were captured in every tow. Densities at station 6 were comparable, but few mysids occurred at station 7. Essentially no changes occurred at station 1 to 7 on September 29.

October 1976

Decreases occurred at all stations on October 5, with the greatest numbers being collected at station 5. At station 1,adults of the 2SG dominated, while juveniles made up more than half of the population at stations 2 to 5. High numbers of juveniles occurred at station 6 on October 19.

Increased numbers were collected on October 25 at stations 1 and 2. The presence of more juveniles and fewer adults indicated the end of

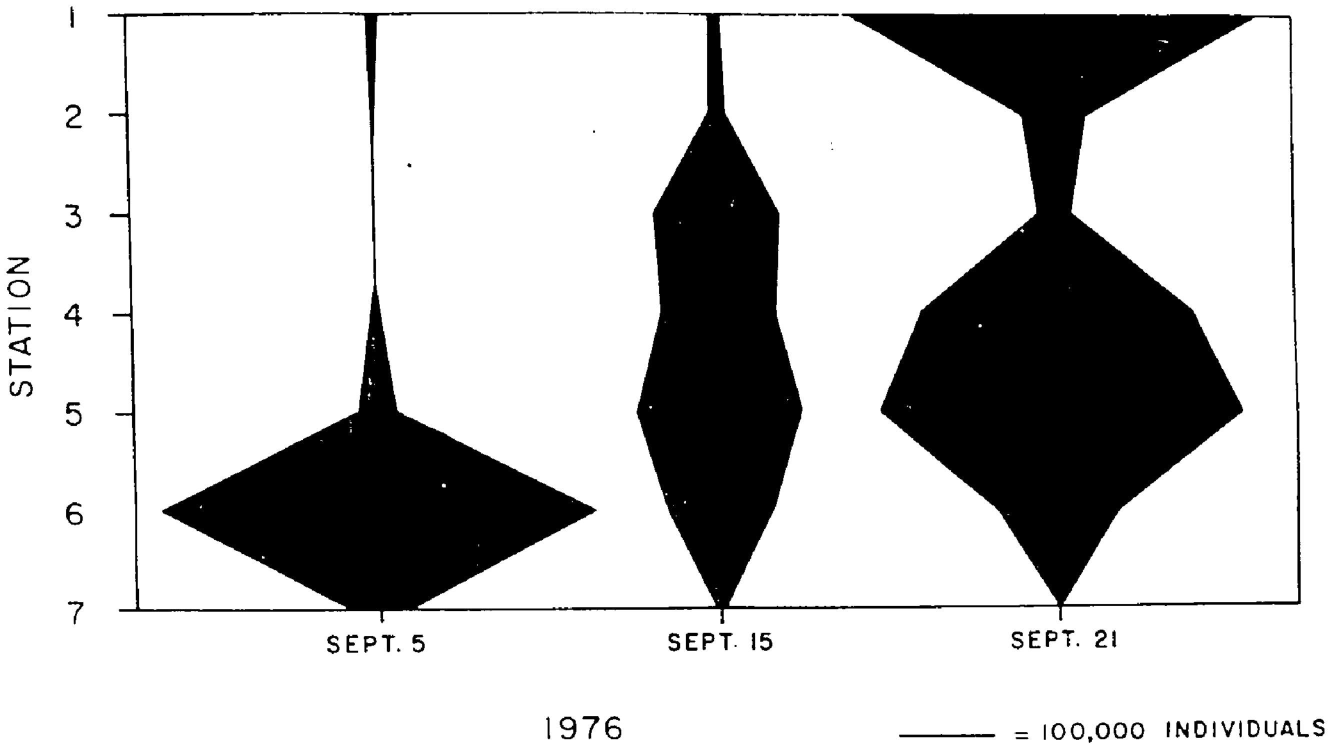

Fig. 17. Spatial and temporal changes in abundance of N. americana at stations 1-7 on cruises in September 1976. Details of the migrations are found in section IV F. .

the fall reproductive activity. No changes were observed at stations 3 to 5.

November 1976

Reduced but moderate numbers were collected inshore on November 3, with matures and immatures being most abundant at stations 2 and 3, and juveniles dominating elsewhere.

On November 14, temperatures had dropped considerably; few mysids were collected at station 1, and the densities at the other stations reached the lowest levels since May. Numbers and compositions were similar at station 6, and only seven individuals were collected at station 7.

Low and stable numbers of juveniles occurred at the inshore stations on November 19 and 26, but large numbers of juveniles were taken at station 6 on November 19.

December 1976

Significant increases were recorded at all stations on December 6 (Fig.16), as a migration from the coastal areas occurred. A sudden change in the inshore population occurred which was similar to the pattern detected in December of 1975. Numbers of immatures and large juveniles which would overwinter penetrated to the upper embayment. The most conspicuous individuals in the samples were large senescent 2SG mysids which had reproduced in the fall.

Supplementary samples collected on December 14 and 29 indicated there were no significant changes in abundance, composition, or distribution of the population. On January 6, 1977, the population was essentially unchanged except for the disappearance of the senescent 2SG.

Spring 1977

On March 4, the first samples were collected following a period when the waterways had been frozen for almost seven weeks. Samples collected showed that the abundances had changed little during this period. Mature WG mysids were dominant in the embayment, but few gravid females or recent young were collected.

On March 21, mature WG (50% brooding), recent juveniles, and numbers of immatures were collected.

Tows made on April 12, 20, and 27 demonstrated that the reproductive peak of the WG occurred during mid April.

May 1977

On May 3, juveniles comprised about 90% of the inshore population, with the greatest numbers occurring at stations 1 and 2. The largest collection was taken at station 6. The composition of the population was similar at all stations.

A large collection of juveniles taken in the southwest corner of Great Sound on May 4 indicated that the progeny of the WG had moved into the warmer shallows.

June 1977

Large numbers of mysids were collected in the upper embayment on June 2. These were mostly juveniles which had moved into the channel during an extended period of cold weather. The temperatures of the shallow sounds had decreased considerably.

Tows taken on June 8 indicated that a penetration of small mature and immature 1SG mysids had occurred at station 5. On June 14, great numbers of these animals were collected at all inshore stations. The maximum number ever collected in a tow in the upper embayment was taken at station 2 on this date. About half of the sample was composed of small adult 1SG mysids, and practically all of the mature females were brooding. Collections from stations 4 to 7 also had large numbers of adults, but were dominated by juveniles.

Samples collected throughout the summer indicated that large numbers of *N. americana* remained in the embayment until the fall.

G. Interactions of N. americana With Other Organisms

Neomysis americana was usually the most abundant macroinvertebrate in the samples collected with the epibenthic sled. In general, the greatest diversity of species occurred at stations 1 and 2, where the largest volumes of detritus were collected. Samples from stations 3 to 7 occasionally contained numbers of other small crustaceans, but more often were low in detrital and animal volumes.

Laboratory observations did not indicate any trophic interactions between mysids and the variety of amphipods, cumaceans, and decapod larvae which were often present in the epibenthic sled collections. Mysids in captivity were preyed upon by the sand shrimp *Crangon septemspinosa*, ctenophores, and fishes.

Crangon septemspinosa was found to be a voracious predator, capable of decimating entire collections of *N. americana* within a short period under laboratory conditions. Large shrimp were very abundant during the colder months and were frequently collected in great numbers with the sled. Gut analyses of specimens collected in the samples usually revealed that they had consumed *N. americana*. The presence of high densities of *C. septemspinosa* at the sampling sites probably influenced the abundance and distribution of *N. americana*. In the laboratory, aggregations of mysids remained further from the bottom in the presence of the shrimp which spent most of its time buried in the substrate. Predation rates in the experimental systems were found to be greatest in the dark at low current velocities.

The ctenophore, *Mnemiopsis leidyii*, was very abundant during the summer of 1975, but was almost absent from the study area during the 1976 and 1977 seasons. The occurrence of high densities of this suspected predator may have influenced the abundance and distribution of the mysids, although no direct evidence was obtained.

Neomysis americana was consumed by most of the species of fishes collected in the baseline finfish survey of the Hereford Inlet Estuary (Allen, et.al., 1977). The salt marsh embayment has been designated an important spawning and nursery area for most of the commercially and recreationally exploited fishes. Mysids were found to be the most important food source for many of these species. Table 8 lists some of the more abundant species of fishes collected in the embayment and the importance of mysids in their diets.

An unidentified ciliate was frequently observed on the exoskeleton of all three mysid species and was especially abundant during the

Table 8

Consumption of Mysids by Juvenile Fishes in the Hereford Inlet Estuary

Species	Common Name	Number of Guts Examined	Percent Incidence of Mysids	Rank in Diet
Urophycis regius	Spotted Hake	101	28	2
Gasterosteus aculeatus	Three Spine Stickleback	18	56	2
Centropristis striata	Black Sea Bass	201	26	1
Bairdiella chrysura	Silver Perch	21	38	1
Cynoscion regalis	Weakfish	86	59	1
Menticirrhus saxatilis	Northern Kingfish	32	3	5
Leiostomus xanthurus	Spot	722	8	6
Prionotus carolinus	Northern Sea Robin	107	36	3
Prionotus evolans	Striped Sea Robin	10	60	2
Ammodytes americanus	Sand Launce	37	3	4
Etropus microstomus	Smallmouth Flounder	161	75	1
Paralichthys dentatus	Fluke	57	40	2
Scophthalmus aquosus	Windowpane	60	65	1

cold months. During the winter, the majority of mysids examined were infected. The colonies were often large enough to be observed on mysids in the maintenance systems and were often dense enough to slow the swimming speeds of the animals.

A little known leech, *Mysidobdella oculata* occurred during each of the four years that the WG of *N. americana* was observed. This highly specialized parasite was species specific for *N. americana* and had not been previously reported from the western North Atlantic Ocean. The leech appeared each November or December with a migration of 2SG animals from the coastal areas, persisted through the winter, and disappeared as temperatures warmed. Warm temperatures were apparently responsible for the absence of the leeches from June to November.

Mysidobdella oculata remained attached to the mysid host with its posterior sucker. Mysids with one to ten parasites attached were maintained in the laboratory for up to three months, indicating the relationship was not acutely lethal for the mysid.

H. Life History of *Mysidopsis bigelowi*

Mysidopsis bigelowi produced three generations per year, and the population dynamics were similar to those of *N. americana*. The timing of the reproductive peaks and the duration of the generations were in close accord.

Figure 18 illustrates the mean monthly percentages of mature, immature, and juvenile *M. bigelowi* collected from July 1975 to November 1976. Immatures dominated the population during most of the year, but the composition was fairly stable from the spring to the

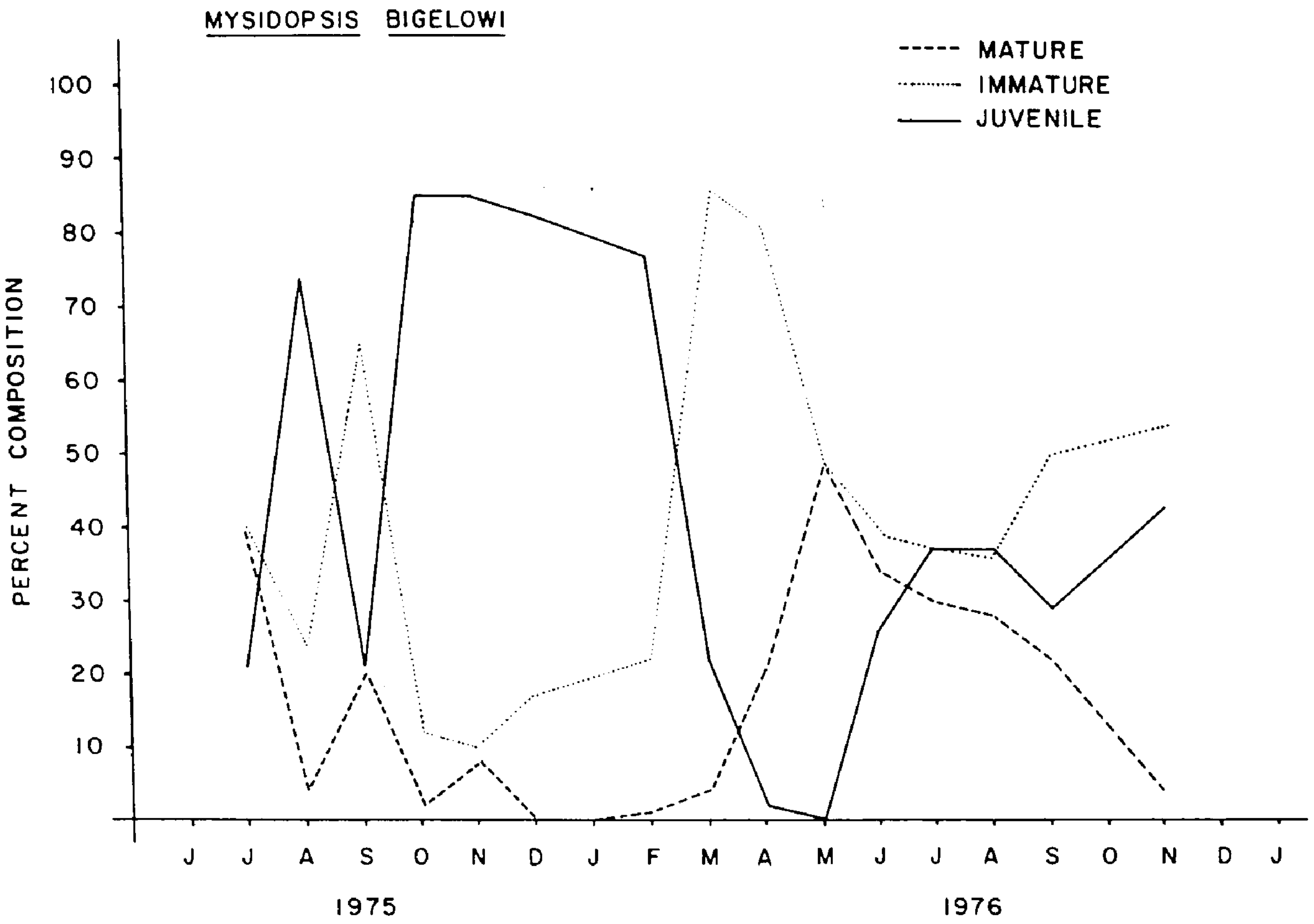

Fig. 18. Mean monthly values of the relative percentages of mature (male and female), immature (male and female), and juvenile *M. bigelowi* composing the sample populations from July 1975 to November 1976.

fall. The percentages of juveniles during most of the warmer months were comparable to those of the immatures and greater than those of the matures.

Table 9 presents the mean lengths of each of the five life stages of _M. bigelowi_. The smallest individuals were about 1.2 mm, and no seasonal variation in the length of the juveniles was observed. The largest individual (7.9 mm) was an overwintering female, which was captured in the early summer.

Gravid females were collected from April to November, and differences in mean length and fecundity of the females of the three generations were observed. The WG animals averaged about 6.4 mm and brooded about 20 young. The 1SG and 2SG had mean lengths of about 5.7 mm and brooded less than 15 young. Reproduction was continuous during the warmer months, with females of the summer generations reproducing more than one time. Mortality rates during incubation appeared to be low, since similar numbers of eggs and late embryos occurred in females of the same length.

An undetermined species of parasitic isopod of the Family Dajidae was frequently observed in the marsupium of mature female _M. bigelowi_. The parasites were most abundant during the summer, and usually occurred in less than 5% of the females.

A large overwintering population of _M. bigelowi_ occurred during the 1975-76 season. The first brooding female was collected on April 27, 1976 at 11°C and, by mid May, almost 100% of the females were brooding eggs or early embryos. The juveniles grew rapidly and, by early June, the first of the 1SG to mature (about 8 weeks old)

Table 9

Mean Length of *M. bigelowi* by Month
Expressed in mm

	♂ Mat.	♂ Imm.	♀ Mat.	♀ Imm.	Juv.
June 1975	-	4.2	-	4.0	2.4
July	6.1	3.8	5.6	4.2	2.5
Aug.	-	3.1	-	3.3	1.8
Sept.	6.1	3.8	-	-	2.0
Oct.	-	-	-	-	2.0
Nov.	5.7	4.3	5.6	-	2.9
Dec.	-	4.8	-	5.1	-
Jan. 1976	-	-	-	-	-
Feb.	-	4.6	-	-	3.4
March	-	4.6	-	4.6	3.2
April	5.8	4.6	5.7	4.6	3.2
May	6.4	4.8	6.4	5.2	2.0
June	6.4	4.0	6.4	4.2	2.2
July	6.2	3.8	6.5	4.2	2.0
Aug.	6.3	3.7	6.2	4.0	2.2
Sept.	6.4	4.0	6.2	4.2	2.0
Oct.	-	-	-	-	2.0
Nov.	-	4.3	-	4.0	2.9

were brooding young. Some very large mature individuals were collected in late June with eggs and brood in early stages of development, indicating that some of the WG reproduced more than one time. The WG was gone by early July, but reproduction within the population was continuous as the 1SG reached its peak activity. Some of the oldest 1SG females were brooding for the second time by late July. By mid August, the first of the 2SG, originating from the 1SG spawn in late June, had matured. An overlap of the summer generations obscured the details of the development of the 2SG, but, during September, the mature and immature constituents of the population belonged to the 2SG. The juveniles resulted from the spawning activity of the last of the 1SG and the earliest of the 2SG. Most of the mature females collected from May to October were gravid. The reproductive activity decreased sharply in late October, and low percentages of matures occurred in November. The last gravid female was collected on November 19 ($8^{o}C$). The December population was composed of 2SG immatures, which had not reached maturity before temperatures declined, and juveniles which resulted from the fall reproductive activity. These animals comprised the overwintering generation. Although there were moderately large numbers of overwintering animals, few _M. bigelowi_ were collected in the spring, summer, and fall of 1977.

I. Abundance and Spatial Distribution of M. bigelowi

Mysidopsis bigelowi was the second most abundant species collected in the Hereford Inlet study area, being taken in 338 of the 424 samples. A total of 380,328 specimens were collected. This accounted for 2.9% of the total number of mysids taken in the investigation. The mean total number of individuals in the 424 samples was 897, and the range was 0 to 162,000.

A high correlation (r= 0.9888) was found between the number of individuals and the calculated density, but, since the density values were unreliable for *N. americana*, the abundance and distribution of *M. bigelowi* were also discussed in terms of numbers of individuals per sample.

Mysidopsis bigelowi was most abundant in the sandy areas of the embayment and adjacent coastal areas. Table 10 summarizes the results of the statistical analysis of the abundance of *M. bigelowi* at the seven stations.

Mysidopsis bigelowi was not collected in intertidal pools or shallow areas less than one meter in depth. The direction of the tide did not seem to affect the abundance or distribution of the species in a regular manner between cruises. The mysids were equally abundant in the upper embayment on the ebb and flood tides and did not move in and out of the embayment with every tidal change.

Table 4 shows *M. bigelowi* was less abundant on the bottom during the evening cruise on August 23, 1976 than during the morning cruise. No specimens were taken in the subsurface samples on either cruise, but the species was collected near the surface in other night tows during the summer of 1976.

Table 10

Statistical Analysis of Abundance of *M. bigelowi* by Station

Station	1	2	3	4	5	6	7	All
Mean Number	27	39	95	498	1455	5887	373	897
Minimum	0	0	0	0	0	0	0	0
Maximum	501	900	2744	12960	57024	161936	4386	161936
Standard Deviation	83	137	355	1760	7055	26498	810	8440
Coefficient of Variation	310	348	373	353	485	450	217	941
Standard Error of the Mean	10	16	43	215	862	4356	117	411
Number of Samples Collected	68	67	67	67	67	36	48	42
Number of Times Occurred	41	44	43	57	61	36	48	338

J. Temporal Distribution of M. bigalowi

Mysidopsis bigelowi was collected every month, but was most abundant from July to September. Table 11 summarizes the monthly abundance of the species. The mean numbers of individuals collected per sample from January to June was consistently low, with the exception of February. The February mean was unusually high because of a single collection in which 7830 specimens were taken. The greatest mean occurred in September (4161).

The monthly analysis was strongly influenced by annual variations in abundance. The mean number of individuals per sample from June to October 1975 was 148, while the value for the same period in 1976 was 2580 per sample. The mean was about 17 times greater in 1976 than 1975.

Figure 19 illustrates the number of mysids collected per sampling date, and Figure 20 shows a log plot of the same data. A low density was observed from June 1975 to June 1976, except for the sporadic peaks described in the account below. M. bigelowi was very abundant during the summer of 1976, but numbers were considerably lower in the fall and remained low through the winter. Unlike the previous year, densities were low in the spring and summer of 1977.

The source of the inshore populations of M. bigelowi was the area outside of Hereford Inlet. Increases in the numbers of individuals collected in the upper embayment never occurred without larger increases at station 5. Increases at station 5 were temporally related to increases at station 6 which, in turn, usually preceded

Table 11

Statistical Analysis of Abundance of _M. bigelowi_ by Month (Jan.-June)

Month	Jan.	Feb.	March	April	May	June
Mean Number	2	498	37	49	40	238
Minimum	0	0	0	0	0	0
Maximum	30	7830	247	332	256	2512
Standard Deviation	6	1833	71	78	66	548
Coefficient of Variation	304	341	210	265	164	229
Standard Error of the Mean	1	432	12	18	13	80

Table 11 cont.

Statistical Analysis of Abundance of _M_. _bigelowi_ by Month (July-Dec.)

Month	July	Aug.	Sept.	Oct.	Nov.	Dec.
Mean Number	742	1672	4161	45	260	265
Minimum	0	0	0	0	0	0
Maximum	14776	57024	161936	536	5264	4386
Standard Deviation	2315	7686	22876	118	904	926
Coefficient of Variation	312	460	550	263	348	350
Standard Error of the Mean	345	1036	3235	22	129	189

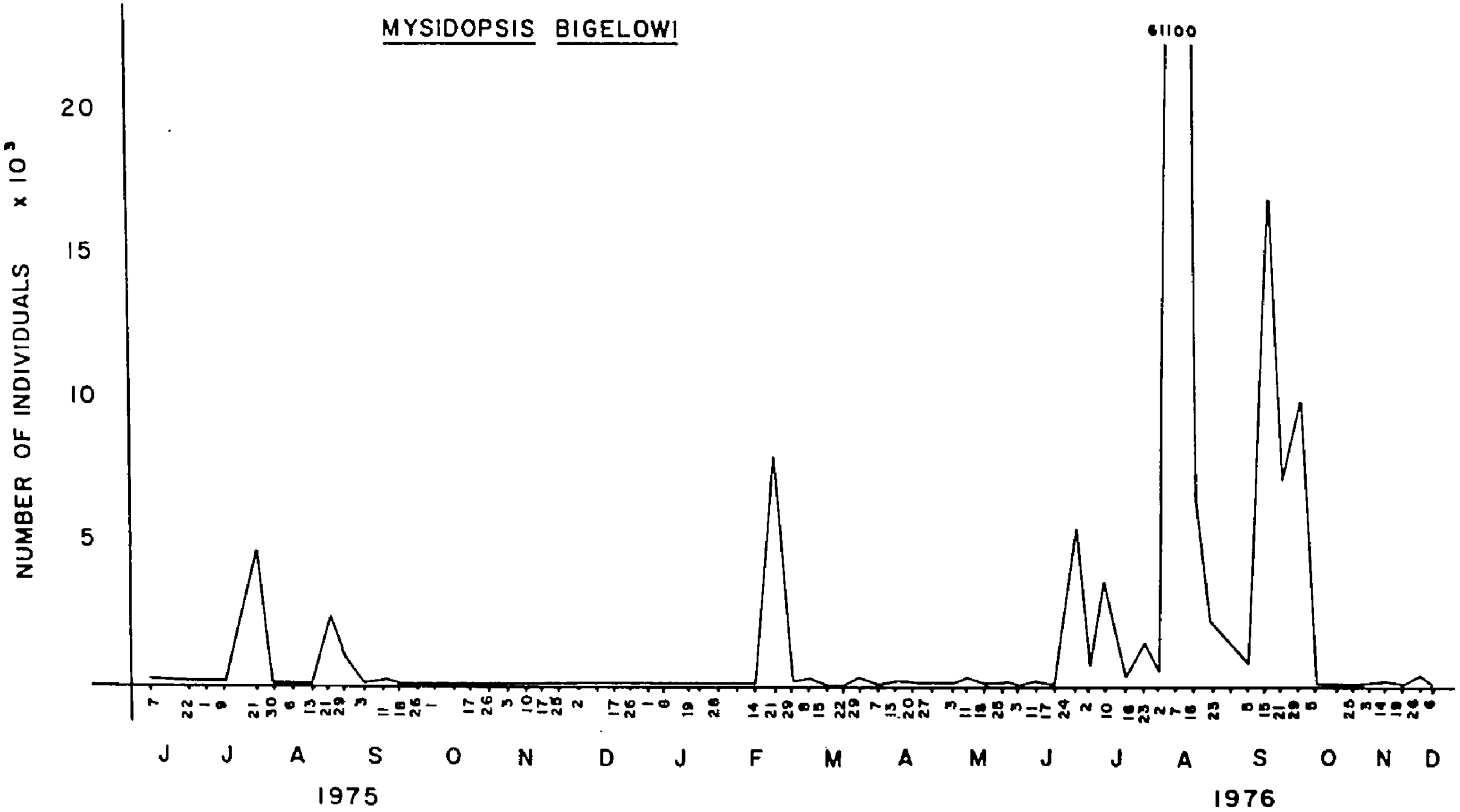

Fig. 19. Total numbers of individuals of M. bigelowi collected at stations 1-5 on cruises from June 7, 1975 to December 6, 1976. Numbers on the vertical scale are times 1000.

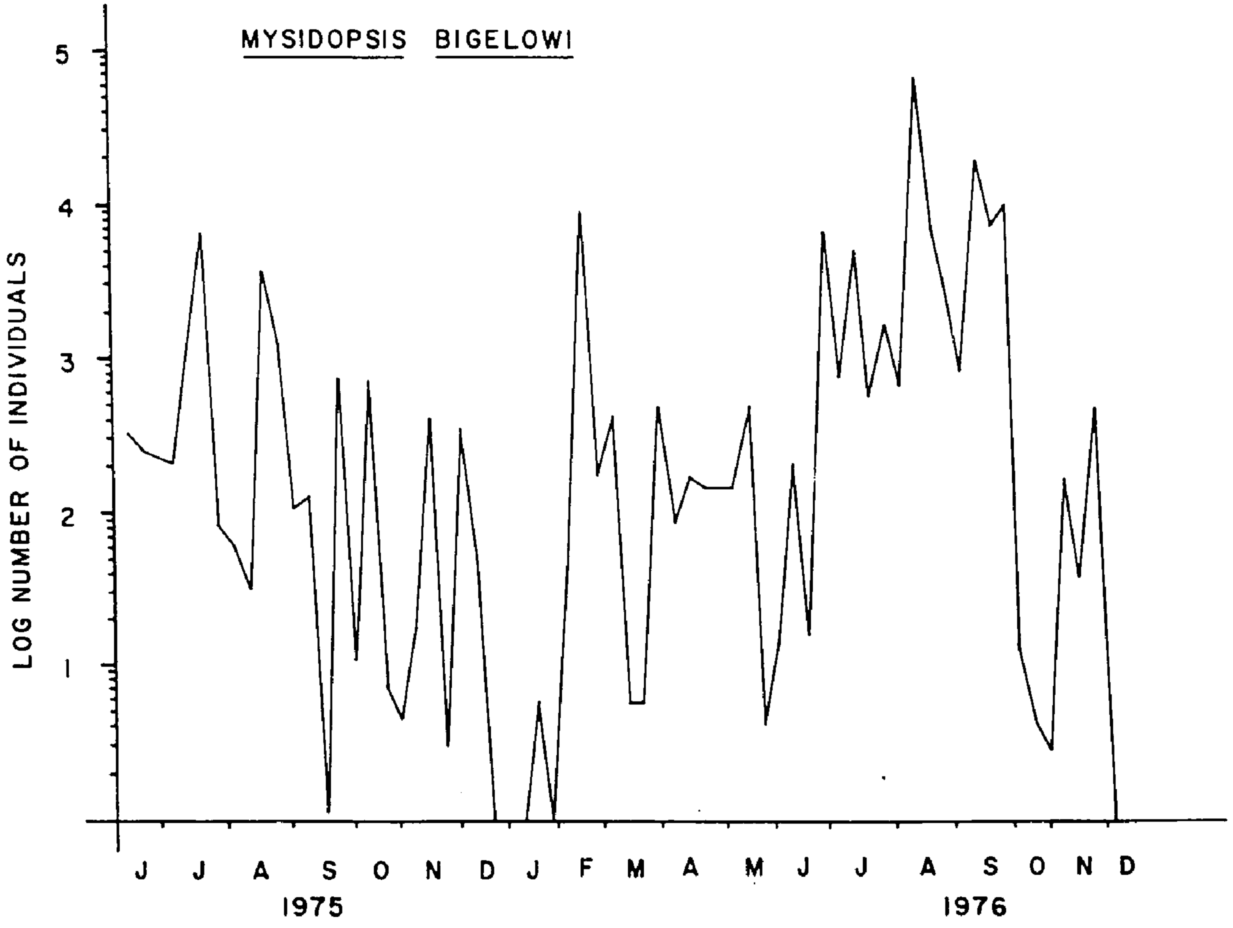

Fig. 20. Log of total number of individuals of *M. bigelowi* collected at stations 1-5 on cruises from June 7, 1975 to December 6, 1976. Numbers on the vertical scale represent powers of ten.

the inshore increases by several days to a week.

Movements of M. bigelowi between the stations were usually rapid. Peak densities often persisted for one or two cruises before rapid reductions were observed.

The description of the spatial and temporal distribution of M. bigelowi, which follows, has been developed from information on the abundance and population dynamics obtained from the sample analyses.

On July 21, 1975 large numbers of M. bigelowi occurred at station 6, where densities had remained low during the late spring and summer. Water temperatures in this area had remained low and stable near 15°C for several weeks. During late July, some of this cool coastal water penetrated at least as far as station 3, and increases in numbers occurred at all inshore stations. The inshore population was dominated by mature animals, while 60% of the offshore specimens were juveniles. The abundance of mysids steadily declined inshore through mid August. By late in the month, the temperatures at station 7 were comparable to those at station 1, and increases in numbers were recorded at stations 4 and 5 after a four week period of low densities. Most of the mysids were juveniles, and high numbers persisted until early September. The population size decreased during the succeeding weeks, and few were collected at stations 1 to 3 during the fall. Increases were observed at all stations on the October 17 cruise, but the species was almost completely absent the next week. While the inshore numbers remained low until early December, the mysids were abundant offshore during the entire period. Juveniles dominated at both station 6 and 7, although some gravid females were present.

On December 2, a huge increase in mysids occurred at stations 6 and 7. Increases were also seen at all of the inshore stations, the numbers at stations 1 and 2 being the highest since July. The temperature differential between stations 1 and 7 was less than 1°C, and at its lowest since the late summer. On December 17, the numbers collected at all stations were sharply reduced and remained low until February 14, when moderately high densities occurred at station 6. Some increases also occurred at the other inshore stations. Samples taken on February 21 contained high numbers at stations 3 to 7, with one of the largest collections of the year occurring at station 5. Temperatures recorded on this date indicated the first increase since the fall. An analysis of the population structure demonstrated that a higher percentage of larger mysids occurred inshore.

Through March, April, and May low and moderate numbers of the overwintering generation remained at all stations, the center of abundance being located near station 5. No major differences in the composition of the population were evident between stations.

On June 24, some of the highest numbers collected in the investigation were taken at all sampling sites. The numbers at stations 1 to 7 were orders of magnitudes greater than the previous week and marked a rapid migration of a large body of _M. bigelowi_ to the area outside of Hereford Inlet, as well as its subsequent migration into the embayment. Inshore water temperatures were nearly 22°C, while those outside were about 15°C.

Great reductions were observed at all inshore stations on July 2, but high densities occurred at station 6. None were collected at station 7. Another migration was observed on July 10, with a number of large animals occurring at station 5. Great fluctuations occurred during the rest of July, and low numbers were collected on August 2. Another large body of mysids penetrated to station 4 by August 7, despite a 5^{o}C temperature differential between stations 5 and 6. The abundance and distribution of M. bigelowi remained unchanged until a reduction was recorded inshore on September 5. On this date, the largest collection of the study (161,936) was taken at station 6. This large body of mysids penetrated the embayment and, on September 15 and 21, the maximum numbers collected at stations 2, 3, and 4 were taken. Sharply declining temperatures in late September were reflected in great reductions of mysids inshore. Virtually none were collected inshore until November 3, when large numbers occurred at station 6. On November 14, increased numbers were found at station 5 and, on November 26 at station 2, indicating a slow inward penetration.

Densities remained low and stable through the winter of 1976-77 and very few mysids were collected in the spring and summer.

K. Interactions of M. bigelowi With Other Organisms

Quantitative information for the utilization of M. bigelowi by predators in the Hereford Inlet system was not obtained, but this mysid was found in the guts of most of the fishes listed in Table 8.

Laboratory observations demonstrated that M. bigelowi was a solitary mysid which did not form spontaneous aggregations in the presence of conspecifics. It showed great affinities for the bottom, and usually oriented into currents. Adult individuals often remained inactive on the bottom for long periods of time, but responded vigorously to disturbances.

The exact nature of the relationship between *M. bigelowi* and *N. americana* could not be determined, but it was evident from the field data that a correlation between the distribution of the two species existed. A comparison of the abundance curves for *M. bigelowi* (Fig. 19 and 20) and *N. americana* (Fig. 13 and 14) demonstrates the simultaneous occurrences of increases and decreases in the inshore densities during most seasons.

Sharp increases in the numbers of both species at the stations nearest the inlet were observed on July 21 and August 21, 1975. Fall densities of *M. bigelowi* were low and no relationship to the distribution of *N. americana* was apparent, but increases in the numbers of both species were recorded at the offshore station on December 2. Simultaneous increases also occurred on February 21, 1976. No distinct migrations of either species were observed during the spring or early summer of 1976. However, on August 7, record numbers of both species were recorded on the same cruise as a major penetration of mysids from offshore occurred. A substantial reduction in the numbers of both species was observed on September 5, and both species were again very abundant on September 15.

L. Life History of *Heteromysis formosa*

Heteromysis formosa was not abundant in the Hereford Inlet area, but sufficient numbers were obtained to determine the life history pattern of the species.

An overwintering generation and one summer generation were observed each year. Immatures dominated during most months, the largest occurring in the winter. The largest mature individuals were collected in the late fall and early spring. Juveniles were relatively abundant from June to October, with the largest being found in the early winter. The ratio of males to females was essentially unity.

The mean lengths of the five life stages are presented in Table 12. The smallest individuals (about 1.7 mm) occurred in the late summer. The largest mature specimen was 9.8 mm and many nearly as large were collected in December and May. The average mysid (mature) was about 6 mm during the summer, although smaller mature individuals occurred in the late summer and fall. Females tended to be slightly larger than males.

The overwintering mysids began to reproduce in late May and continued to produce young until early August. The females of the WG brooded more than one time before dying off in mid summer. Large females were seldom observed without brood during the reproductive season, with some of the largest females carrying newly laid eggs in July. The incubation period appeared to be on the order of 15 to 25 days.

Table 12

Mean Length of H. formosa by Month
Expressed in mm

	♂ Mat.	♂ Imm.	♀ Mat.	♀ Imm.	Juv.
July 1975	5.4	3.7	6.0	4.3	2.3
Aug.	5.4	3.5	5.7	4.1	2.7
Sept.	5.7	4.1	6.0	4.5	2.3
Oct.	5.7	4.1	5.8	4.3	2.7
Nov.	6.8	5.4	6.8	5.8	3.7
Dec.	7.0	5.7	7.2	5.8	4.1
Jan. 1976	-	5.8	-	6.8	-
Feb.	-	-	-	-	-
March	-	-	-	-	-
April	-	-	-	-	-
May	-	3.7	-	-	-
June	5.7	3.7	6.8	4.8	2.7
July	5.8	4.5	6.0	4.7	2.5
Aug.	5.2	4.1	5.8	4.5	2.7
Sept.	5.7	3.9	6.0	4.3	2.3
Oct.	5.8	4.3	6.2	4.8	2.7

In August 1975, most of the WG had disappeared from the collections and the first of the summer generation (now 10-12 weeks old) was approaching maturity. In early September, mature females from 5.5 to 9.0 mm were brooding young. Most of the smaller individuals were reproducing for the first time and carried 6 to 9 eggs or embryos. Similar numbers of eggs and embryos were collected in females of the same size, indicating low marsupial mortality. There was little variation in the number of brood the females were incubating.

In October 1975, reproductive activity was suppressed and the few remaining gravid females were carrying advanced embryos. Late in the month, gravid females were very scarce and the large females in the population were without oostegites. Few large mysids occurred in November. Juveniles and immatures comprised the overwintering generation. The occasional occurrence of large females in the winter samples indicated that some of the individuals which reproduced in the fall did overwinter. The first spawning female collected in the spring was one of the largest specimens observed in the study.

Heteromysis formosa was less abundant during the spring and summer of 1976, but the pattern of growth and reproduction was almost identical to the previous season. The last brooding female was collected on October 25 (14°C).

Very low numbers of _H. formosa_ occurred from December, 1976 to November, 1977.

M. Abundance and Spatial Distribution of H. formosa

Heteromysis formosa was the least abundant mysid in the Hereford

Inlet system, comprising less than 0.1% of the total number of individuals collected. A total of 8904 specimens were taken in 140 of the 424 samples. The mean number collected per sample was 21 and the range was 0 to 1088 per tow.

A high correlation (r= 0.8543) was found between the number of individuals and the calculated density, but since the density values were not always reliable, the abundance and distribution of *H. formosa* is described in terms of numbers per sample.

Table 13 summarizes the results of the statistical analysis of *H. formosa* by station. This species occurred almost exclusively in the upper embayment, where it was frequently taken from debris laden bottoms. Individuals were occasionally collected in intertidal areas during the warmer months.

Laboratory observations demonstrated *H. formosa* was a solitary species which spent most of the daylight period hidden among bottom debris. After dark, the mysids began to roam randomly about the bottom. The mysids were much more active in static water than in the presence of currents. Table 4 demonstrates the increase in the number of *H. formosa* collected during the evening cruise on August 23, 1975.

Heteromysis formosa was not observed to interact with other mysids maintained in the laboratory systems, and no relation was found between its distribution and that of the other species.

N. Temporal Distribution of *H. formosa*

Heteromysis formosa was collected every month, but was most

Table 13

Statistical Analysis of Abundance of *H. formosa* by Station

Station	1	2	3	4	5	6	7	All
Mean Number	48	75	2	1	1	<0.1	0.2	21
Minimum	0	0	0	0	0	0	0	0
Maximum	552	1088	31	49	20	2	8	1088
Standard Deviation	108	191	6	6	3	0.4	1.2	92
Coefficient of Variation	221	255	258	613	311	448	511	448
Standard Error of the Mean	13.1	23.3	0.7	0.7	0.4	<0.1	0.2	4.5
Number of Samples Collected	68	67	67	67	67	36	48	421
Number of Times Occurred	45	43	22	8	15	3	4	140

abundant from June to December. The number of individuals collected per cruise is shown in Figure 21. The statistical analysis of the abundance of H. formosa by month is summarized in Table 14.

Annual fluctuations in the abundance of H. formosa in the study area were great and strongly influenced the monthly means. A mean of 64 per sample was determined for the period from June to November 1975, while a mean of less than nine individuals per collection occurred for the same period in 1976.

In general, a change in the distribution occurred in the fall as water temperatures in the upper embayment fluctuated greatly. Reductions in densities were recorded at stations 1 and 2,and some mysids were collected at stations 3 to 7. Heteromysis formosa was collected at station 7 only in November and December 1975 and November 1976. In the fall, H. formosa was collected at stations 4, 5, and 6 only on cruises with the ebbing tide. None were taken on flooding tide cruises either in the fall of 1975 or 1976. Although H. formosa was almost always associated with large collections of coarse bottom detritus, no accumulations of materials occurred with the fall mysid collections at stations 4 to 7.

Heteromysis formosa was not collected at stations 1 and 2 on two cruises in June 1975, but did occur in samples taken at these sites in mid July. The abundance of mysids was greater in late July as water temperatures reached a high of 25°C. The increased densities were primarily due to recruitment by the winter generation spawn. Individuals were collected at all inshore stations on August 6 after

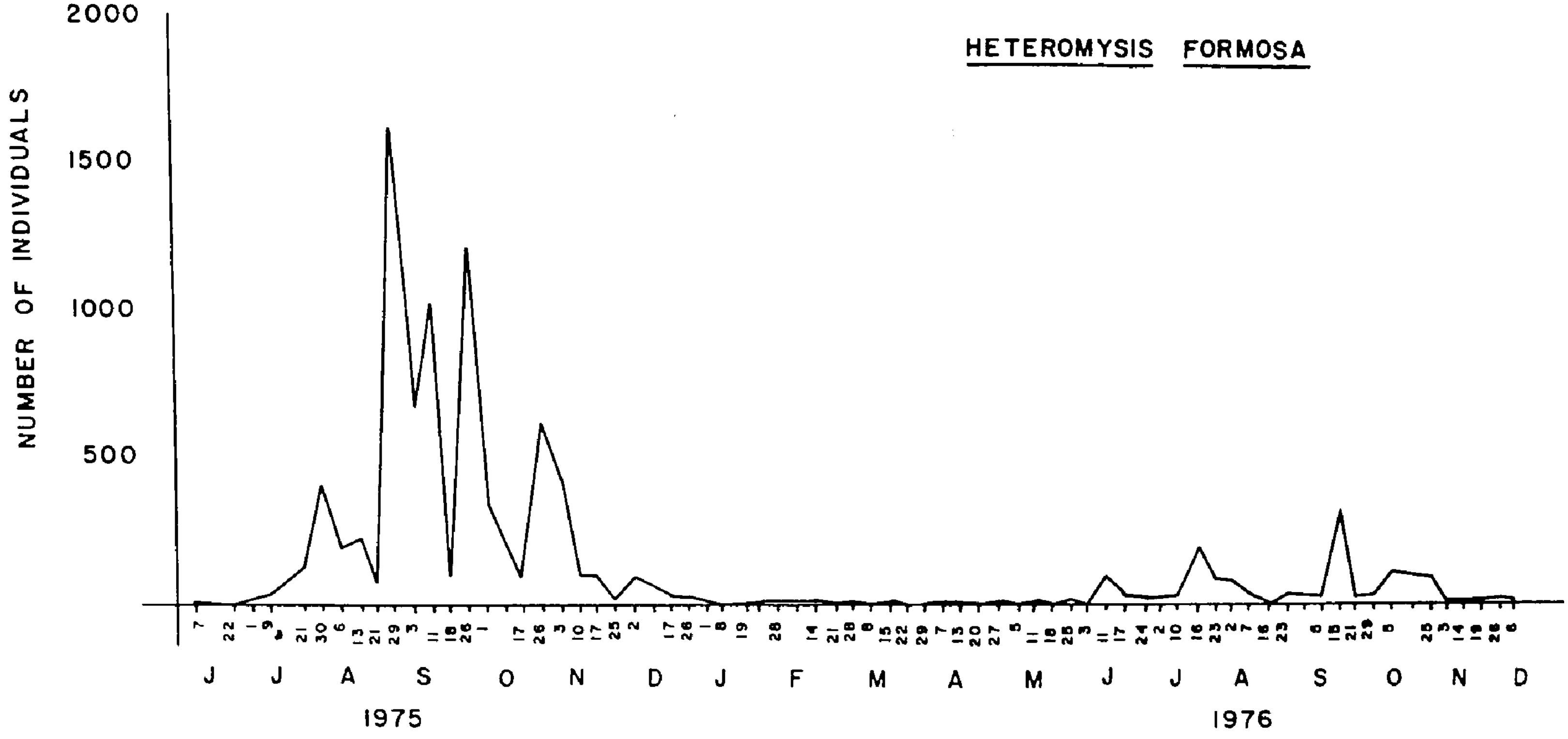

Fig. 21. Total number of individuals of H. formosa collected at stations 1-5 on cruises from June 7, 1975 to December 6, 1976.

Table 14

Statistical Analysis of Abundance of *H. formosa* by Month (Jan.-June)

Month	Jan.	Feb.	March	April	May	June
Mean Number	0.3	0.1	<0.1	0.5	0.6	2.6
Minimum	0	0	0	0	0	0
Maximum	2	1	1	4	7	90
Standard Deviation	0.6	0.3	0.2	1.1	1.7	13.3
Coefficient of Variation	202	291	600	214	305	503
Standard Error of the Mean	0.1	<0.1	<0.1	0.3	0.3	1.9

Table 14 cont.

Statistical Analysis of Abundance of *H. formosa* by Month (July-Dec.)

Month	July	Aug.	Sept.	Oct.	Nov.	Dec.
Mean Number	19.5	40.8	67.8	40.1	12.9	5.6
Minimum	0	0	0	0	0	0
Maximum	312	1088	850	394	305	37
Standard Deviation	54.6	161.3	173.4	84.8	45.8	9.7
Coefficient of Variation	280	395	256	209	354	173
Standard Error of the Mean	8.1	21.8	24.5	15.5	6.6	2.0

cold weather had caused the temperatures in the upper embayment to decline. Some mysids were collected at stations 3 to 5 during August, but the densities at stations 1 and 2 were consistently high. The maximum numbers collected in the investigation were taken at these stations on August 29.

In early September, temperatures decreased in the upper embayment, and samples taken on September 3 indicated that increased numbers of mysids were present at stations 4 and 5. Inshore densities fluctuated during the remainder of the month, and the first individual collected offshore was taken on September 21. *Heteromysis formosa* remained abundant in the upper embayment through October and early November and, as temperatures dropped during November, mysids were collected at all inshore stations. Increased numbers occurred at the offshore stations during late November and December. Almost no mysids were collected in the upper embayment during January and February 1976, although occasional individuals occurred in samples collected at stations 2 to 6. Only a single individual was collected in the four March cruises, and the densities in April and May were extremely low.

The abundance of *H. formosa* in the summer of 1976 was about seven times less than in 1975, but the trends appeared to be similar. Without exception, the numbers were greatest at stations 1 and 2. Peak abundances occurred in early July when the WG had releaseo numbers of young and in mid September when juveniles from the SG spawn were numerous.

V. DISCUSSION

Neomysis americana was omnipresent and abundant in the tidal embayment and adjacent coastal waters at Hereford Inlet. Mysids were collected in every epibenthic sled tow in the major waterways of the study area; however, their clumped distribution and high motility presented a major problem in the assessment of their numerical abundance.

Laboratory experiments demonstrated that water currents induced ordered aggregations of mysids which oriented into and maintained positions against the currents. Field studies indicated similar aggregations probably occurred in the tidal embayment. The spatial and temporal characteristics of captive aggregations were primarily regulated by current velocity and were secondarily modified by light and temperature. Observations on the responses of aggregations to changes in current velocity were instrumental in the design of a sampling program which minimized many sources of variability. Two major sources of error involved with sampling mysid aggregations in the embayment were related to mysid avoidance of the sampling apparatus and to changes in the vertical position of the aggregations with respect to current velocity. Net avoidance was minimized by towing the sled in the same direction the current was moving. Since the height of the sled was fixed at 30 cm,and the distance the mysids remained above the bottom was variable, the proportion of the aggregation which was available to the collection apparatus was not consistent. The vertical dimensions of the aggregations were controlled by current velocity and light so that it appeared essential to collect the samples at the same stage of the tide throughout the study period. Since this sampling procedure minimized a significant source of error, more realistic comparisons of abundance could be made.

Attempts to use other sampling devices to collect mysids indicated that none were as effective as the epibenthic sled. Samples collected with subsurface ring nets under a variety of conditions of current and light demonstrated the vast majority of mysids in the water column were near the bottom. The abundance of mysids in a sled sample was always orders of magnitude greater than that taken in a simultaneous subsurface net tow. While it is not possible to directly compare the abundance of *N. americana* determined in the study to that reported by other investigators from other sections of the coast, the densities reported by Fish (1925), Cowles (1933), and Whitely (1948) using subsurface ring nets in coastal waters are probably meaningless in terms of actual abundance. It is not likely the abundance reported by Hulburt (1957), using a Clarke-Bumpus sampler with a five inch aperature, was representative of the abundance of *N. americana* in Delaware Bay. Hopkins (1958) attempted to determine the abundance of the species in the surface waters of Indian River Inlet, Delaware by hanging a twelve inch ring net into tidal currents from a bridge. The present investigation demonstrates the necessity of carefully designed and executed sampling programs for the best possible assessments of mysid abundance and distribution.

The spatial distribution of N. americana in the study area was not homogeneous with respect to numbers of individuals or relative percentages of life stages at any point in time. Comparisons of estimates of abundance and population structure at a particular sampling site at varying intervals were difficult to interpret because of the dynamic nature of the aggregations. Temporal fluctuations in the abundance and life stage composition of the populations were caused by variable birth and death rates as well as by changes in the horizontal distribution of the motile aggregations.

The life history pattern of N. americana in southern New Jersey waters is similar to that reported for other areas in the western North Atlantic, although there is some disagreement about the temporal nature of the 2SG. Hopkins (1958) determined the 2SG reproduced and died before the early fall, and he did not discuss the origin of the overwintering generation. In the present investigation, the major brood release of the 2SG occurred in the late fall before water temperatures began to decline, and those 2SG animals which had not matured by this time overwintered to reproduce the following spring. Herman (1962) determined a similar temporal pattern for the 2SG in Narragansett Bay.

Because of continuous reproduction and considerable individual variations in growth rates, it is difficult to investigate many aspects of the population dynamics of *N. americana*. Laboratory experiments were conducted to facilitate the interpretation of the field data. One significant aspect of the reproductive behavior which was determined in the laboratory was the ability of females to reproduce more than one time. This fact has not been reported for *N. americana* and figures as an important factor in assessments of the dynamics of populations. Hopkins (1965) and Herman (1962) suggested that females probably died shortly after their first brood release.

Tattersall and Tattersall (1951) concluded that temperature was the primary factor which influenced various aspects of the growth and reproduction of temperate mysids. Seasonal variations in apparent growth rates and the size at which individuals reached sexual maturity were determined from the field sample analyses in the present study. A comparison of the life history patterns of *N. americana* determined for populations at various locations along the east coast demonstrates variations in the timing of major brood releases,and other aspects of the population dynamics,which are probably related to geographical variations in temperature regimes.

To the author's knowledge,there are no detailed published accounts of the life histories of either *Mysidopsis bigelowi* or *Heteromysis formosa*. The life history pattern determined for *M. bigelowi* in southern New Jersey substantiates the limited information reported by Hopkins (1965), Wigley and Burns (1971) and Williams (1972). The length of the spawning period of *H. formosa* (June to September) reported by Wigley and Burns (1971) was consistent with observations made in Hereford Inlet.

Factors related to the spatial and temporal fluctuations in abundance rendered the patterns of distribution of N. americana in the tidal embayment difficult to interpret. The physical and numerical dimensions of the aggregations were extremely variable and were determined by complex interactions of physical, chemical, and biological factors. Tidal currents appeared to be among the primary physical determinants of both the short term (daily and weekly) and long term (monthly and seasonally) distributions of aggregations within the embayment. Sampling programs which investigated the responses of the field populations to tidal currents indicated that the aggregations usually maintained positions at the sampling sites over the daily tidal cycle. The overall abundance of mysids at the various stations was correlated with the strength of the local tidal currents, so that abundance was most variable in the lower embayment (strongest tidal currents) and least variable offshore (weakest tidal currents). The length of time that an aggregation remained at a sampling site appeared to be related to the local current structure; however, light, temperature, food supply, and predator concentration were probably influential.

The ultimate source of the inshore populations was the coastal area outside of Hereford Inlet. Migrations of aggregations into the embayment occurred during all seasons. The numbers of mysids involved in such movements were highly variable as were the rapidity and horizontal extent of the penetrations, but occasionally these migrations could be followed to the upper embayment over a period of days or weeks.

Temperature was clearly the most important factor influencing mysid movements between the coastal areas and the embayment. Migrations occurred in the early winter after inshore temperatures stabilized, and, in the early summer, after the period of most rapid warming. In June 1975 and 1977, large masses of *N. americana* arrived outside of Hereford Inlet before the sharp temperature gradient was established, and massive penetrations occurred without delay. In June of 1976, a large mass of 1SG mysids arrived outside of the inlet after the temperatures inshore had warmed sufficiently to establish a considerable thermal discontinuity between the two areas. High numbers of mysids remained offshore all summer and within two days after the gradient broke down in early September, a massive penetration to the upper embayment occurred.

Several migrations of temperate mysids have been reported from European waters (Kinne, 1938; Holthuis, 1954; Van der Baan and Holthuis, 1971; and Hesthagen, 1973), but no such movements have been documented for *N. americana* or *M. bigelowi* in the western North Atlantic. The only species of mysid from this area which has been reported to migrate was *Mysis stenolepis* in Passamaquoddy Bay, New Brunswick (Amaratunga and Corey, 1975). None of these reports offers detailed analyses of the spatial and temporal characteristics of the seasonal migrations or the factors which induced them.

The factors which initiated the migrations into the embayment could not be precisely determined. Most migrations occurred during periods when there was no significant difference (less than 1 or 2^{o}C) in temperature between the coastal and inshore waters, indicating temperatures may have been more a limiting factor than an initiating factor. Since inward penetrations were of greater magnitude and frequency than outward migrations, it appears likely that some stimulus must be detected by mysids outside of the embayment before an inshore penetration ensues. It seems likely the offshore animals may respond to concentrations of dissolved and suspended organic materials which are flushed from the productive salt marsh embayment with the ebbing tide. Clutter (1969) found food supplies may have been a primary factor determining the distribution of *Metamysidopsis elongata*.

The mechanism by which mysid aggregations moved within the study area could not be determined and probably involved complex behavioral patterns related to the animals' responses to current, light, temperature, and other factors. The means of dispersal in the tidal area may involve a tendency of the animals to maintain positions into currents of tolerable physical and chemical properties and a tendency to drift with currents which have unsuitable qualities.

Short term sampling studies showed aggregations maintained positions over tidal cycles during the day, but dispersed in darkness. Similar observations were made in the laboratory, where the majority of individuals maintained positions into the currents in darkness, while others drifted passively. The nocturnal orientations were less precise and such behavior may be important in determining the distribution of mysids in the embayment. Penn (1975) determined the interaction of nocturnal vertical migrations of larval penaeid shrimps and flooding tides which dominated during the evening were responsible for the influx of the larvae into Shark Bay, Australia. Much information which would facilitate the understanding of the mechanics underlying the migrations and short term displacements of mysid aggregations in the Hereford Inlet study area may be obtained through careful laboratory investigations.

Although aggregations which migrated into the embayment were usually composed of mysids of all sizes, there was a tendency for larger animals to penetrate more quickly. Within the study area, the mean lengths of adult animals of both sexes were greater in the upper embayment. A similar trend was observed by Hulburt (1957) in Delaware Bay. Without considering the swimming capabilities of *N. americana*, Hulburt attributed the attentuation of larger animals upestuary to passive transport with the saline bottom currents typical of the Delaware Estuary. Although the means by which larger mysids arrived in the upper embayment of the Hereford Inlet study area could not be established, it was apparent these accomplished swimmers remained in the area by choice. Unlike the Delaware Estuary, the bottom current structure of the upper reaches of the Hereford Inlet embayment did not have a net inward flow.

A resident population of _N. americana_ remained in the upper embayment during the summer and winter. The mean lengths of the individuals were usually greater than those in other parts of the embayment and may have been related to the higher concentrations of filterable organic materials in the area. Temperatures during the summer were generally highest in the upper embayment and may have influenced growth and reproductive rates. Differences in the timing of major brood releases of the generations between the upper embayment and offshore populations may have been related to differences in thermal regimes.

Although many environmental factors determined changes in the distribution of mysids in the study area, fluctuations in abundance between stations were often correlated with changes in temperature. Temperature variations on a daily basis were not of sufficient magnitude to influence the distribution of the aggregations, but fluctuations compounded over days or weeks had marked effects on the abundance of mysids in the upper embayment. This was particularly evident in the spring and fall when the rates of temperature change were greatest. During the spring, considerable fluctuations in abundance in this area occurred as juveniles moved into the shallow sounds during warm periods and returned to the more thermally stable channels when cold weather decreased the water temperatures in the sounds. Mauchline (1970) demonstrated that _Schistomysis ornata_ left the flats as temperatures declined in the fall to overwinter in the depths.

In the upper embayment of the Hereford Inlet area, juveniles remained after the adults had moved toward the inlet with rapidly declining temperatures in the fall. Kinne (1955) observed the fall migration of N. vulgaris (N. integer) from the shallows of Kiel Canal (Germany) and concluded that the young were less sensitive than adults to temperature fluctuations. Herman (1962) found that young N. americana were less sensitive than adults since they crossed thermoclines in their vertical migration when larger forms could not.

Neomysis americana is one of the major components of the trophic structure of the salt marsh ecosystem of southern New Jersey. As an omnivore which filters particulate organic materials and phytoplankton and captures small zooplankters, this mysid constitutes an important link by making the productivity of the salt marsh system available to higher trophic levels.

Neomysis americana occupies a unique habitat by remaining oriented into tidal currents just above the bottom. There is no other species of small invertebrate in the study area which is as abundant or readily available to predators feeding near the bottom. Mysids are ubiquitous in the major waterways of the embayment and in the adjacent coastal waters. They provide one of the most significant sources of food for the majority of commercially and recreationally important species of fishes which utilize the inshore waters as nursery grounds during all seasons.

The ecological significance of mysids in temperate coastal waters cannot be overemphasized. Further investigations on all aspects of the biology and ecology of mysid crustaceans will contribute information which is essential to the understanding of the complexities of shallow temperate ecosystems.

VI. SUMMARY

1. The population dynamics and spatial and temporal distributions of *Neomysis americana*, *Mysidopsis bigelowi*, and *Heteromysis formosa* were investigated.

2. Quantitative samples were collected with an epibenthic sled in a tidal embayment and the adjacent coastal areas at Hereford Inlet, New Jersey. Tows were made at seven stations several times a month from June 1975 to June 1977.

3. *Neomysis americana* was the most abundant mysid in the study area, occurring in each of the 424 samples. It accounted for 97% of the mysids collected, and was most abundant from June to October. The mean number per sample was 29,113.

4. *Neomysis americana* reproduces throughout the year, the greatest activity occurring from April to October. Three generations occur per annum. An overwintering generation (WG) spawns in the spring giving rise to a first summer generation (1SG). The 1SG mysids spawn from June to August,and their progeny constitute a second summer generation (2SG). Those 2SG which mature in the fall bear young which, in addition to the immature 2SG, overwinter to brood the next spring.

5. Juveniles dominated most of the samples, immatures (and occasionally matures) comprising the greatest percentages during

the winter and early spring

6. Mysids (1SG) originating from the WG spawning peak in April reached maturity in the early summer and died by late August, indicating a longevity of three to four months. The first born 2SG mysids (in June) reached maturity in the fall and were three to four months old when they died. Those 2SG animals which overwintered (=WG) had a longevity of six to nine months. It is unlikely any mysids lived more than one year.

7. The size range of *N. americana* was 1.6 to 15.2 mm, with the largest individuals of each life stage category occurring in the winter. Females were larger than their male counterparts.

8. Gravid WG females were about 11 mm and carried an average clutch of 37 brood. Spawning females of the 1SG and 2SG had a mean length of about 8 mm. Gravid 1SG mysids brooded about 15 young, while the 2SG had an average clutch size of 11.

9. Laboratory and field evidence indicated that two or more broods were produced by females of the 1SG. Most of the WG females spawned once, as did most of the 2SG mysids which were reproductively active in the fall.

10. *Neomysis americana* was difficult to maintain for extended periods in the laboratory due to its susceptibility to mechanical damage during collection.

11. Mysids in still water swam almost continuously, remaining close to the bottom in assay tanks maintained in shaded sunlight. All individuals swam in erratic paths at cruising speeds which varied between individuals of different sizes. In darkness, mysids remained higher in the water column and swam at slower speeds.

12. In experimental systems, individuals responded to water movement immediately. Mysids swam into currents, forming ordered associations of individuals oriented parallel to one another. Aggregations maintained stable positions with respect to the bottom in currents which did not carry them away.

13. *Neomysis americana* was found to be an accomplished swimmer capable of avoiding adverse conditions. Swimming behavior was primarily influenced by currents, but light, temperature, and density related factors modified the rheotactic responses.

14. Mature animals were more motile than young and could tolerate stronger velocities. Mysids of different sizes showed preferences for currents of different velocities in the experimental gradient systems.

15. The responses of current induced aggregations to disturbances were studied to provide information which facilitated the interpretation of the results of the field sampling program.

16. In the laboratory, changes in current velocities altered the horizontal and vertical dimensions of the oriented aggregations. Sampling programs designed to assess the effect of varying tidal speeds on the abundance and distribution of _N. americana_ produced results that were consistent with these laboratory observations.

17. Uniform sampling procedures with respect to tidal currents were essential. Greatest numbers per sample were collected when the epibenthic sled was towed in the same direction the tide was flowing. More mysids were collected with moderate velocities than with peak velocities. Lowest numbers were taken at slack tide.

18. While aggregations usually maintained positions into tidal currents in the embayment during the day, there was a tendency to disperse and move away from the bottom at night. This was also observed in the laboratory.

19. The distribution of _N. americana_ in the study area was found to be non-random. Large spatial and temporal variations in abundance and population structure occurred between adjacent stations over short periods.

20. The size, composition, and longevity of the aggregations could not be examined in detail because of their great motility, but it was evident these characteristics were highly variable.

21. The coastal waters were the ultimate source of the mysid populations in the embayment. Migrations of animals to the inshore waters occurred after masses of animals arrived outside of Hereford Inlet.

22. The largest migrations occurred during the warmer months, when the abundance inshore increased by three or more orders of magnitude over days or weeks. Such migrations were responsible for the repopulation of the embayment in June 1975 and 1977.

23. The extent of the penetrations into the upper embayment depended on the size of the migrating aggregations and the thermal regimes of the study area. Temperature influenced the distributions between stations over short periods (tides, days, weeks) as well as over long periods (months, seasons, years). Juveniles appeared to be less sensitive to temperature change than adults.

24. A resident population remained in the upper embayment during the summer and dispersed during the fall cooling period. An early winter penetration repopulated the area and the WG population remained until spring. Tidal current strengths were less and the food supply was greater in this area than in the lower embayment. Aggregations did not remain in the lower embayment for long periods of time.

25. Differences in the mean lengths of individuals and the timing of the major brood releases between the inshore and coastal waters

reflected the influence of the respective thermal regimes on the population dynamics. Differences in size and reproductive condition made it possible to determine movements of mysids between the two areas.

26. The ubiquity and abundance of *N. americana* in the Hereford Inlet area, and the great extent to which it is consumed by juvenile fishes, indicate its great significance in the productivity of the temperate marsh system. This organism is one of the major components of the trophic structure of the system during all seasons.

27. *Mysidopsis bigelowi* comprised less than 3% of the total number of mysids collected and was most prevalent in the sandy areas. Greatest numbers were collected during the warmest months. Three generations were produced per annum and its abundance and distribution in the lower embayment were related to those of *N. americana*.

28. *Heteromysis formosa* was almost entirely confined to the upper embayment and was most abundant in the summer and fall. This secretive species hid among debris during the day and roamed the bottom in darkness. Its reduced abundance during the winter, and sporadic occurrence near the inlet and offshore during the early winter, indicated seasonal migrations may occur.

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Appendix 1. Bottom water temperatures (°C) corresponding to epibenthic sled samples at time of collection.

Station	1	2	3	4	5	6	7
6/7/75	21.5	20.0	19.0	18.7	19.3	-	-
6/22	22.4	22.5	21.7	21.5	21.7	-	14.0
7/7	24.0	24.1	24.3	23.4	23.7	-	14.0
7/21	22.8	21.9	19.0	19.3	18.4	-	15.0
7/30	25.2	24.6	22.3	20.7	20.1	-	14.7
8/6	22.2	23.0	21.9	21.6	21.8	-	15.4
8/13	26.3	25.8	24.7	23.9	23.9	-	22.8
8/21	24.9	25.2	25.0	25.0	25.2	-	24.7
8/29	25.6	26.5	25.8	24.9	24.8		22.7
9/3	21.6	21.6	21.6	21.9	21.6	-	22.0
9/11	21.6	21.6	21.4	21.8	21.9	-	-
9/18	20.5	20.1	20.4	20.5	20.6	-	-
9/21	-	-	-	-	-	-	20.6
9/26	23.7	23.0	22.0	22.0	21.9	-	-
10/1	21.0	21.2	21.0	21.1	21.0	20.8	20.8
10/17	18.0	18.0	18.1	17.6	18.0	-	-
10/26	19.4	18.7	18.5	18.3	18.3	-	18.0
11/3	15.6	15.5	15.1	15.3	15.2	-	15.5
11/10	17.9	17.8	17.4	17.2	17.2	-	-
11/17	11.8	10.9	11.8	12.5	11.9	13.1	14.1
11/25	8.8	8.5	10.4	10.8	11.0	-	-
11/29	-	-	-	-	-	11.2	11.5
12/2	9.8	9.3	9.8	10.0	9.0	10.6	10.6

Appendix 1. cont. Bottom water temperatures (^{o}C) corresponding to epibenthic sled samples at time of collection.

Station	1	2	3	4	5	6	7
12/17/75	8.2	8.2	8.1	8.0	8.0	-	-
12/26	3.4	3.9	3.9	5.0	5.0	-	-
12/29	-	-	-	-	-	5.1	4.9
1/8/76	2.0	2.3	2.5	3.0	3.3	-	-
1/16	3.0	2.8	2.8	2.9	2.9	-	-
1/29	3.1	3.0	3.1	2.0	3.0	-	-
1/30	-	-	-	-	-	2.2	2.3
2/14	3.8	3.0	3.0	3.0	3.0	-	-
2/15	-	-	-	-	-	3.0	-
2/21	7.0	6.4	5.8	4.7	4.6	4.6	4.2
2/29	5.5	6.4	6.3	5.4	6.0	-	-
3/8	8.0	7.9	7.4	6.7	6.6	6.6	6.3
3/15	6.0	6.0	6.3	6.0	6.4	-	-
3/22	8.1	8.2	7.6	7.0	6.8	-	-
3/29	10.3	10.4	9.2	8.3	8.4	8.4	8.0
4/7	11.1	10.8	11.3	9.2	10.4	-	-
4/13	8.2	8.0	8.4	8.4	8.6	-	-
4/15	-	-	-	-	-	9.2	9.1
4/20	16.3	15.6	15.0	12.5	11.9	-	-
4/30	-	-	-	-	-	11.1	10.1
5/5	14.1	14.0	13.7	12.7	12.6	-	-
5/11	14.7	14.8	13.9	13.8	14.0	-	-
5/13	-	-	-	-	-	12.8	13.0

Appendix 1. cont. Bottom water temperatures (°C) corresponding to epibenthic sled samples at time of collection.

Station	1	2	3	4	5	6	7
5/18/76	17.8	16.7	-	13.5	14.0	-	-
5/25	16.1	16.1	14.8	13.9	14.0	-	-
6/1	-	-	-	-	-	17.4	17.4
6/3	17.0	17.2	16.4	15.4	15.3	-	-
6/11	19.9	20.9	20.0	19.5	19.5	18.3	16.4
6/17	21.7	21.7	21.2	19.8	19.4	18.9	18.8
6/18	-	-	-	-	-	20.7	16.7
6/24	22.9	23.0	22.2	21.1	21.6	-	-
6/25	-	-	-	-	-	15.8	15.8
6/28	-	-	-	-	-	14.4	14.4
7/2	22.5	20.7	17.3	15.9	16.1	14.5	14.8
7/6	-	-	-	-	-	14.0	13.9
7/10	19.3	19.7	18.1	16.6	18.0	16.8	14.4
7/16	21.8	20.0	19.8	17.7	17.2	-	-
7/21	-	-	-	-	-	16.0	16.2
7/23	23.2	23.0	21.8	20.3	20.3	-	-
8/2	24.5	24.5	23.2	22.3	22.3	22.2	17.5
8/7	24.4	23.9	24.1	23.3	23.6	-	-
8/11	-	-	-	-	-	21.5	21.5
8/16	24.5	23.9	23.5	21.4	21.5	21.0	21.0
8/23	24.4	24.3	24.0	23.3	24.3	23.6	23.8
8/31	-	-	-	-	-	22.2	20.8

Appendix 1. cont. Bottom water temperatures (°C) corresponding to epibenthic sled samples collected at same time.

Stations	1	2	3	4	5	6	7
9/5/76	22.2	22.2	21.9	21.9	21.9	23.4	22.9
9/11	-	-	-	-	-	22.0	-
9/15	23.0	22.6	22.4	21.6	21.0	21.5	22.3
9/21	22.0	21.9	21.3	21.2	21.5	-	-
9/23	-	-	-	-	-	19.5	19.5
9/29	19.3	19.3	18.8	18.6	18.7	18.8	18.8
10/5	17.5	17.5	16.9	17.1	17.0	-	-
10/19	-	-	-	-	-	14.6	14.8
10/25	14.1	14.2	14.4	14.5	14.0	-	-
11/3	9.2	9.2	8.7	10.0	9.2	-	-
11/4	-	-	-	-	-	11.6	12.1
11/14	5.7	5.9	6.6	8.4	7.6	7.8	8.9
11/19	7.3	7.4	7.3	8.0	7.9	9.8	9.8
11/26	6.4	6.8	7.2	7.1	8.3	-	-
12/6	4.2	4.3	4.3	4.9	4.4	-	-
1/6/77	0.7	0.6	0.6	0.6	0.9	-	-
3/4	4.6	4.6	4.0	3.9	3.8	-	-
3/21	7.0	6.8	6.2	6.2	5.8	5.8	5.5
5/3	17.3	16.3	14.0	13.9	14.3	12.5	11.8
6/2	17.2	16.7	16.0	15.3	15.5	-	-
6/14	21.2	21.9	19.7	18.6	19.3	17.2	16.9

Appendix 2. Total numbers of _N. americana_ collected per sample.

Station	1	2	3	4	5	6	7
6/ 7/75	18616	210896	2591	478	33832	-	-
6/22	208968	75424	221	8622	46216	-	-
7/7	85572	88080	4034	3894	5586	-	23904
7/21	58400	37912	35052	11198	546696	-	27940
7/30	1112	18520	10326	4675	570	-	20226
8/6	9449	3786	1488	886	10562	-	41804
8/13	3380	2426	11750	211304	1460	-	6851
8/21	5656	105360	36776	59396	93984	-	57108
8/29	21605	3672	19242	9874	3371	-	1028
9/3	16916	1634	7328	5312	3219	-	24889
9/11	248	4484	17426	1460	475	-	-
9/18	214	180	26	662	67	-	-
9/21	-	-	-	-	-	-	2053
9/26	2026	3234	83648	49048	20138	-	-
10/1	22826	40228	60	1190	46660	196480	24768

Appendix 2. cont. Total numbers of *N. americana* collected per sample.

Station	1	2	3	4	5	6	7
10/17/75	9042	56636	4172	69632	22364	-	-
10/26	8280	3744	15682	14460	5390	-	13622
11/3	7080	4169	609	2379	4420	-	3575
11/10	812	482	980	512	426	-	-
11/17	64	69	8	16	643	653	3265
11/25	310	224	212	74	126	-	-
11/29	-	-	-	-	-	181	3848
12/2	105	47	11	19	88	1275	5704
12/17	4885	529	1	521	1020	-	-
12/26	16648	4200	1126	3520	214	-	-
12/29	-	-	-	-	-	1151	30952
1/8/76	16864	8792	5570	1190	1046	-	-
1/16	2082	956	7	30	272	-	-
1/29	1978	1570	22	88	1729	-	-
1/30	-	-	-	-	-	8803	3269

Appendix 2. cont. Total numbers of _N. americana_ collected per sample.

Station	1	2	3	4	5	6	7
2/14/76	5388	2378	94	34	163	-	-
2/15	-	-	-	-	-	4516	-
2/21	18484	3892	4482	830	7253	4752	5240
2/29	1111	209	26	92	516	-	-
3/8	3188	2792	328	268	1060	1068	13381
3/15	1879	204	42	85	122	-	-
3/22	202	614	293	184	78	-	-
3/29	2329	223	28	35	132	1358	9222
4/7	6520	1832	17	65	582	-	-
4/13	982	127	72	130	16	-	-
4/15	-	-	-	-	-	12613	12664
4/20	882	1120	107	146	181	-	-
4/30	-	-	-	-	-	2160	9126
5/5	106	215	490	165	1246	-	-
5/11	24	-	74	22	582	-	-

Appendix 2. cont. Total numbers of *N. americana* collected per sample.

Station	1	2	3	4	5	6	7
5/13/76	-	-	-	-	-	5443	31519
5/18	380	68	-	76	180	-	-
5/25	2807	297	24	32	15	-	-
6/1	-	-	-	-	-	3734	7552
6/3	3794	651	158	428	232	-	-
6/11	7878	5330	64	85	3957	-	5593
6/17	243	6302	6470	2340	497	920	15
6/18	-	-	-	-	-	40368	29760
6/24	920	23432	3084	230	3101	-	-
6/25	-	-	-	-	-	3944	3326
6/28	-	-	-	-	-	25224	22328
7/2	20604	17481	4440	6213	26520	55064	103
7/6	-	-	-	-	-	22360	32488
7/10	4284	5410	2606	1851	10474	25496	2784
7/16	6764	12645	11560	16201	12416	-	-

Appendix 2. cont. Total numbers of N. americana collected per sample.

Station	1	2	3	4	5	6	7
7/21/76	-	-	-	-	-	96512	2960
7/23	22484	31304	1360	4207	127696	-	-
8/2	22764	3560	21040	9640	31646	49472	8720
8/7	43292	19560	39	140892	1337600	-	-
8/11	-	-	-	-	-	12560	45104
8/16	40960	65472	118080	103056	972800	299712	20224
8/23	4210	42800	4326	48880	499392	276224	41024
8/31	-	-	-	-	-	38120	12211
9/5	3064	2280	810	2519	34108	440320	75640
9/11	-	-	-	-	-	129168	-
9/15	12840	18368	125520	118628	173200	109936	6525
9/21	418080	62480	30960	281536	385936	-	-
9/23	-	-	-	-	-	107568	13
9/29	140960	31248	34000	11816	89960	84976	12682
10/5	3970	4254	93	5344	24874	-	-

Appendix 2. cont. Total numbers of *N. americana* collected per sample.

Station	1	2	3	4	5	6	7
10/19/76	-	-	-	-	-	31127	2891
10/25	15325	20832	2481	5435	9126	-	-
11/3	2936	3198	236	2107	8725	-	-
11/4	-	-	-	-	-	8122	7811
11/14	92	3032	2136	1860	5160	3478	8
11/19	351	6364	385	873	2117	63444	620
11/26	57	1652	422	1120	530	-	-
12/6	10220	15480	2520	5871	3433	-	-
1/6/77	8424	12416	4522	1632	3942	-	-
3/4	1126	4870	432	1554	1442	-	-
3/21	2488	1240	101	106	292	1426	1
5/3	4966	2734	14	454	1420	49008	3591
6/2	98248	33044	1840	420	1022	-	-
6/14	152960	374752	3160	4120	11272	67760	9791

VITA

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