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ECOLOGICAL STUDIES ON THE SAND BEACH AMPHIPOD AMPHIPOREIA VIRGINIANA SHOEMAKER, 1933 (CRUSTACEA: HAUSTORIIDAE)

RICHARD PERRY HAGER

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AMPHIPOREIA VIRGINIANA SHOEMAKER, 1933
(CRUSTACEA: HAUSTORIIDAE).

University of New Hampshire, Ph.D., 1977
Zoology

ECOLOGICAL STUDIES ON
THE SAND BEACH AMPHIPOD
AMPHIPOREIA VIRGINIANA SHOEMAKER, 1933
(CRUSTACEA: HAUSTORIIDAE)

by

RICHARD P. HAGER
B.S. Bates College, 1969
M.S. University of New Hampshire, 1971

A THESIS

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In Partial Fullfillment of
The Requirements for the Degree of

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This thesis has been examined and approved.

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Feb. 4, 1977

Date

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THE SAND BEACH AMPHIPOD
AMPHIPOREIA VIRGINIANA SHOEMAKER, 1933
(CRUSTACEA: HAUSTORIIDAE)

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RICHARD P. HAGER

Amphiporeia virginiana inhabits sand beaches from eastern Nova Scotia to northern South Carolina and is the dominant macroinfaunal resident of high energy beaches in northern New England. In southern Maine, the species displayed bivoltine reproduction with an overwintering generation that bred in late spring and a summer generation that bred in the fall. Differences in brood size and maturation rates were apparent between the two generations. Females had faster growth rates and attained larger sizes than males, and the species showed within-habitat aggregations separable by sex and size. The amphipods were found to be unspecialized detritus feeders that maintain only a loose affinity with the substratum by only burrowing superficially, and frequently swimming.

The annual abundance of *A. virginiana* varies from late winter-early spring minimal levels, to late spring-summer maximal levels in response to life history events. More erratic population fluctuations were evident on a high energy beach, where it was found that the abundance of the species could be temporarily reduced by the sedimentary processes that occur during beach deposition or erosion. *Amphiporeia virginiana* was normally distributed over the entire lower foreshore, but aggregated near the mean low water level when avoiding unfavorable conditions higher up the beach. Both in the laboratory and in the field the species proved capable of surviving a wide range of salinity for brief periods, but for time periods longer than 96 hours, the species is stenohaline and requires a salinity range from 25 to 35 ^{o}/oo. A poor tolerance of sediment desiccation appeared to ultimately restrict the distribution of the species within its habitat.

Preliminary analysis of the longshore distribution of *A. virginiana* and its associated fauna along an environmental stress gradient on the Saco Bay shoreline implied that the sand beach community structure is controlled by the amount of wave action and resultant sedimentary dynamics. The number of species in the community was reduced in areas with steep beach slopes and large grain sizes. *Amphiporeia virginiana* was absent from sheltered and stable areas with more complex communities, but was found to be one of the only species that could successfully inhabit the most exposed and unstable areas of the beach.

Amphiporeia virginiana was the dominant macrofaunal species in the tidal plankton over the high energy beach at Ocean Park, Maine. Unlike many intertidal sand-burrowing peracaridean crustaceans that vertically migrate into tidal waters, _A. virginiana_ did not display day-night or lunar periodicity in its swimming behavior. Rather, the species swam during each tidal cycle and accomplished diurnal migrations over the beach foreshore. Laboratory populations of _A. virginiana_ displayed endogenous swimming rhythms in synchrony with the tidal cycle, but the rhythm deteriorates rapidly in the absence of natural stimuli. The pelagic behavior of the amphipods increases potential mating encounters between the sexes that are segregated when burrowed into the sand, and serves as a behavioral mechanism that allows the species to inhabit high energy beaches.

SECTION I

HABITAT DYNAMICS

INTRODUCTION

Ecological studies on sand beaches, although often accompanied with measurements of pertinent physical factors, rarely consider the effects of beach cycles and sedimentary processes on the fauna. The following section provides data on both physical factors and long term beach processes for interpreting population data concerning the amphipod, *Amphiporeia virginiana* and associated sand beach macroinfauna.

A marine sand beach is one of the most dynamic and variable of all landforms. A complex of energy and sedimentary factors result in drastic geomorphic changes, often measurable over short time spans. The need for beach landings during the second World War stimulated intense research on the processes influencing the morphology of beaches and offshore topography. As a result, the ensuing field and wave tank studies developed the concept of a series of beach processes, determined by the net effect of waves arriving at the beach after they were altered by the topography of the surrounding coastal landforms. The classical studies on beach processes are extensively reviewed by King (1972) and Ingle (1966) and the principal concepts are summarized in Bascom (1964) and Shepard (1973).

Seasonal beach cycles of winter erosion and summer accretion were noted for New England beaches by Darling (1964) and Goldsmith et al. (1972). The wave characteristics responsible for beach erosion or accretion were determined by Munk (1949) and the studies of Johnson (1949) and King and Williams (1949) explained the role of subtidal bars in maintaining long term sediment equilibrium during beach cycles.

MATERIALS AND METHODS

STUDY AREAS

The principal study areas were the beaches of Saco Bay, Maine. Additional data were collected at Long Sands Beach, York, Maine (Fig. 1). The shoreline of Saco Bay forms a seven mile arc of sand, interrupted by two estuaries at opposite ends of the arc and a tidal creek in the center (Fig. 2). This area has a diversity of sand habitats ranging from a low energy sandflat environment at Prout's Neck to a high energy barrier beach along the Ocean Park section of Old Orchard Beach. More typical beach profile features, as illustrated in Figure 3, are found in the higher energy environments.

In contrast, Long Sands Beach is a homogeneous sandflat with direct exposure to the Atlantic Ocean (Fig. 4). This beach receives less energy than most beaches in Saco Bay as evidenced by its extensive width, gentle slope, fine grained deposits, and lack of "typical" beach morphology. This partly results from protection provided by Cape Neddick

Fig. 1. Map of southern Maine showing Saco Bay (1) and Long Sands Beach (2).

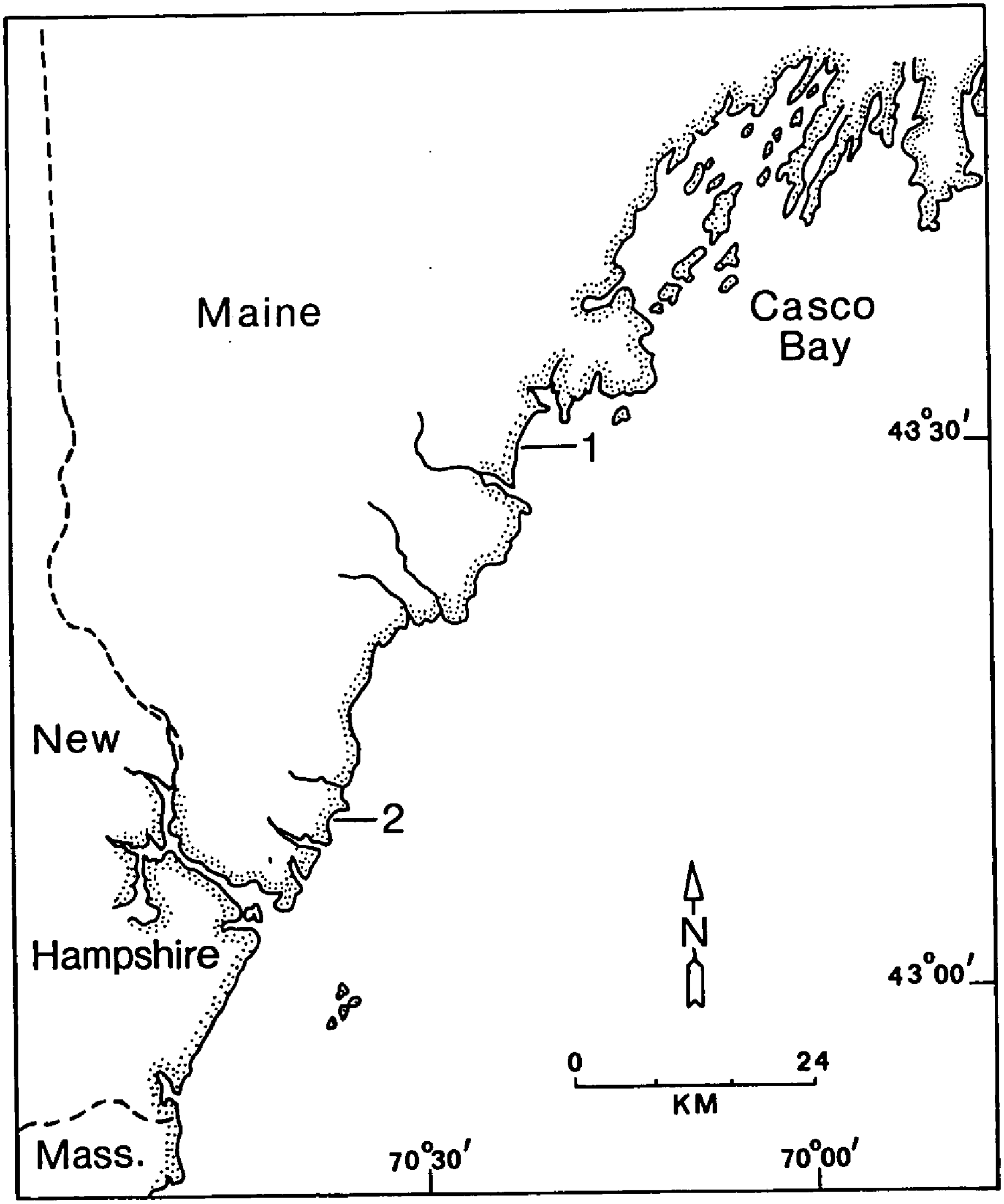

Maine
Casco
Bay
1
43°30′
New
Hampshire
2
N
43°00′
0
24
KM
Mass.
70°30′
70°00′

Fig. 2. Map of Saco Bay showing positions of Ocean Park and Grand Beach transects and the seven longshore stations.

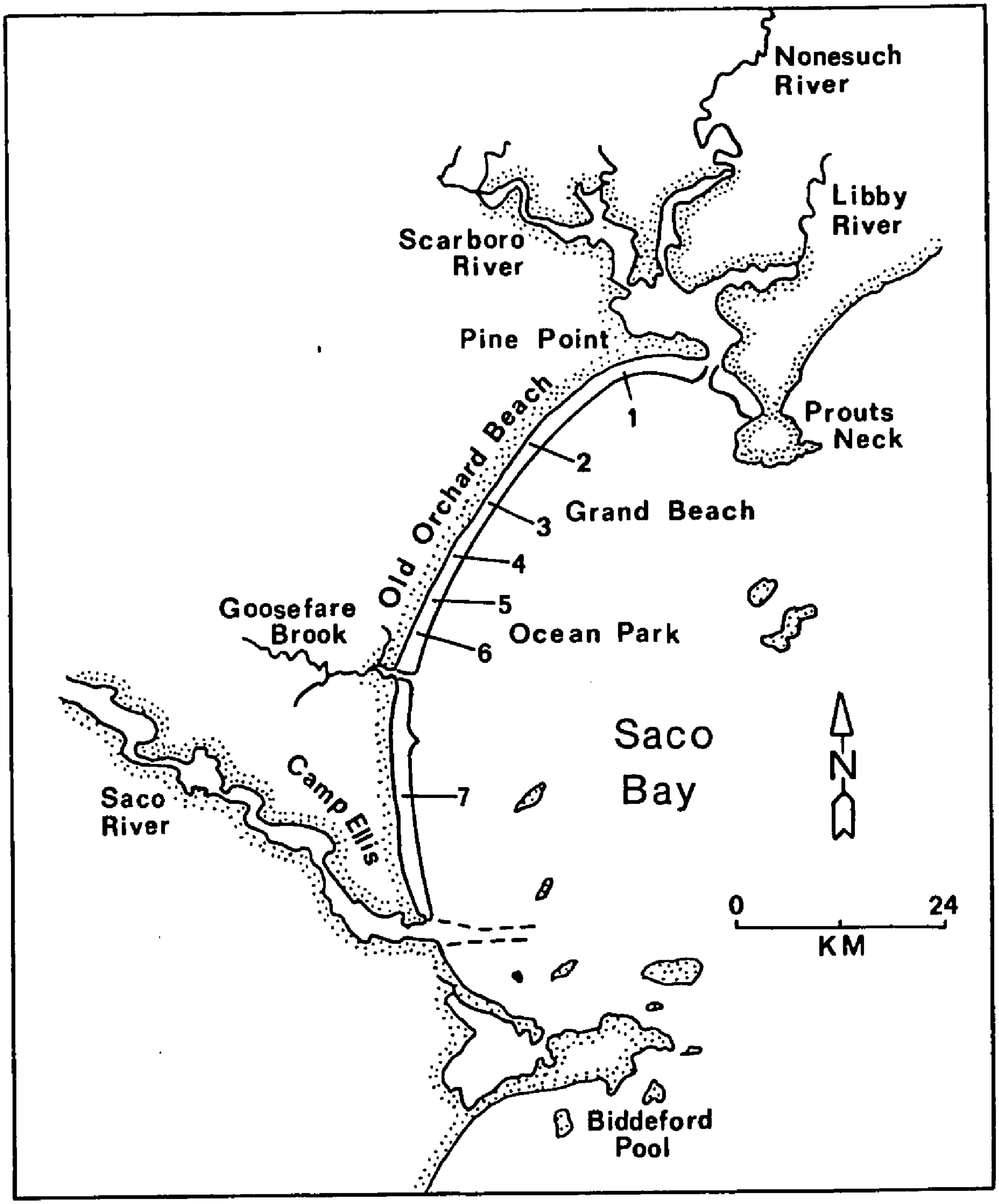

Nonesuch River
Libby River
Scarboro River
Pine Point
Prouts Neck
Old Orchard Beach
1
2
3
Grand Beach
4
5
Goosefare Brook
Ocean Park
6
Saco Bay
N
Camp Ellis
Saco River
7
0
24
KM
Biddeford Pool

Fig. 3. Beach features and descriptive terminology (After Shepard, 1974). Positions of the 4 foreshore stations are indicated by their repective numbers.

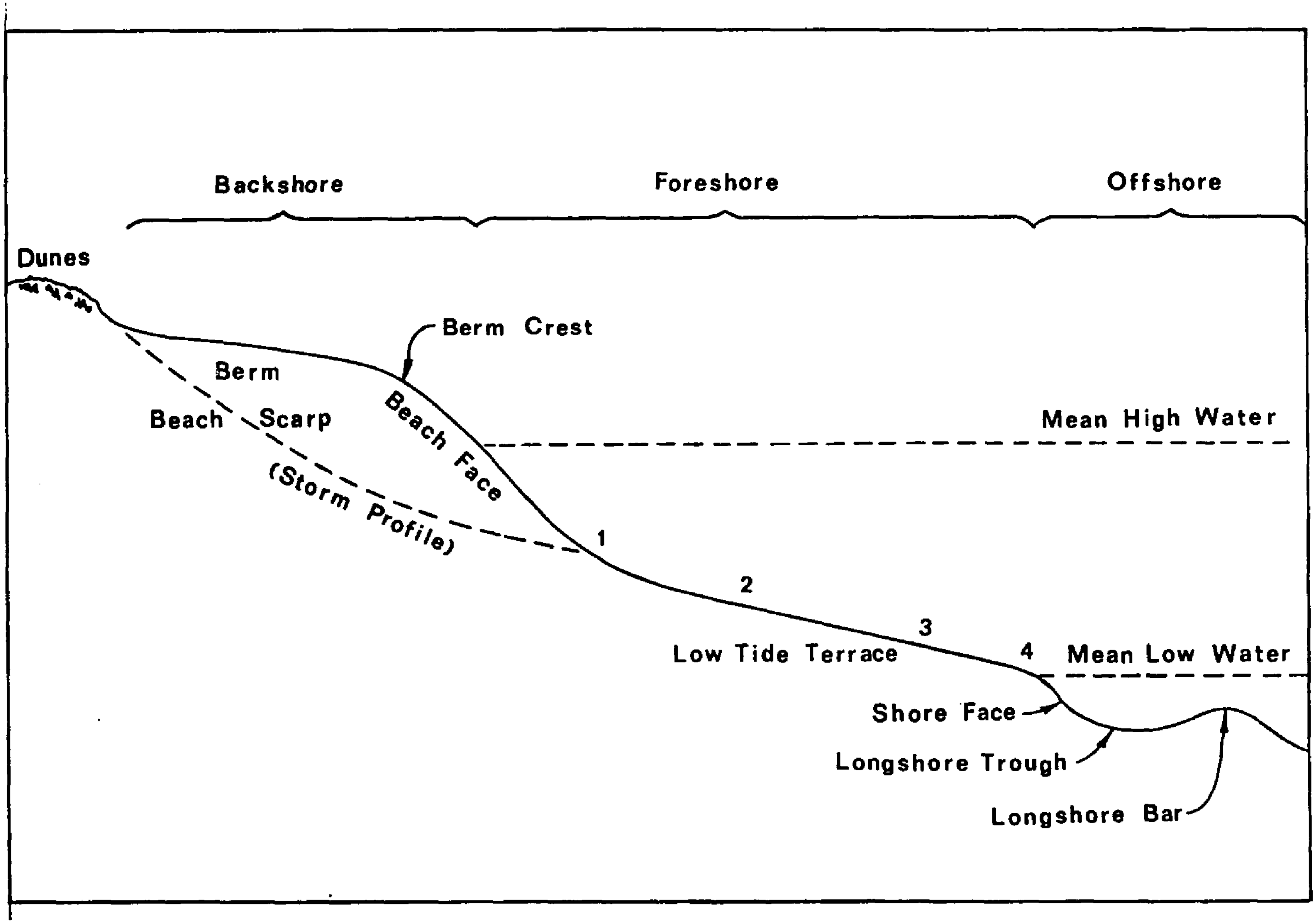
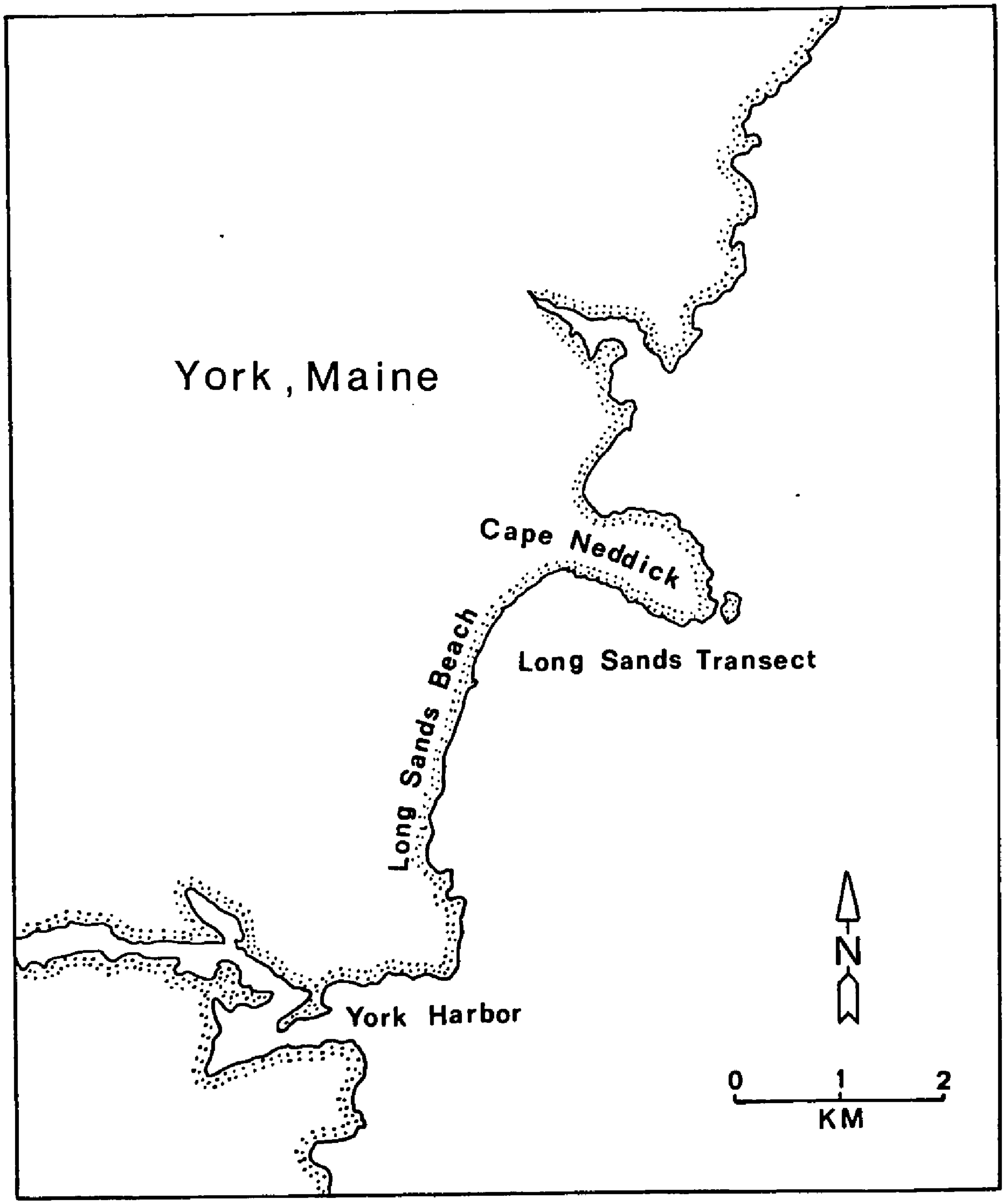

Backshore
Foreshore
Offshore
Dunes
Berm Crest
Berm
Beach Scarp
(Storm Profile)
Beach Face
Mean High Water
1
2
3
4
Low Tide Terrace
Mean Low Water
Shore Face
Longshore Trough
Longshore Bar

Fig. 4. Map of Long Sands Beach showing location of study transect.


York , Maine
Cape Neddick
Long Sands Beach
Long Sands Transect
York Harbor
N
0
1
2
KM

from northeast storm seas.

FIELD STUDIES

Transects were established in the Ocean Park section of Saco Bay, and at Long Sands Beach (Figs. 2 and 4). Data were collected from Ocean Park at monthly intervals from July, 1971 to September, 1972. Since Long Sands is a more stable beach than Ocean Park, data were only collected on four occasions; July and October, 1971, January and May, 1972.

Variations in beach habitats along the shoreline of Saco Bay were investigated by establishing a series of longshore stations where data were collected during March and August, 1972 (Fig. 2). Samples were collected from the mean low water level at each station. At station 3 (Grand Beach) and station 6 (Ocean Park) data from complete transects (four levels of the foreshore) were obtained. Additional data on longshore beach variability in Saco Bay were available from Farrell (1970, 1972) and Croker (unpublished).

Beach profiles were obtained with a hand-held transit and a tidal staff using daily low water predictions as a reference point. The foreshore portion of each transect (the area populated with macroinfauna) was divided into four relatively equal zones; measurements and sand samples were taken at a station established within each zone. The relative positions of the stations are given in Figure 3 and can be considered as: station 1, upper foreshore, just seaward of beach face; station 2, upper middle section of low tide terrace; station 3, lower foreshore, near low water neap; station 4, mean low water or slightly below. At Long Sands Beach a fifth station was established to more adequately sample its extensive width.

At each station, surface (upper 5 cm) sediment samples and interstitial water samples were collected. The temperatures of the air, sediment surface, and sediments at a 5 cm depth were measured with a Yellow Springs telethermometer equipped with appropriate thermistors. Surf temperatures and salinities were also measured from samples collected in water 0.5 m deep. Interstitial water samples were collected with a specially adapted syringe, and salinities were determined either by silver nitrate titration or with an American Optical Co. refractometer.

Daily fluctuations in temperature, salinity, and water content of the Ocean Park foreshore sediments were measured during January and August, 1972, and March and November, 1973. At each station on the transect the temperature of the air, sediment surface, and sediments at a 5 cm depth were recorded every hour throughout one 12 hour tidal cycle. Interstitial water samples were collected at hourly intervals. Water content of sediments was calculated through weight loss measurements of sediment samples.

SEDIMENTARY PARAMETERS

The mean grain size, sorting coefficient, skewness, and coarse sand components were calculated for each foreshore sediment sample as outlined by Krumbein (1939), Inman (1952), and Morgans (1956). After air drying each sample, two subsamples of approximately 3 gm each were taken and separated with an Emory settling tube (Emory, 1938). The use of settling tubes for exact size determination is somewhat controversial (Gibbs, 1972), but in this study the relative differences between sand grain categories was most important, and therefore the less precise method was chosen to permit analysis of more samples. A mean cumulative frequency distribution for each sample was calculated and the resultant cumulative frequency curve was plotted on normal probability paper. The various parameters were calculated using the graphic methods of Folk (1968). Sediment data are based on analyses of 160 samples.

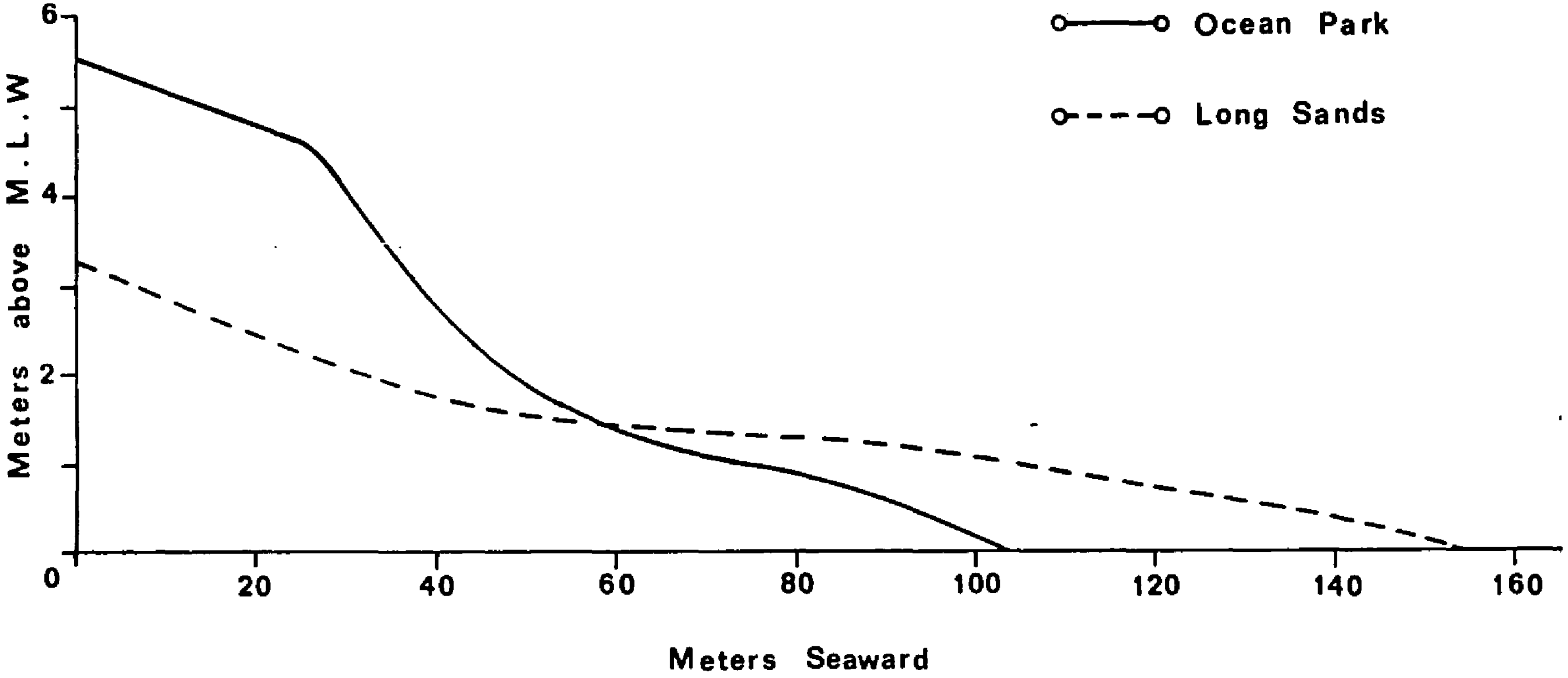
RESULTS

BEACH MORPHOLOGY

Profiles of the two transects show marked differences in beach morphology (Fig. 5). Ocean Park has a steep overall slope of 1 in 23 and a profile with a pronounced morphology. In contrast, Long Sands has a gentle slope, 1 in 55, and its flat profile does not display a berm or other features characteristic of high energy beaches.

Since preliminary observations indicated that the Ocean Park transect undergoes drastic and rapid changes in morphology from sediment movement, this site was selected for study of beach cycles. Beach profiles for 12 consecutive

Fig. 5. Summer profiles of the Ocean Park (July 25, 1971) and Long Sands (July 26, 1971) transects.


Ocean Park
Long Sands
Meters above M.L.W
6
4
2
0
20
40
60
80
100
120
140
160
Meters Seaward

months are shown in Figure 6 and demonstrate the classical progression in beach dynamics. The summer (non-storm) beach is characterized by a steep beach face, a very obvious berm crest, and a flattened, well-pronounced berm. The winter (storm) beach shows the results of berm erosion. The berm crest is no longer evident, and instead there is a continuous slope from the dunes to the low tide terrace. The fall and spring profiles are less stable than the winter and summer profiles, showing intermediate stages. In general, the fall profiles reveal a net erosion of the berm, while the spring profiles indicate net deposition or buildup of the berm.

Intertidal profiles do not illustrate the important beach features of subtidal, longshore bars. Observations of subtidal bars were noted at Ocean Park to assist in the interpretation of the grain size data. Bars were most frequently noted during winter, particularly following periods of heavy surf action. After formation, the bar was observed to slowly drift landward and to the north. Within four or five weeks of the subtidal formation of a bar, it had migrated across the low tide terrace and joined with the beach face.

This beach cycle of erosion and subsequent deposition through return of sediments by migrating foreshore bars is typically seasonal, but can be observed occurring over shorter time periods associated with storm activity. The erosional actions of storm waves and the subsequent initiation of sediment return is evident in Figure 7. A severe

Fig. 6. Beach profiles of the Ocean Park, Maine transect during 1971-72. (vertical scale exaggerated)

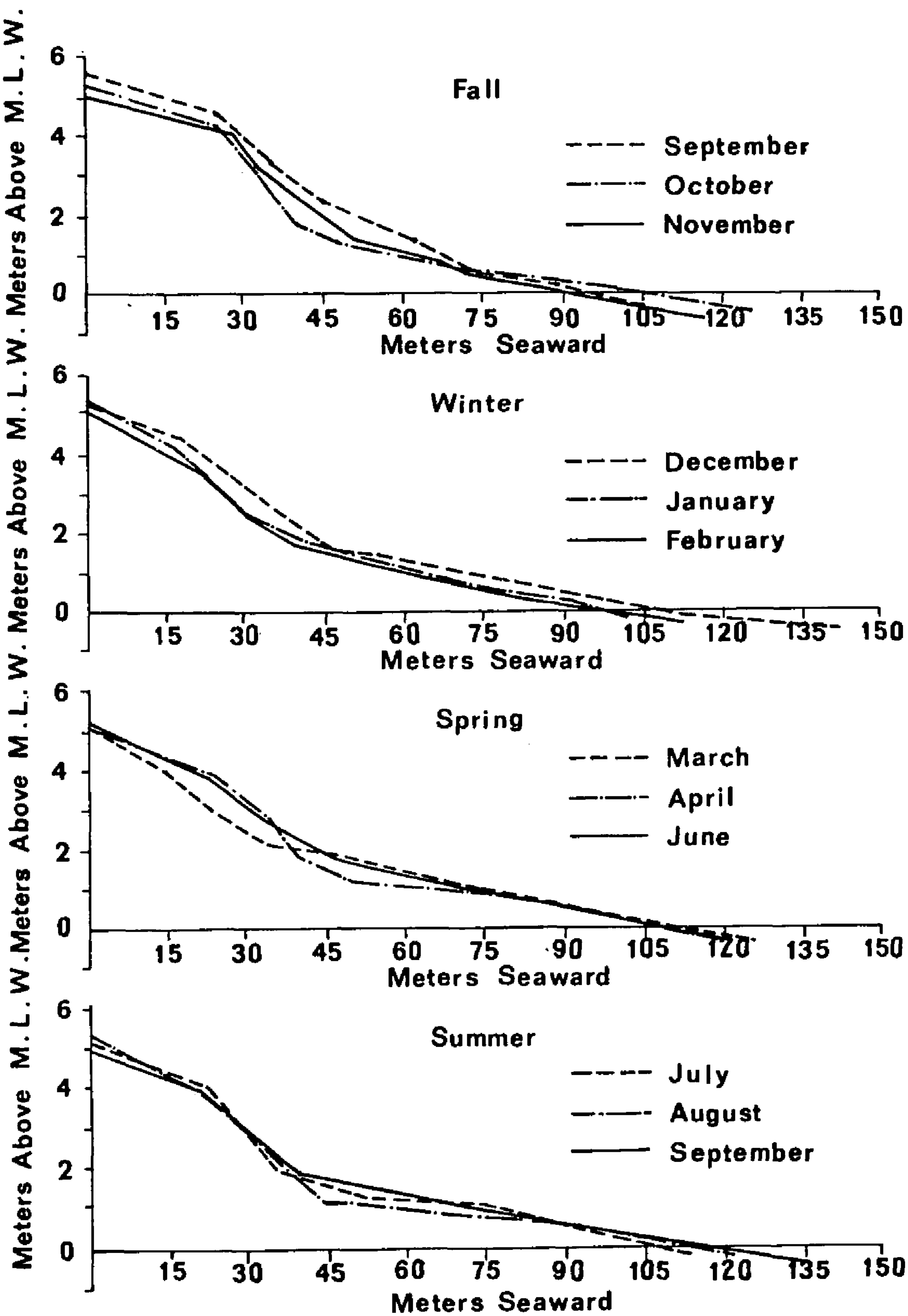
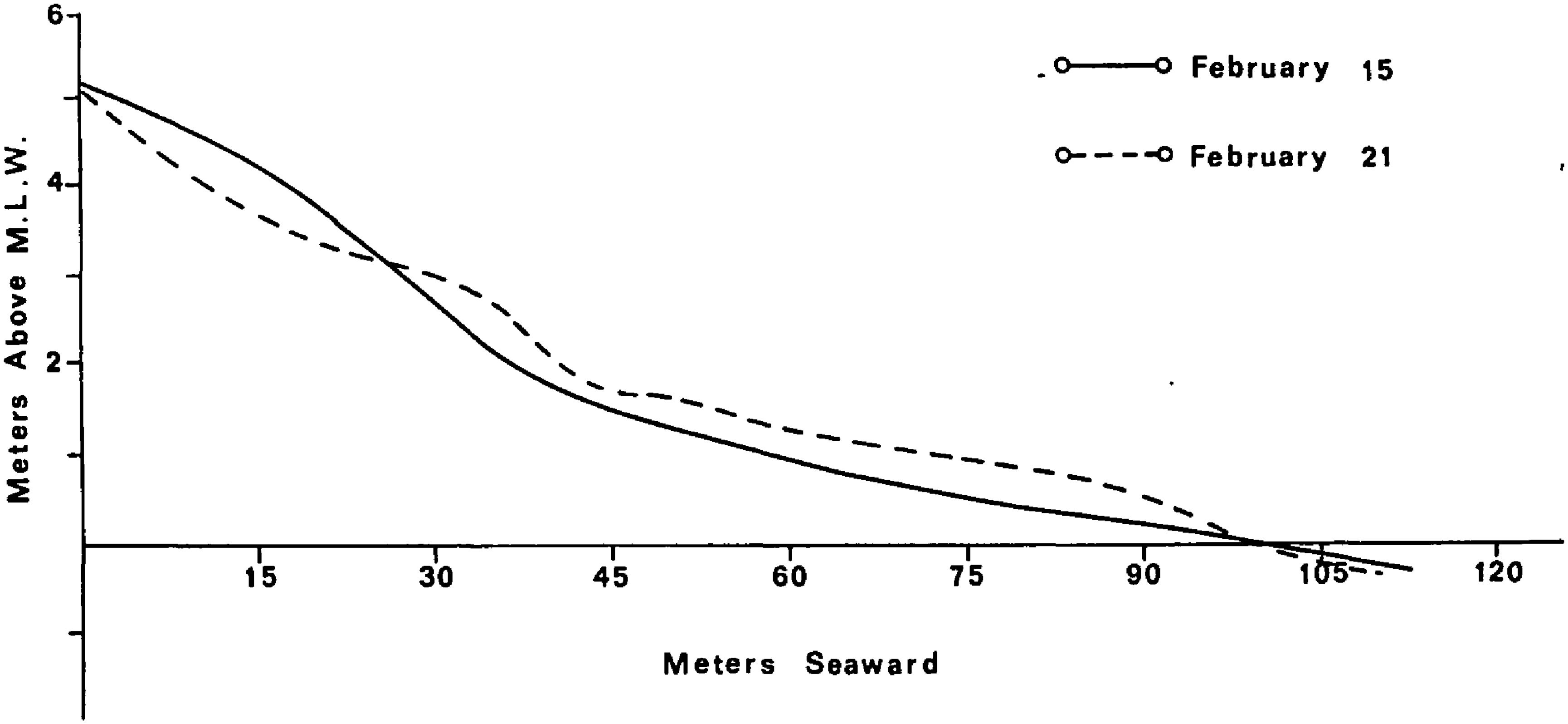

Fall
---- September
—·— October
—— November
Meters Above M.L.W.
6
4
2
0
15 30 45 60 75 90 105 120 135 150
Meters Seaward
Winter
---- December
—·— January
—— February
Meters Above M.L.W.
6
4
2
0
15 30 45 60 75 90 105 120 135 150
Meters Seaward
Spring
---- March
—·— April
—— June
Meters Above M.L.W.
6
4
2
0
15 30 45 60 75 90 105 120 135 150
Meters Seaward
Summer
---- July
—·— August
—— September
Meters Above M.L.W.
6
4
2
0
15 30 45 60 75 90 105 120 135 150
Meters Seaward

Fig. 7. Pre-storm (Feb. 15, 1972) and post-storm (Feb. 21, 1972) profiles of the Ocean Park transect. The post-storm profile demonstrates severe erosion of the berm and sediment deposition in the foreshore.



February 15
February 21
Meters Above M.L.W.
6
4
2
Meters Seaward
15
30
45
60
75
90
105
120

winter storm struck the southern Maine coast on February 19, 1972. The U. S. Coast Guard at Portland Light Ship reported winds of 90 M.P.H. and seas 5 feet above predictions with surf in excess of 15 feet. Figure 7 compares the pre-storm beach condition (Feb. 15, 1972) with the post-storm condition (Feb. 21, 1972). Although the beach was in a winter profile, the storm further eroded the sediments from the berm and deposited them in the sublittoral region. The foreshore area in the Feb. 21 profile is occupied by a landward migrating sand bar. The slow migration of this bar ultimately resulted in the extreme accretion of the berm between the March and April profiles (Fig. 6).

The erosional effect of storms on sand beaches has long been noted through post-storm qualitative studies (Brown, 1939, Nichols and Marston, 1939), but rarely studied with the aid of before and after quantitative data. Following the destructive effect of storms, restoration to a pre-storm condition is generally accomplished within a relatively short time span (Blumenstock et al., 1961). Ziegler et al. (1959) noted that restoration of beaches following storms may begin so rapidly that the true extent of severe erosion often escapes measurement. Storms may not always be destructive to a beach, e.g. High (1969) presented evidence that in some geographic areas severe storms serve as a depositional agent in sedimentary processes.

The Ocean Park post-storm profile, measured within two tidal cycles of the storm, indicates a fast restorative process. The April profile, two months after the storm, shows a complete restoration to a summer (non-storm) profile. Data compiled over a five year period at Saco Bay beaches indicated that despite periodic severe winter storm erosion, there was no net landward retreat occurring (Farrell, 1972).

FORESHORE SEDIMENTS

Disruption of sediments by wave action initiates sediment movement (Kolman, 1973, Schiffman, 1965). With the exception of storm waves, wave action largely disturbs only the upper few centimeters of the sedimentary surface (King, 1951). Since this surface sediment layer is the most transitory and often contains large numbers of animals, the characteristics of the surface sediments of the foreshore were examined.

The Ocean Park foreshore was composed of medium to coarse sand (size range: 2.27-0.73 ϕ), generally moderately well-sorted (sorting coefficient range: 0.85-0.34 ϕ). The flat Long Sands Beach was composed of well-sorted fine sand with a mean grain size range of 2.47-2.07 ϕ and a sorting coefficient range of 0.48-0.33 ϕ. Trends occurring in the foreshore sediments in relation to beach processes are illustrated by considering the Ocean Park data.

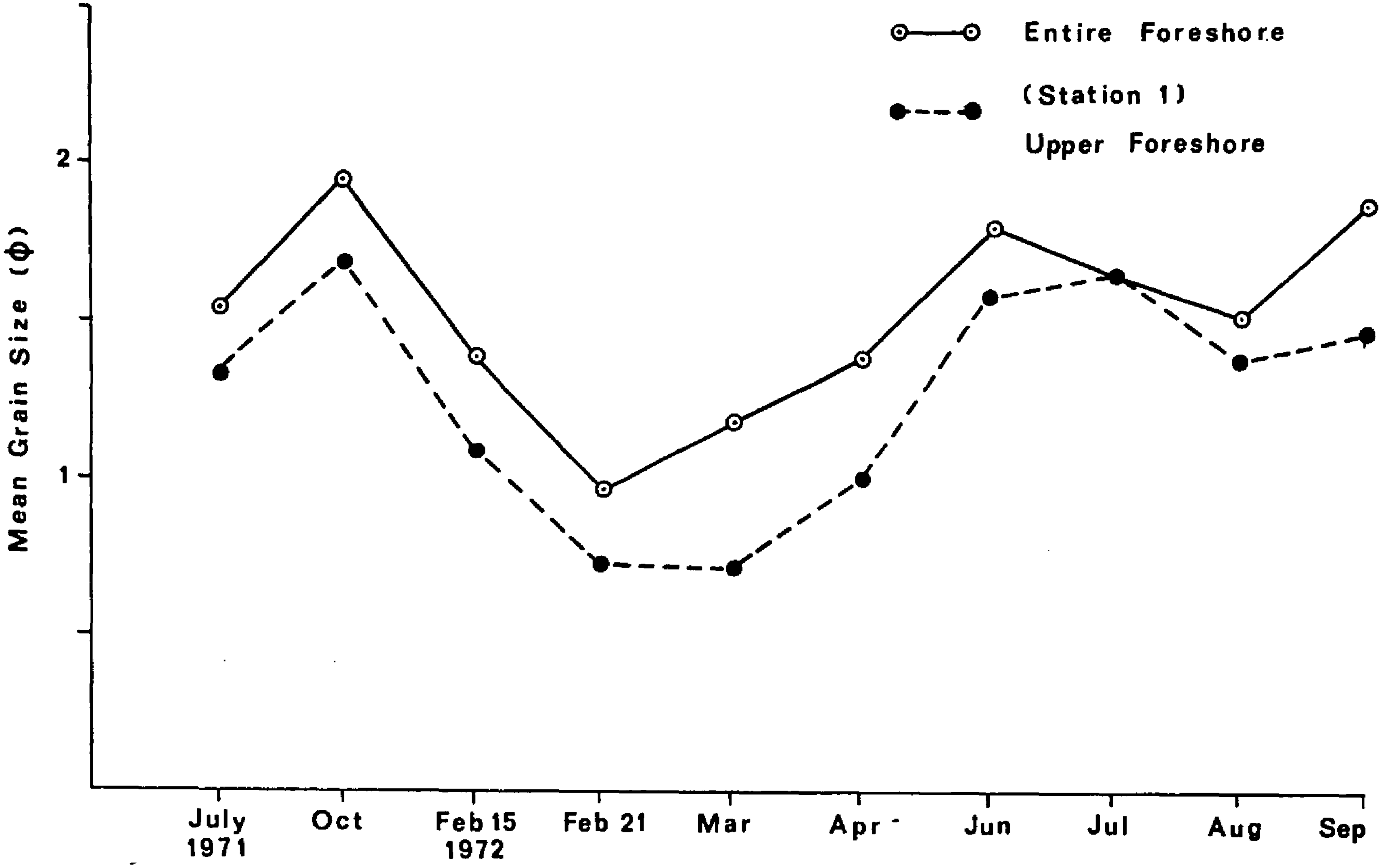
The foreshore sediments typically display an increase in mean grain size and an increase in the percentage of the coarse sand category from the low water mark toward the backshore. Similar grain size distributions were reported by

Bascom (1951) and Miller and Ziegler (1958). A seasonal pattern is also evident (Fig. 8) with coarser sediments present following periods of winter storm erosion. The effects of storm on the sediment texture was apparent, i.e. the percentage of coarse sand on the foreshore increased from 29.3% to 50.4% following the storm of February 19, 1972.

The migratory return of berm sediments across the foreshore can be followed by examining the mean grain size of the foreshore sediments. Sonu (1972) demonstrated that beaches in the southeastern U. S. have fine grained foreshore deposits, but preceding periods of accretion, the foreshore sediments take on a bimodal size frequency distribution, the coarse mode reflecting the migratory sediments soon to build the berm. Ocean Park had a negligible fine grain component, and no evidence of bimodality preceded periods of accretion. However, preceding berm deposition, foreshore sediments had an increase in mean grain size, apparently analogous with the appearance of bimodal distributions found by Sonu.

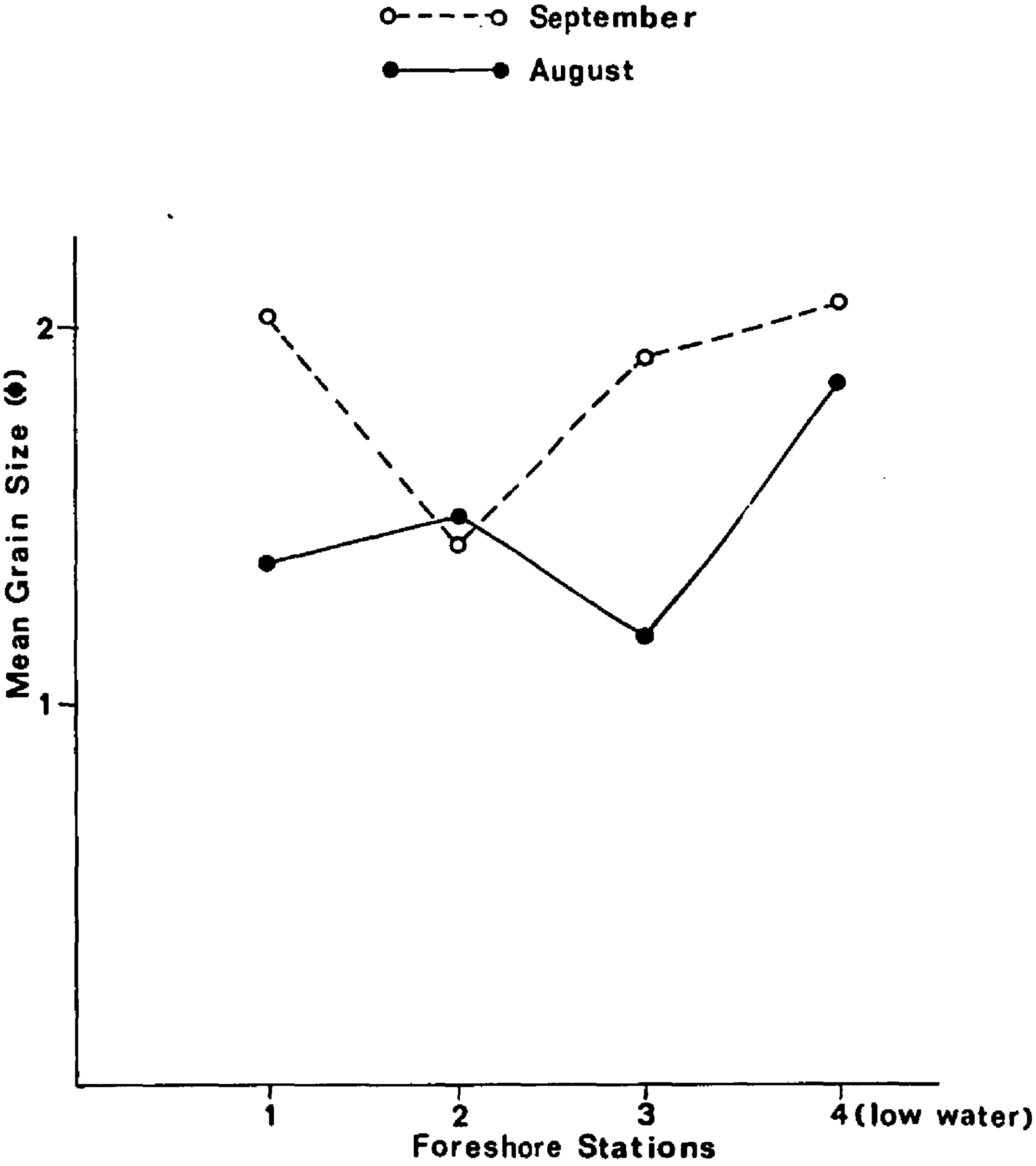
The observed bars are also apparent in the grain size data. When a sand bar was migrating landward, the data deviated from the normal pattern of a continuous seaward decrease in mean particle size and percentage of coarse sand. Figure 9 illustrates the presence of a bar and traces its landward movement. The August profile of grain size distribution shows coarser sediments in zone 3, where a sand bar was located. The September profile shows that the sand bar had moved landward to zone 2, with a resultant increase in

Fig. 8. Temporal trends in grain size of foreshore sediments at Ocean Park, 1971-72. Upper foreshore sediments (Station 1) are consistently coarser than mean grain size of entire foreshore.



Entire Foreshore
(Station 1)
Upper Foreshore
Mean Grain Size (ϕ)
2
1
July
1971
Oct
Feb 15
1972
Feb 21
Mar
Apr
Jun
Jul
Aug
Sep

Fig. 9. Spatial trends of foreshore sediment mean grain sizes at Ocean Park, August 27 and September 24, 1972. The landward shift of the coarsest sediments from Station 3 (Aug.) to Station 2 (Sept.) corresponds to the movement of a migrating sand bar.


○- - - -○ September
●——● August
Mean Grain Size (ϕ)
2
1
1
2
3
4 (low water)
Foreshore Stations

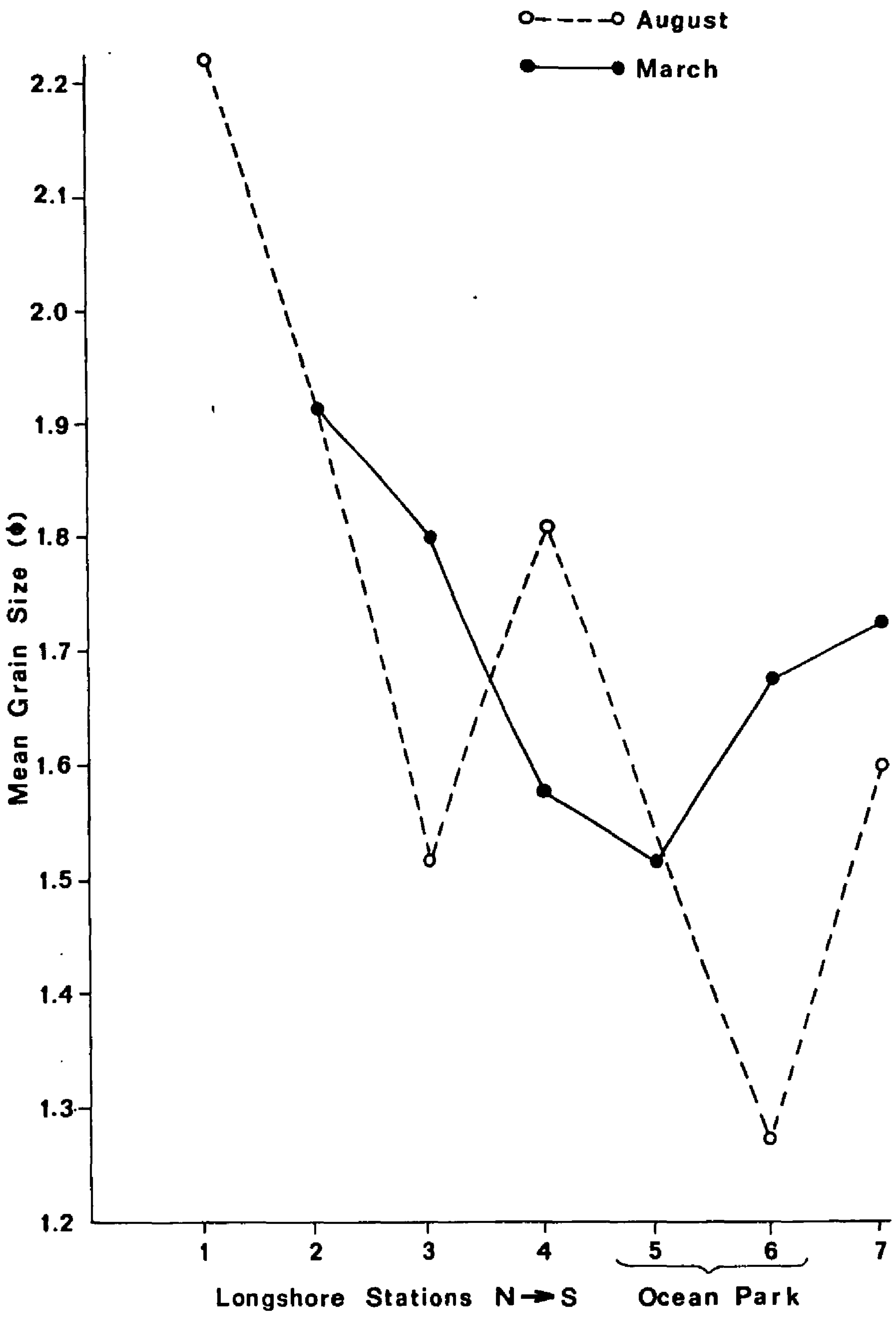
mean grain size at that station.

LONGSHORE SEDIMENT TRENDS

The seven mile long shore of Saco Bay displays a variety of beach types along its arc. To the north of the Grand Beach transect (slope 1 in 31) the beach becomes increasingly flat and wide (Pine Point beach slope 1 in 37, Prout's Neck beach slope 1 in 64) (Fig. 2). To the south, the beach becomes increasingly narrow and steep, attaining its steepest profile along the Ocean Park section, with slopes as steep as 1 in 17. Sediment samples were collected from just above mean low water (0.0-0.3 meters above mean low water) in March and August, 1972 at the 7 longshore stations illustrated in Figure 2.

The mean grain size of Saco Bay beach sediments was coarsest in the Ocean Park section and became progressively finer in both the northerly and southerly directions (Fig. 10). Farrell (1970, 1972) reported a similar longshore grain size distribution for Saco Bay, and with the aid of aerial photographs and wave refraction diagrams, made predictions on wave energy dissipation along the Saco Bay shores for various wave types and angles of attack. Under most non-storm sea conditions observed in Saco Bay, refraction patterns imply energy is greatest at Ocean Park and progressively diminishes to the north and south. This theoretical pattern of energy dissipation is supported by the observed patterns

Fig. 10. Longshore distribution of mean sediment sizes near mean low water at Saco Bay, March 20 and August 27, 1972.



August
March
Mean Grain Size (Φ)
2.2
2.1
2.0
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1
2
3
4
5
6
7
Longshore Stations N → S
Ocean Park

of sediment distribution and beach morphology along the shore of Saco Bay.

The works of Einstein (1948), Johnson (1956), Tanner (1958), Cherry (1966), Goldsmith and Colonell (1970), and Inman and Brush (1973) provided explanations of the various processes influencing longshore sediment distributions and morphological variations along continuous beach shorelines. However, the work of Sonu (1973) presents theoretical interrelationships between various beach processes, emphasizing the potential for error in interpretations of longshore data.

TEMPERATURE STUDIES

Temperature measurements made at the Ocean Park transect during 1971-1972 indicate potential thermal stress for animals living within the upper layers of intertidal sands. The intertidal sand beach assumes the temperature and salinity characteristics of adjacent coastal waters during high tide, but during exposure at low tide, conditions are modified by prevailing weather. Areas landward of the foreshore, i.e. the upper beach face and berm, may be virtually uninhabitable to marine life, due to a combination of complete drainage during each tidal cycle and the resultant temperature fluctuation of the dry sand. The berm may be frozen for periods of weeks in the winter, and during summer was found to undergo temperature fluctuations of 30°C within a few hours, reaching maximum temperatures in excess of 45°C. The low tide terrace retains some water throughout the tidal cycle, and presents a temperature range suitable to sand macroinfauna. The temperature data, (Figs. 11-14) are based on recordings taken at the foreshore transect stations at Ocean Park.

The monthly recordings of surf temperature at Ocean Park (Fig. 11) are indicative of temperatures on the beach when submerged. However, microhabitat temperature fluctuations of exposed beach sediments present limiting factors to the fauna. Monthly measurements of the temperature of the air 15 cm above the sediment surface, the sediment surface, and sediments at a 5 cm depth were recorded for each foreshore transect station at the time of low water. Only contrasting winter and summer data will be considered here to illustrate the extreme conditions possible.

The temperature profiles (Fig. 12) are typical of beach conditions in winter and summer. The July profile shows a typical warm weather trend with sediments reaching temperatures intermediate between the cooler water and the warmer air. The landward stations are slightly warmer than seaward stations, and deeper sediment layers remain cooler than surface sediments. The March profile is typical of winter days with direct sunlight. Under these conditions the sediments absorb the heat of insolation and may rise considerably above air and sea temperature. A more typical winter stratification is produced on cold overcast days when the sediments are close to the freezing point. In this instance, the landward stations in the foreshore occasionally

Fig. 11. Monthly low tide water temperature at Ocean Park, 1971-72.

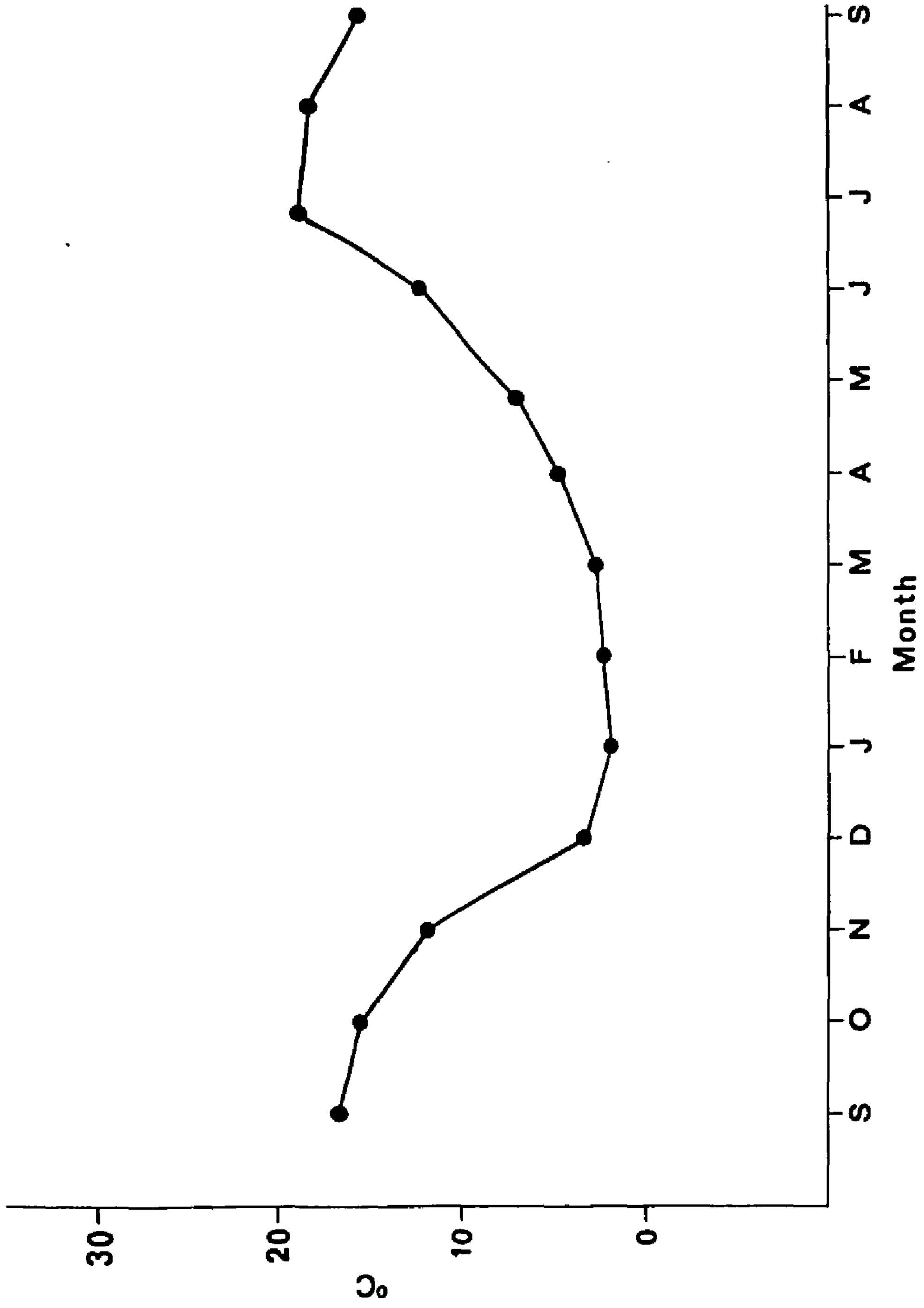
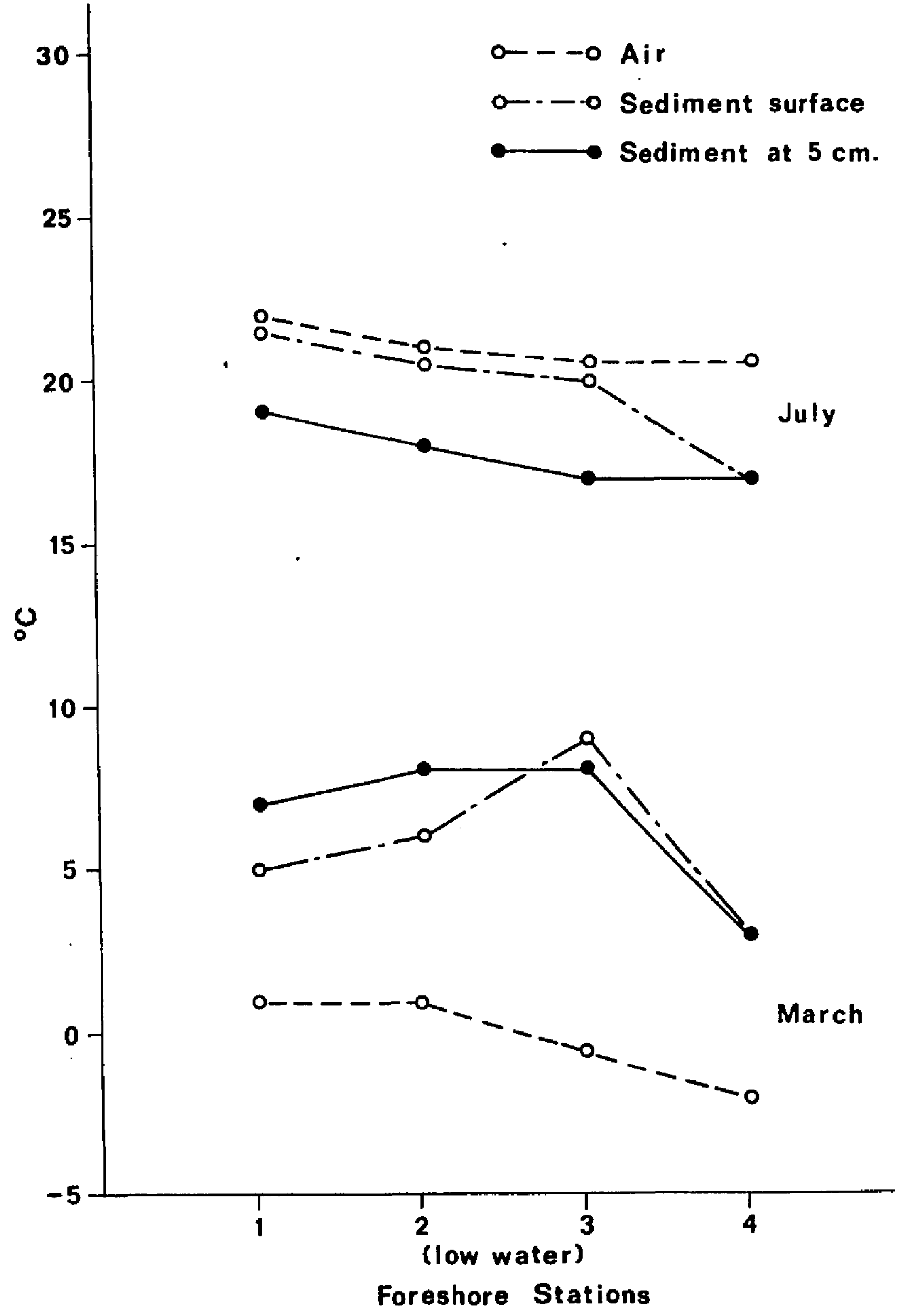

°C
30
20
10
0
S
O
N
D
J
F
M
A
M
J
J
A
S
Month

Fig. 12. Temperature profile of Ocean Park foreshore stations on July 25, 1971 (surf temp. = 15°C) and March 20, 1972 (surf temp. = 3°C).


Air
Sediment surface
Sediment at 5 cm.
30
25
20
15
°C
10
5
0
-5
July
March
1
2
3
4
(low water)
Foreshore Stations

freeze while exposed, but seaward stations generally remain above freezing due to the effects of brief exposure time, poor drainage, and proximity to seawater.

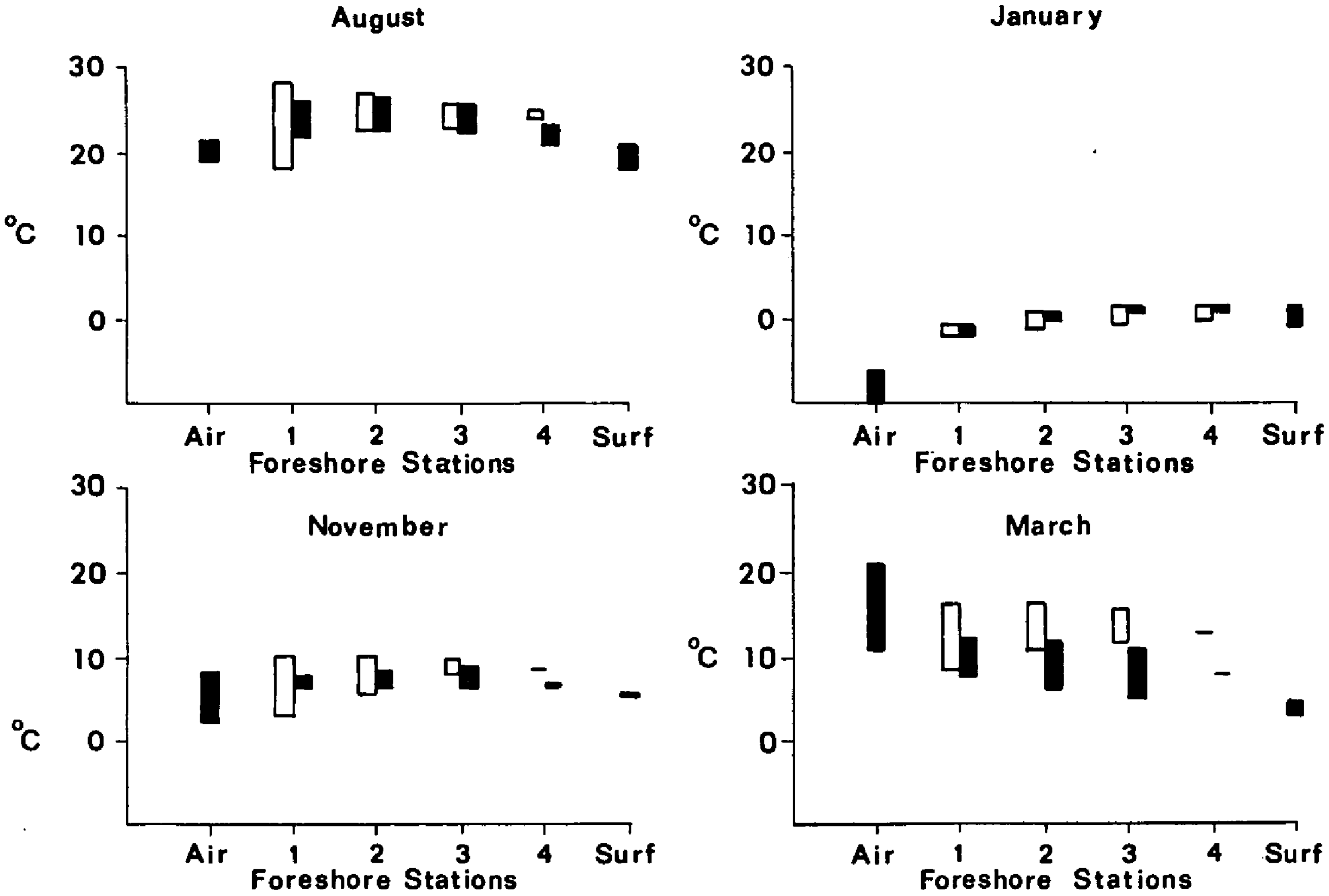
Daily temperature fluctuations of various portions of the foreshore were studied during each season by recording temperatures at exposed stations hourly over one twelve hour tidal cycle. The temperature ranges of sediments exposed to air during low tide are presented in Fig. 13. The seaward stations experience the smallest temperature range and remain closer to seawater temperature during one to two hours of exposure. The landward stations show greater variability, often in excess of $10^{o}C$ during approximately 7 hours of exposure. The sediments at a 5 cm depth have a much smaller temperature range than surface sediments, and remain closer to seawater temperatures.

The rate of temperature change within intertidal sand is also important. Field estimates of rate of temperature change can be obtained from tidal cycle temperature data (Fig. 14). These data, collected on a warm day with air temperatures of $22^{o}C$, show that sand can be heated at rates as rapidly as 6.5 C^{o} in 15 minutes. Since many summer days are warmer than $22^{o}C$, more rapid heating rates are undoubtably common.

INTERSTITIAL WATER

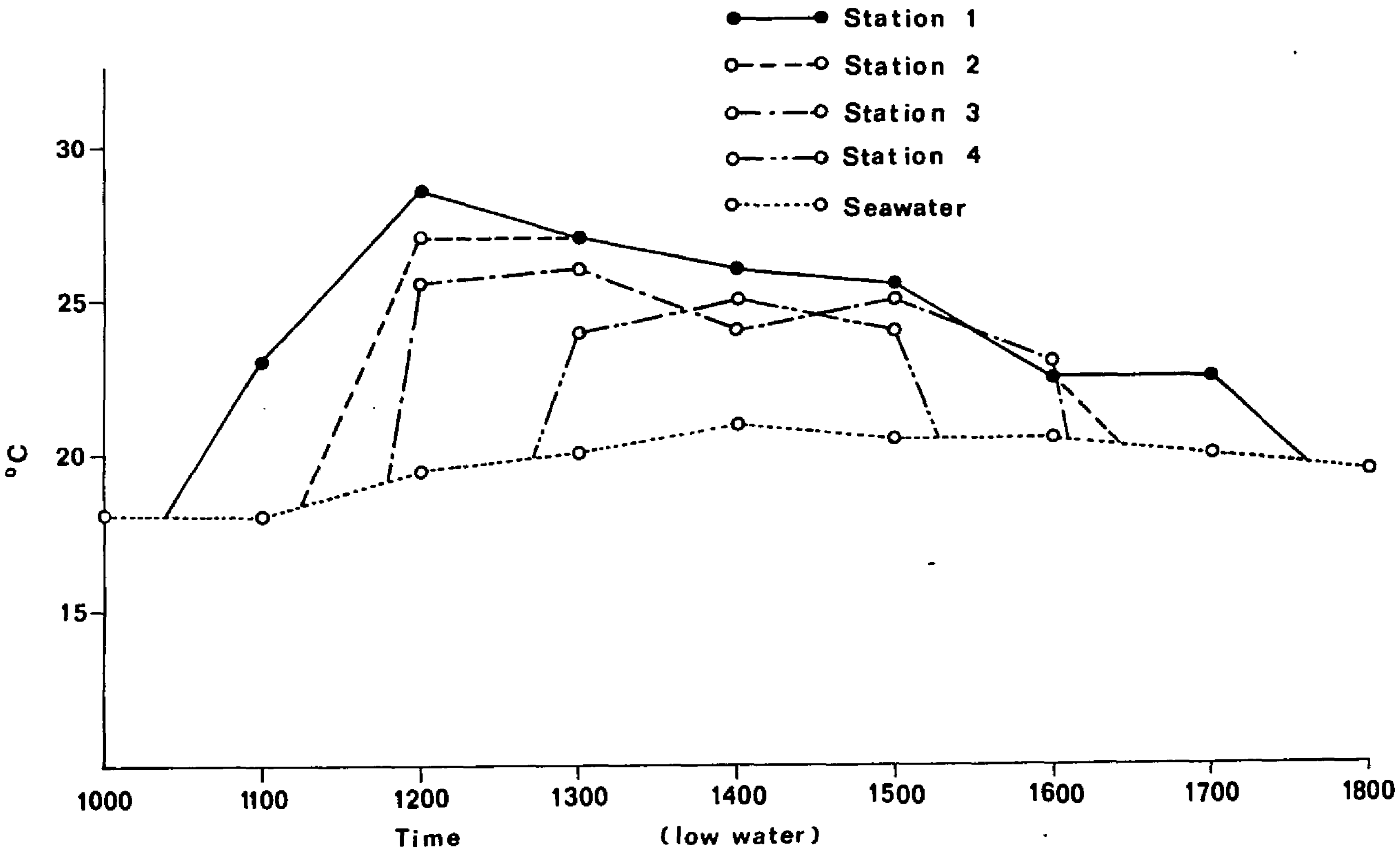
The water content of the foreshore sediments at Ocean Park varied from 10 to 30% by weight loss determinations. The average water content of the sand was approximately

Fig. 13. Temperature ranges at Ocean Park foreshore stations during tidal cycles on August 5 and January 26, 1972; November 19 and March 13, 1973.



Shaded Bar = Sediment 5 cm. Unshaded Bar = Sediment Surface

Fig. 14. Ocean Park foreshore temperature fluctuations during a summer tidal cycle on August 5, 1972.


Station 1
Station 2
Station 3
Station 4
Seawater
30
25
20
15
°C
1000
1100
1200
1300
1400
1500
1600
1700
1800
Time
(low water)

20%. The data collected display no discernible trends in water content, but this property appears to be related to drainage patterns and sediment characteristics of the beach, factors undergoing daily changes. Time of exposure is important, since upper foreshore sediments lost from 30 to 50% of their interstitial water during a tidal cycle, while lower foreshore sediments lost less than 10%.

The studies of Kindle (1936), Trefethen (1941), Emery (1945), and Chapman (1949) considering the various aspects of thixotrophic and dilitant sands, especially the entrapment of air and water in the interstices between sand grains, and studies by Emery (1948) and Isaacs and Bacon (1949) on water table fluctuations beneath sand beaches, shed little light on the interrelations involved in beach drainage patterns. The factors explaining available interstitial water in surface sediments are complex, undoubtably including relationships between grain size, pore space, packing criteria, water table fluctuations, and temperature.

The salinity of interstitial water in beach sediments underwent daily fluctuations similar to temperature and water content. Mean annual surf salinity at Ocean Park was 29.3 ^{o}/oo (range 27.5 to 31.0 ^{o}/oo). Salinity measurements of interstitial water samples from the upper 5 cm of sand at each station, drawn at the time of low water, indicate that the interstitial water becomes slightly more saline (up to 3 ^{o}/oo) than the adjacent seawater. This results from evaporation, with upper foreshore stations generally more saline than stations with less exposure.

Reid (1930, 1932) illustrated the limited exchange between marine sands and overlying fresh water. Salinity measurements of Ocean Park foreshore sediments recorded during periods of heavy rainfall also indicated that the rain does not percolate extensively into the sediment. However, interstitial water in surface sediments during a rain storm on May 15, 1972 showed a lowered salinity range of 24.2-27.3 ^{o}/oo), when compared to a clear day (surf salinity 29.0 ^{o}/oo) with a range of 29.2-33.0 ^{o}/oo. Such temporary dilutions could affect more stenohaline species.

DISCUSSION

The abundance of sand beach meiofaunal populations is known to be under the control of available pore space (Jansson, 1967a) and sediment sorting (Hulings and Gray, 1976). No comparable set of habitat features can explain the abundance of intertidal sand macroinfauna. The importance of temperature and salinity fluctuations was noted (Johnson, 1965, 1967), as has sediment oxygen content (Gordon, 1960; Brafield, 1964). Other workers have noted such factors as mean grain size, organic content of sediments, or tidal cycles and currents (Meadows and Campbell, 1972).

On high energy beaches, profiles and sediment texture are constantly changing through seasonal and storm related cycles. Cyclical habitat changes have been recorded over time spans as brief as a few minutes (Ziegler and Tuttle, 1961; Farrell, 1972). Infaunal populations on high energy beaches require behavioral mechanisms to survive the rapid sedimentary changes during beach cycles, a factor less important to populations on beaches with stable profiles. The frequency and extent of sedimentary cycles, therefore, becomes a principal limiting factor to populations of sand beach macroinfauna.

SECTION II

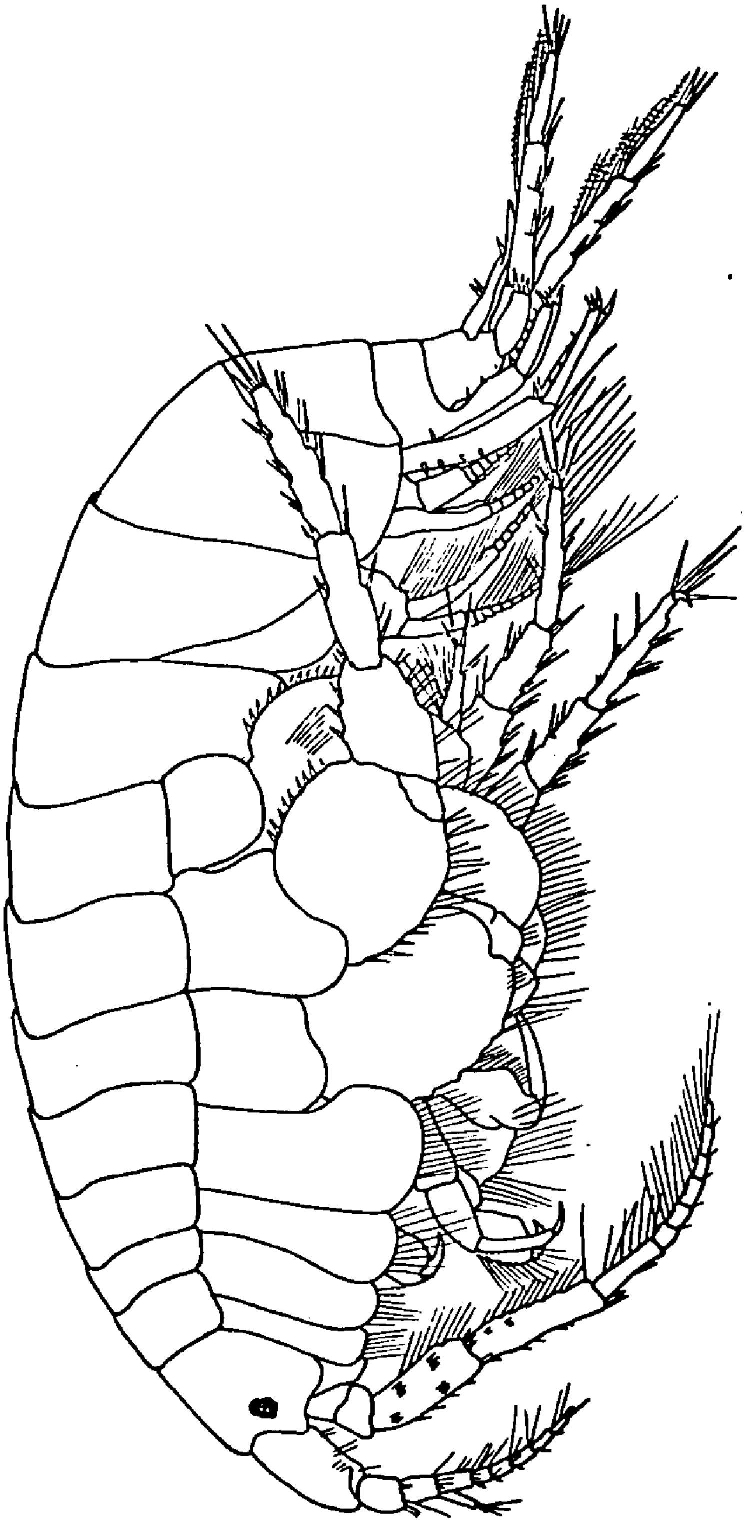
LIFE HISTORY AND GENERAL BIOLOGY

INTRODUCTION

Haustoriid amphipods are common inhabitants of intertidal sands along the western North Atlantic coast, and are frequently the dominant component of the sand beach macroinfauna (Croker et al., 1975). Despite the abundance and wide geographic occurrence of haustoriids, the life histories and general biology of many species is not known. The work of Croker (1967a, 1967b), Dexter (1967, 1971), and Sameoto (1969a, 1969b) provides detailed studies on the life histories and biology of several haustoriid amphipod species in the western North Atlantic beyond the general outlines provided by Bousfield (1965, 1973).

The genus *Amphiporeia* was erected by Shoemaker (1929) and *A*. *virginiana* (Fig. 15), the most common of the three known species in the genus, was described by Shoemaker in 1933. *Amphiporeia* *virginiana* is endemic to the western North Atlantic (Bousfield, 1970), with a geographic range from eastern Nova Scotia (Bousfield and Laubitz, 1972) to northern South Carolina (Dexter, 1967). The species is the dominant inhabitant of high energy sand beaches over most of its geographical range. Until now the life history of *A* *virginiana* was unknown, although ecological data on the species were

Fig. 15. *Amphiporeia virginiana* X 40 (drawing by R. A. Croker).



Amphiporeia virginiana Shoemaker

provided by Dexter (1967), Lemire (1968), Croker (1970), Gnewuch and Croker (1973), and Croker et al. (1975). The present study concerns the life history and general biology of A. virginiana based on studies in southern Maine during 1970-74.

MATERIALS AND METHODS

Specimens were collected from Ocean Park and Long Sands beaches in southern Maine (Figs. 2 and 4). Collections were taken from Ocean Park at monthly intervals from July, 1971 to September, 1972. Long Sands was sampled during four seasons: July and October, 1971, and January and May, 1972.

The beach foreshore was divided into four (Ocean Park) or five (Long Sands) zones. At random within each zone, triplicate 0.04 m^2 samples were taken by forcing a metal square into the sand and removing the sediments to a 10 cm depth. Sediments were sieved in the field with a 0.5 mm mesh screen. Animals were immediately removed from the coarse residue by elutriation and preserved in 5% formalin buffered with hexamine. The efficiency of this sampling scheme is discussed in Croker et al. (1975).

For each collection, 50-200 animals from each tidal zone were measured and sorted into life stage categories. Samples containing an unmanageable number of specimens were subsampled with a Folsom Plankton Splitter. A preliminary statistical analysis of the Folsom Splitter indicated that this is a sufficiently reliable device for numerical subsamples and accurately maintains the relative proportions of various size classes. Animals from Ocean Park (5,159) and Long Sands (1,228) yielded by the Folsom Splitter were measured and assigned to life stage categories. The use of subsamples to obtain similar numbers of specimens from each tidal zone would introduce errors when the zones were combined to compute statistical parameters on the entire population. To avoid this, extrapolations were made from subsamples to represent the original sample size. The extrapolated number of specimens used for statistical purposes were 12,966 from Ocean Park and 9,764 from Long Sands.

Animal length was measured from the tip of the rostrum to the base of the telson using an ocular micrometer with an accuracy to 0.08 mm. The following life stage categories were determined:

juvenile- no discernible secondary sexual characteristics.

male- testicular papillae present at the base of pereopod 7.

female- oostegites present (generally on pereopods 2-5)

ovigerous female- a brood of eggs or juveniles present.

post-reproductive female- oostegites with setae present, no brood.

Broods were removed from ovigerous females and the eggs or juveniles present were counted and measured.

Data from each collection were organized into population components according to life stage category and tidal zone occupied. A series of computer programs was designed that computed 13 basic statistics, a frequency histogram, as well as various combinations of components. This allowed examination of within-habitat population variability, and was performed on 278 components from 13 Ocean Park collections, and on 78 components from 4 Long Sands collections. The significance of observed differences between population components was examined using t tests.

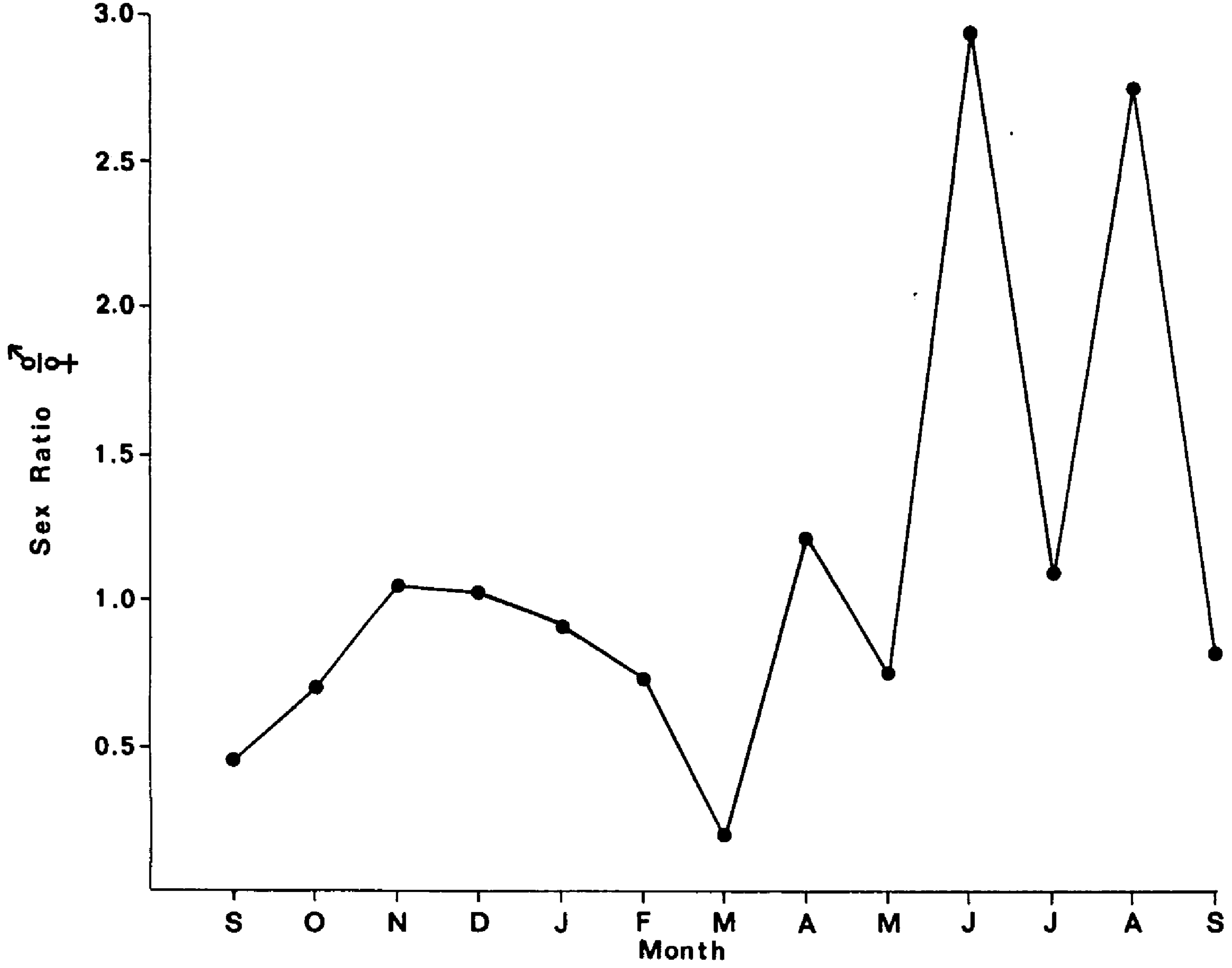
Laboratory populations of A. virginiana were maintained, and behavioral observations were made frequently on individual specimens or small groups of animals isolated in small vessels. Observations were always made with, and without a sand substratum present.

RESULTS

LIFE CYCLE

Analysis of monthly collections from the Ocean Park transect illustrates the life cycle patterns of A. virginiana. Sex ratios displayed seasonal reversals since fall and winter months displayed either a predominance of females or a 1:1 ratio, while late spring and summer populations were male-dominated (Fig. 16). Males of the species were not collected

Fig. 16. Monthly sex ratios (male/female) of *A. virginiana* at Ocean Park, 1971-72.


3.0
2.5
2.0
1.5
1.0
0.5
Sex Ratio ♂/♀
S
O
N
D
J
F
M
A
M
J
J
A
S
Month

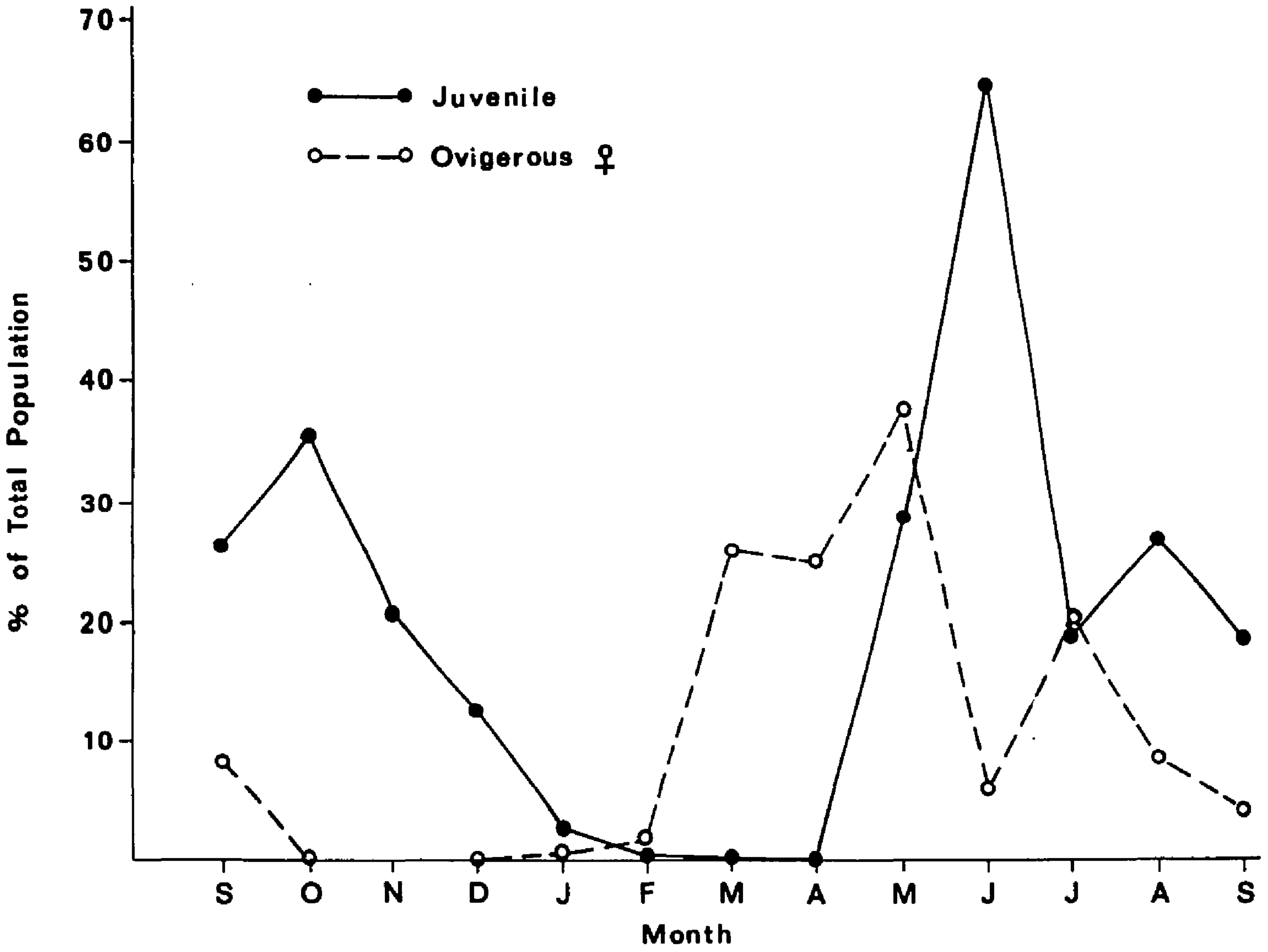
by Shoemaker (1933) and were considered rare until their description by Bousfield (1956). The sudden shift in the sex ratio and the former lack of records of male *A. virginiana* can be attributed to smaller size, micro-habitat distribution, seasonal population movements, and female mortality, as will be presently shown.

Ovigerous females occurred in the population from January to September, with peak breeding occurring during May (Fig. 17). Juveniles were abundant from May to January and were most abundant during June and October.

Amphiporeia virginiana has two annual generations; a rapid growing, short-lived summer generation, and a slower growing, longer-lived, overwintering generation (Figs. 18a and 18b). Females of the winter generation produced broods as early as February and released young during May and June. These young grew rapidly and the females matured and produced broods during July and August, releasing their young during August, September, and October. Figure 17 also illustrates the transition between the generations with two periods of maximum abundance of ovigerous females clearly separated by a period of low occurrence in June, and two peaks of maximum recruitment in June and October.

Data from Long Sands (Fig. 19) supports the described life cycle. May was dominated by breeding females from the winter generation. They released young resulting in July recruitment. The July population had a low occurrence (2%) of ovigerous females, yet the October population

Fig. 17. Percent contributions of juveniles and ovigerous females to monthly populations of _A_. _virginiana_ at Ocean Park, 1971-72.



70
60
50
40
30
20
10
% of Total Population
Juvenile
Ovigerous ♀
S
O
N
D
J
F
M
A
M
J
J
A
S
Month

Fig. 18a. Monthly size distributions of juvenile, male, female, and ovigerous female populations of *A. virginiana* at Ocean Park. Relative abundance of each category is evident by comparing sample sizes (N).

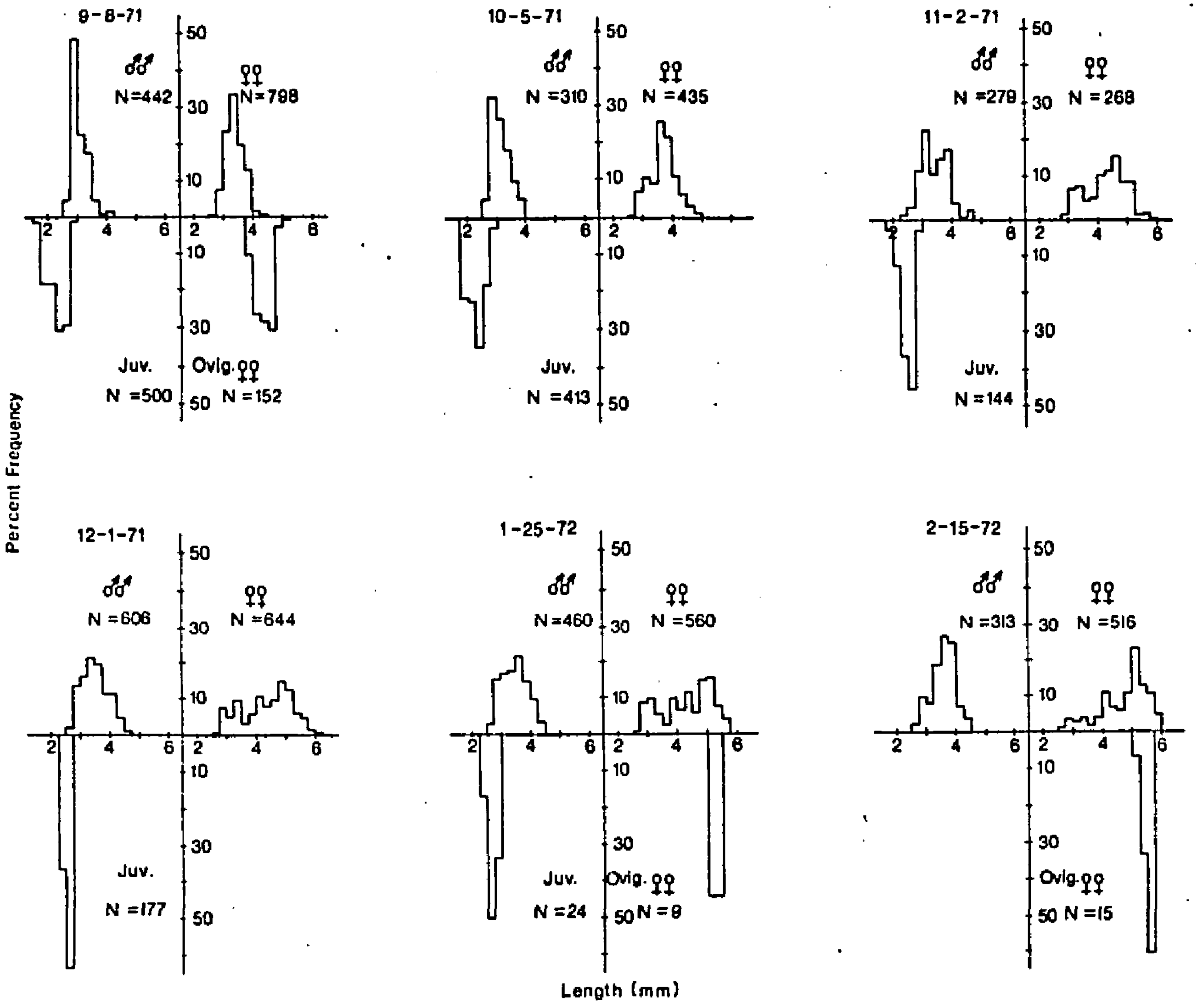

9-8-71
♂♂
N=442
♀♀
N=798
Juv.
N =500
Ovig.♀♀
N =152
10-5-71
♂♂
N =310
♀♀
N =435
Juv.
N =413
11-2-71
♂♂
N =279
♀♀
N =268
Juv.
N =144
12-1-71
♂♂
N =606
♀♀
N =644
Juv.
N =177
1-25-72
♂♂
N=460
♀♀
N =560
Juv.
N =24
Ovig.♀♀
N =8
2-15-72
♂♂
N =313
♀♀
N =516
Ovig.♀♀
N =15
10
30
50
2
4
6
8
Percent Frequency
Length (mm)

Fig. 18b. Monthly size distributions of juvenile, male, female, and ovigerous female populations of *A. virginiana* at Ocean Park. Relative abundance of each category is evident by comparing sample sizes (N).

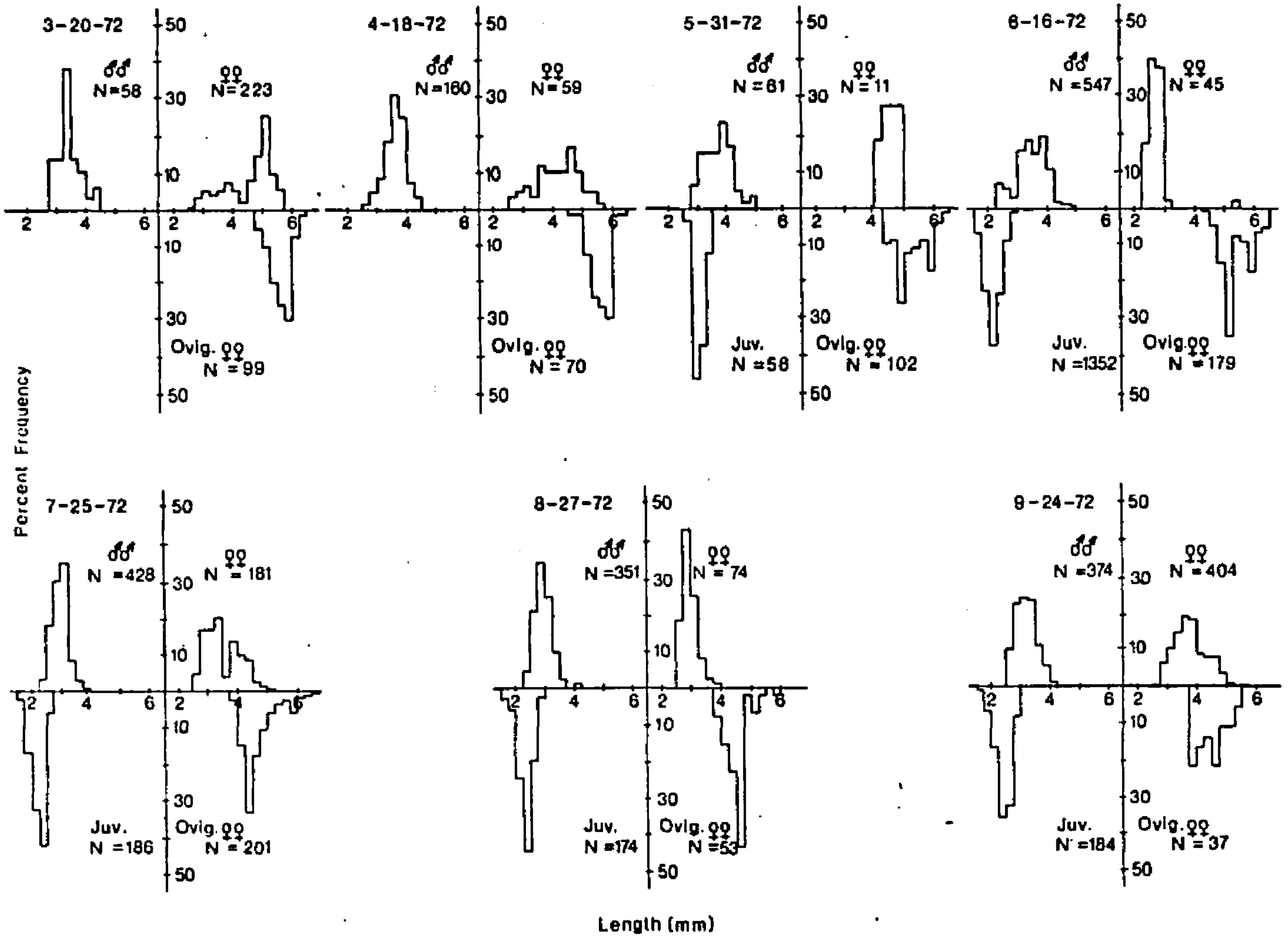
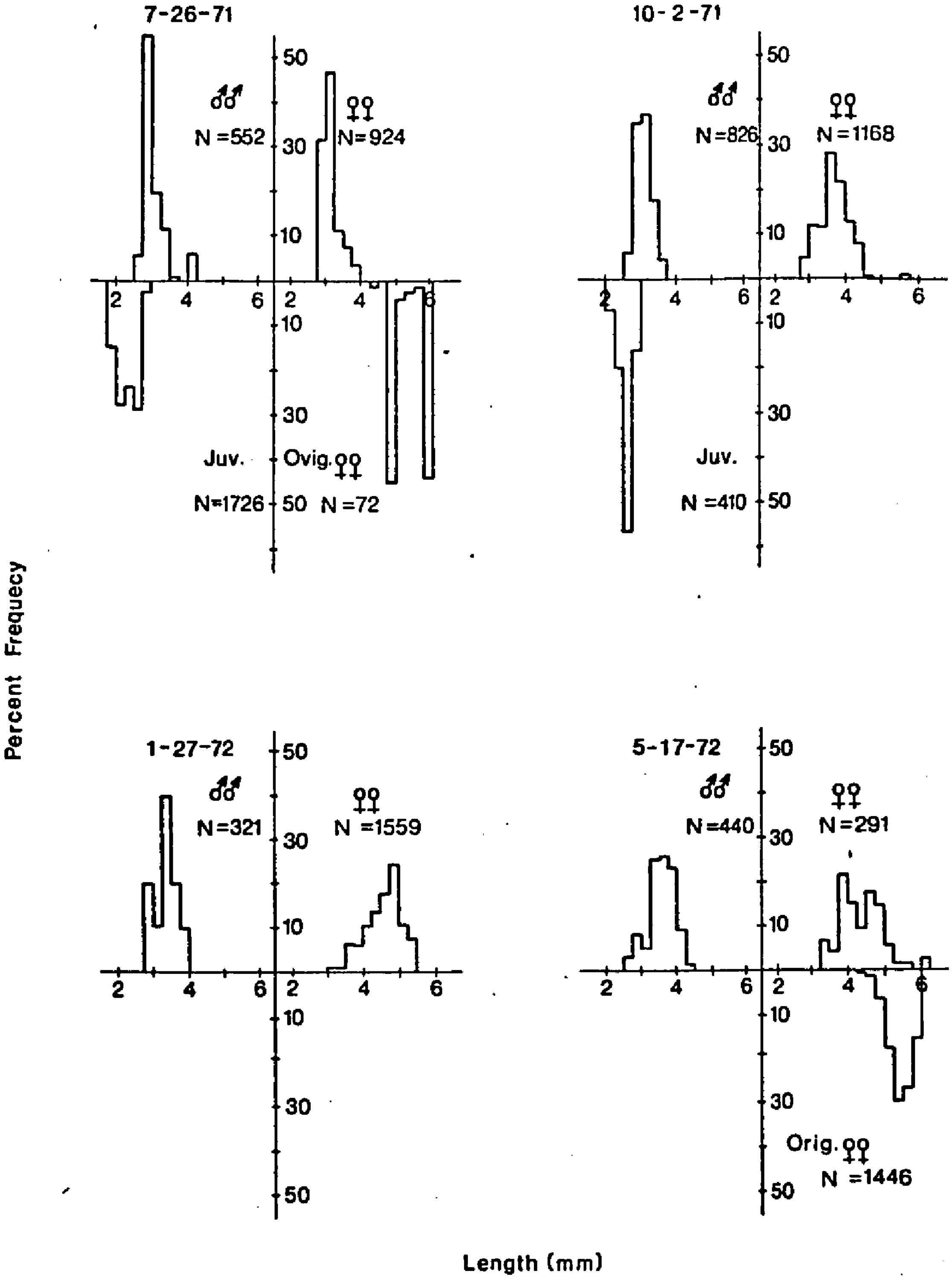

3-20-72
♂♂ N=58
♀♀ N=223
Ovig. ♀♀ N=99
4-18-72
♂♂ N=160
♀♀ N=59
Ovig. ♀♀ N=70
5-31-72
♂♂ N=61
♀♀ N=11
Juv. N=58
Ovig. ♀♀ N=102
6-16-72
♂♂ N=547
♀♀ N=45
Juv. N=1352
Ovig. ♀♀ N=179
7-25-72
♂♂ N=428
♀♀ N=181
Juv. N=186
Ovig. ♀♀ N=201
8-27-72
♂♂ N=351
♀♀ N=74
Juv. N=174
Ovig. ♀♀ N=53
9-24-72
♂♂ N=374
♀♀ N=404
Juv. N=184
Ovig. ♀♀ N=37
50
30
10
2
4
6
Percent Frequency
Length (mm)

Fig. 19. Monthly size distributions of juvenile, male, female, and ovigerous female populations of A. *virginiana* at Long Sands. Relative abundance of each category is evident by comparing sample sizes. (N).


7-26-71
♂♂ N =552
♀♀ N=924
Juv. N=1726
Ovig.♀♀ N =72
10-2-71
♂♂ N=826
♀♀ N=1168
Juv. N =410
1-27-72
♂♂ N=321
♀♀ N =1559
5-17-72
♂♂ N=440
♀♀ N=291
Orig.♀♀ N =1446
10
30
50
2
4
6
Percent Frequecy
Length (mm)

had a substantial number (17%) of juveniles. Since juveniles released in early summer would have matured prior to October, these October young were produced by a second population of ovigerous females that matured during August and September.

The size distribution histograms presented in Figures 18a, 18b, and 19 show the growth characteristics of the species. Free-living specimens of A. virginiana ranged in size from 1.52 to 6.80 mm. Following recruitment, the months from October to March showed successive increases in mean population lengths. The appearance of juveniles in the population was accompanied by a decrease in monthly mean lengths from March to June, indicating recruitment of the summer generation. Rapid growth of individuals was evident from June to July as the summer generation matured. A July to August decrease in mean length followed, when the summer generation bred to establish the over-wintering population.

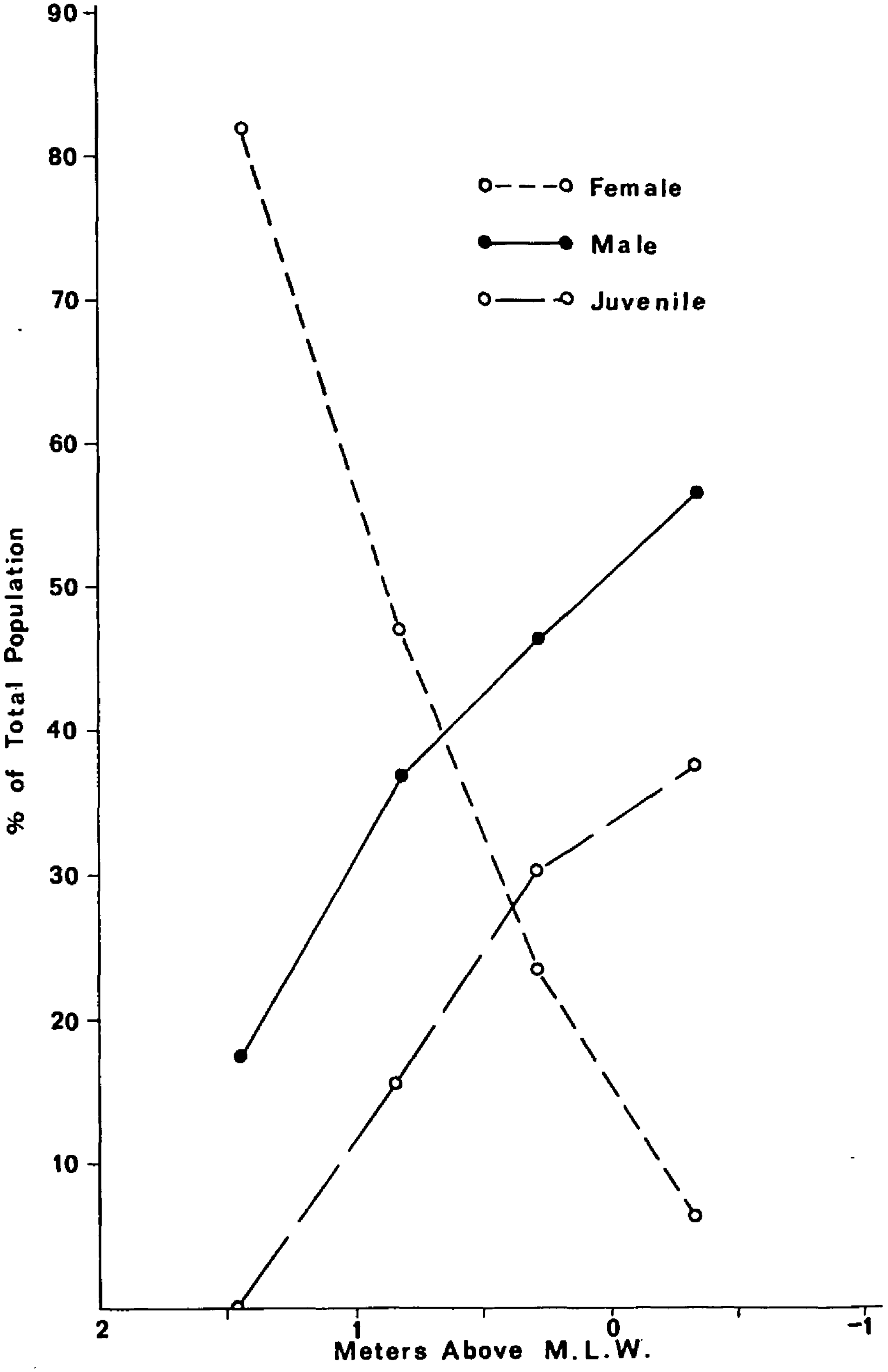
The four major life stage categories generally had significantly ($p<0.001$) different mean lengths, with ovigerous females attaining the largest sizes. Females were significantly larger than males, except during the months of June and August. The female population during June was primarily comprised of small, rapidly maturing individuals, the larger size classes being absent due to death following the breeding period. Mortality in the larger overwintering males occurred over a longer period of time, hence the mean monthly lengths of males decreased more gradually over the breeding season. For this reason, males were more abundant than females in the spring and occasionally displayed a larger population mean length.

It is evident from Figures 18a and 18b that females displayed a faster growth rate than males. By late summer, both male and female segments of the population were composed of small individuals (approximately 3 mm), but rapid growth of the females during the fall allowed the female population to attain individual sizes of approximately 1 mm larger than males by early winter. The most rapid-growing of these females produced broods earliest in the reproductive season (January-April). During May and June the remainder of the overwintering females bred, regardless of size. Newly recruited females were evident in June, and their rapid growth and breeding activity is apparent in the July-September histograms.

WITHIN-HABITAT POPULATION DISTRIBUTION

Populations of A. virginiana typically inhabit the entire low tide terrace with peak abundance in the lower foreshore (0.0 to 0.6 m tidal level). Analysis of populations revealed within-habitat distribution by life stage category and size. Figure 20 illustrates the percent contribution of males, females, and juveniles at various tidal levels of the foreshore of Ocean Park on September 24, 1972. This distribution is typical for all collections from Ocean Park and Long Sands, and clearly indicates that females aggregated in the upper foreshore, while juveniles and males

Fig. 20. Percent composition of the *A. virginiana* population in relation to tidal level. September 24, 1972, Ocean Park.



% of Total Population
90
80
70
60
50
40
30
20
10
2
1
0
-1
Meters Above M.L.W.
Female
Male
Juvenile

aggregated near the low water mark.

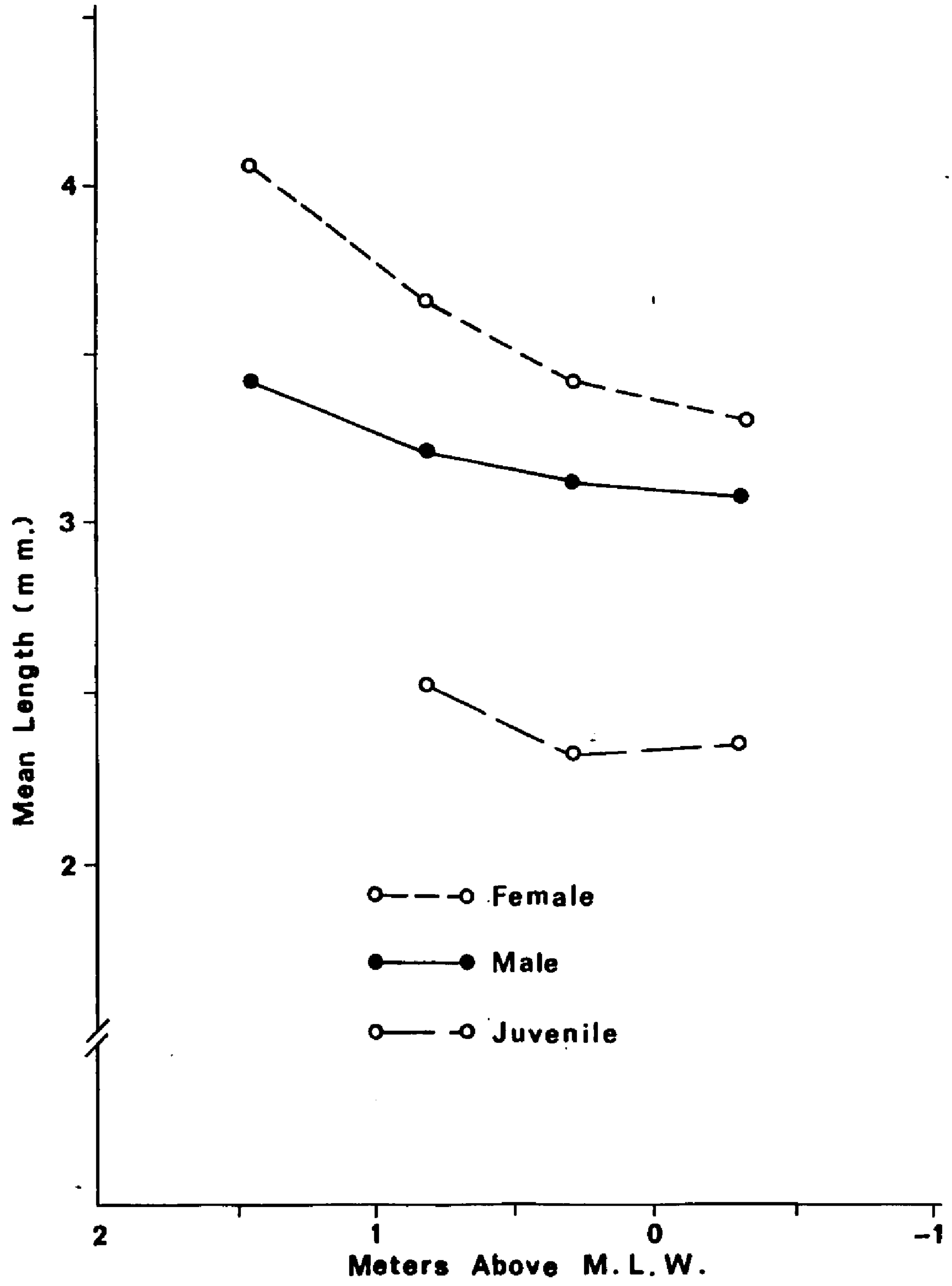
Since females were largest, larger animals would generally be found higher in the intertidal zone than smaller animals. However, each life stage category also showed a trend for its own larger animals to occur higher in the intertidal zone (Fig. 21). This distribution was evident in all collections, although successive landward increases of mean length were often slight. Mean lengths of each life stage category from the upper and lower foreshore were compared for each month. Significantly larger individuals were present at higher tidal levels in 87% of the collections for juveniles, in 50% of the collections for females, and in 41% of the collections for males ($p<0.05$, t test). Ovigerous females did not display this pattern, since they were generally confined to the upper tidal levels only.

FECUNDITY

Ovigerous females carried from 1 to 21 eggs or juveniles with a pronounced reduction of fecundity in the late summer breeding population (Fig. 22). Mean brood sizes ranged from 10 to 11.9 eggs or juveniles per female during the February to June breeding period, followed by mean brood sizes of 4.6 to 7.3 eggs or juveniles per female for the July to September period.

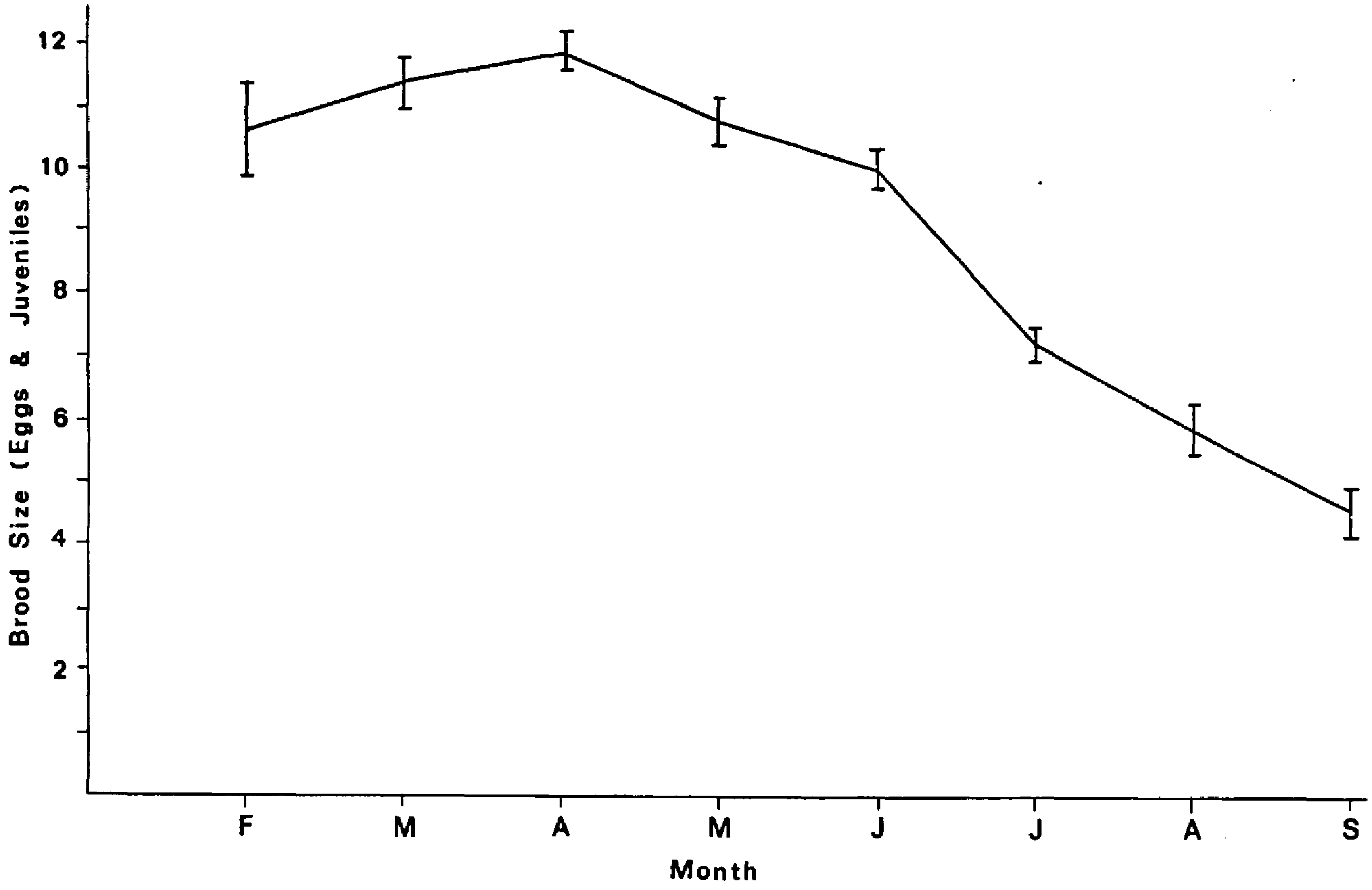
The number of eggs or juveniles in a brood had a significant positive correlation ($p<0.01$, regression analysis) with animal length when all ovigerous females were

Fig. 21. Mean length of juvenile, male, and female populations of A. virginiana at various tidal levels. September 24, 1972, Ocean Park.



4
3
2
Mean Length (m m.)
2
1
0
-1
Meters Above M. L. W.
Female
Male
Juvenile

Fig. 22. Mean brood sizes of ovigerous females at Ocean Park, 1972. Vertical lines indicate ± standard error.

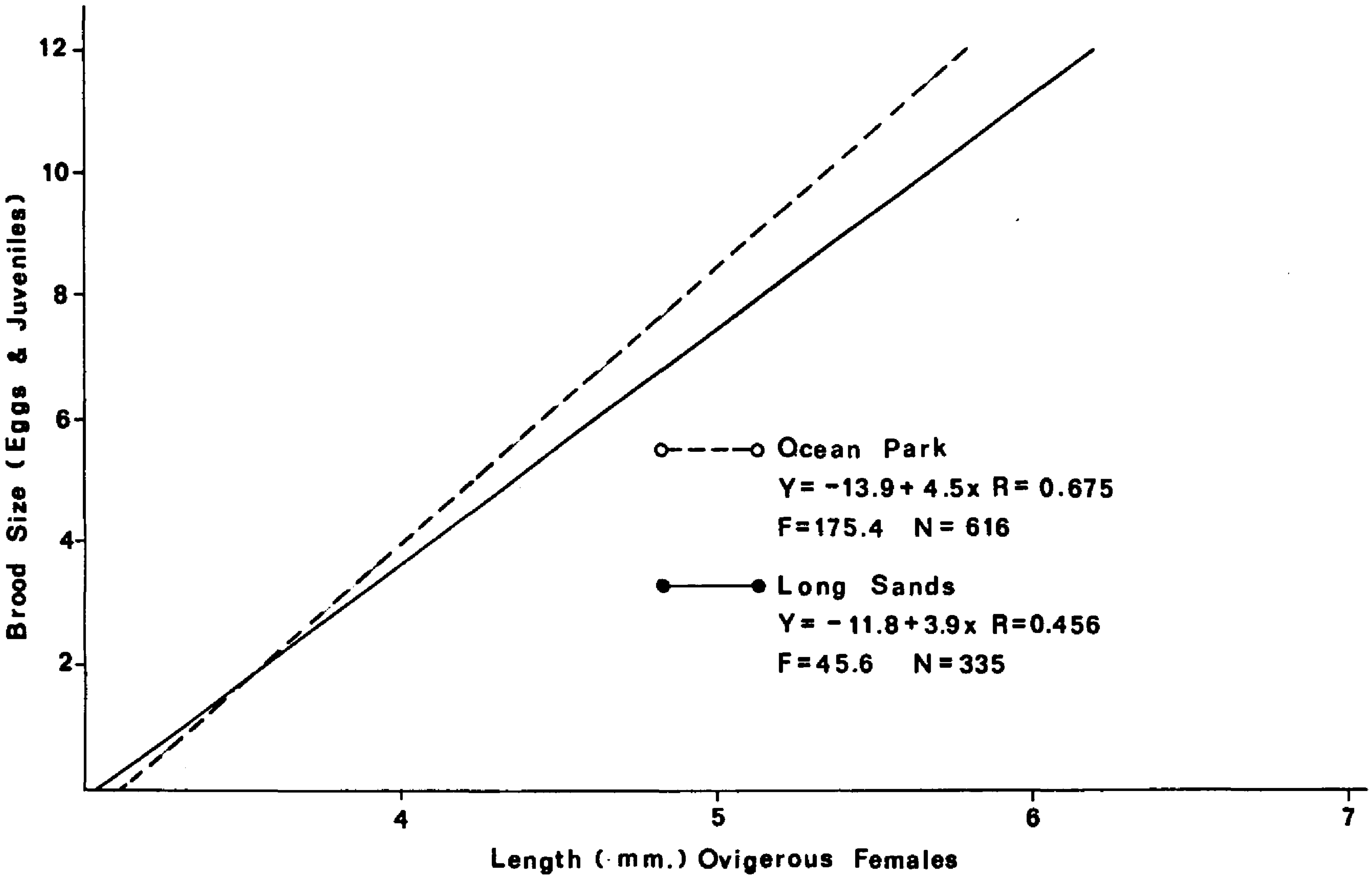

Brood Size (Eggs & Juveniles)
12
10
8
6
4
2
F
M
A
M
J
J
A
S
Month

considered (Fig. 23). Regression analysis of individual months indicated a non-significant ($p>0.05$) relationship between brood size and female length during four of the eight breeding months at Ocean Park. Differences in fecundity are obviously related to the occurrence of two separate breeding generations, rather than the simultaneous presence of different size classes. Fish (1975) has shown similar variations in fecundity between overwintering and summer breeding generations of sand beach amphipods in the genus *Bathyporeia*.

There was no evidence that females produced more than one brood during their life span. As the breeding season progressed, there was a continuous decrease in mean length of ovigerous females (Fig. 18). The most rapid decline in mean length of ovigerous females occurred between June and July, interpreted as the appearance of the second breeding generation. Significant differences in length were found between the two generations ($p<0.001$, t-test). Animals breeding in May had a mean length of 5.20 mm, while the August breeders had a mean length of 4.54 mm.

Post-reproductive females rarely formed more than 0.5% of the total population, and it is probable that these females normally die within a few weeks after releasing their broods. Oostegites deteriorate shortly after the young are released, rendering the post-reproductive female category somewhat artificial.

Fig. 23. Relationship of brood size to length of ovigerous females at Ocean Park and Long Sands. Regression lines for all specimens examined.


12
10
8
6
4
2
4
5
6
7
Brood Size (Eggs & Juveniles)
Length (mm.) Ovigerous Females
Ocean Park
Y= -13.9 + 4.5x R= 0.675
F=175.4 N= 616
Long Sands
Y= - 11.8 + 3.9x R=0.456
F=45.6 N=335

DEVELOPMENT

Eggs are produced in the gonadal tissues of the dorsal thoracic segments, and are deposited in the brood chamber formed by the oostegites as the female molts during the copulatory process. Eggs had a size range from 0.40 to 0.48 mm with no significant variation in size apparent over the breeding season. Development progressed with no readily apparent external changes of egg morphology until an embryo was visible and the eggs enlarged to 0.6-0.7 mm. Eggs containing well-formed embryos were not encountered frequently; thus development progresses rapidly through the final stages. Newly hatched juveniles ranged in length from 0.96 to 1.04 mm and grew rapidly. Juveniles were retained in the brood chamber until they attained a length greater than 1.5 mm. Secondary sexual characteristics were usually distinguishable when free-living young reached a length greater than 2.6 mm. Since hatched juveniles were found less commonly in the broods than eggs, it can be assumed that juveniles are released quite soon after hatching. However, it is possible that there is a substantial loss of the larger, hatched embryos from the brood as suggested by Fish (1975). Temporal spacing in the population peaks of juveniles and ovigerous females (Fig. 17) implies that the entire developmental sequence required 1 to 2 months in early spring, and a somewhat shorter time span during the summer months. The rapid increase in numbers of ovigerous females during March, April, and May coincided with spring increase in coastal water temperature.

MORTALITY

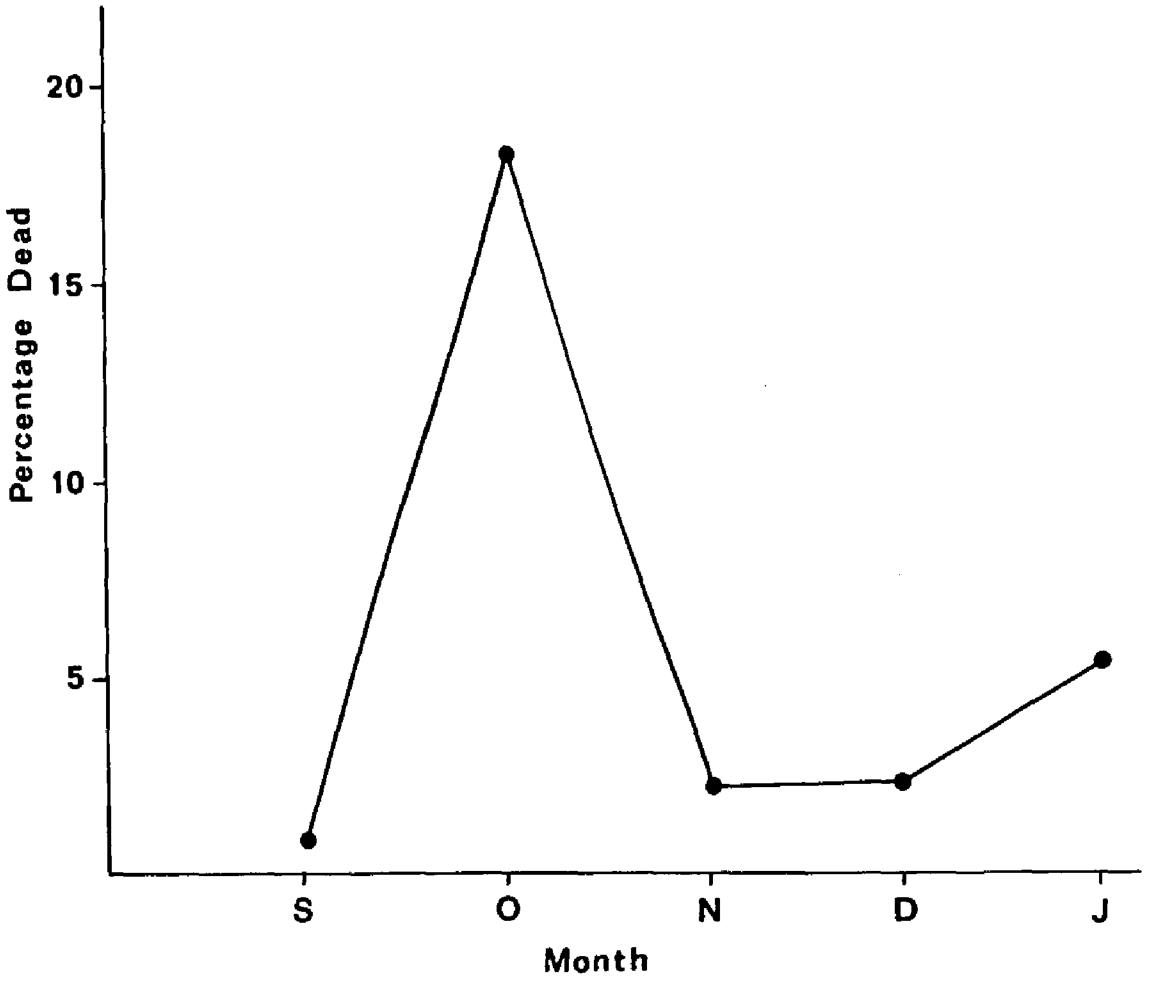
Animals that had died prior to collection were recognized by noting general external appearance and deterioration of internal structures. Significant occurrence of dead animals was limited to collections during the months of September to January (Fig. 24). Peak mortality occurred in October when 18.2% of the animals collected were found dead. Mortality was highest at the upper station, where from 30 to 90% of the animals collected were found dead (September - January). Lower stations yielded a mortality rate of less than 4% during the same months.

Confinement of mortality to upper levels of the foreshore implies that the larger animals were dying; thus the peak mortality in October undoubtably represents the termination of the summer generation, rather than deaths of the smaller sized members of the overwintering generation. It remains unclear why a similar mortality peak was not observed in June or July marking the end of that generation.

FEEDING

Laboratory observations of adult _A_. _virginiana_ showed that the species is a detritivore. No feeding was observed when animals were presented with large pieces of algae or animal tissue, but the amphipods occasionally ate

Fig. 24. Percent contribution of dead individuals to monthly collections at Ocean Park, 1971-72.


Percentage Dead
20
15
10
5
S
O
N
D
J
Month

finely ground pieces of organic material. There was no evidence of filter feeding or mechanical removal of organic matter from sand grains.

Animals isolated for a week with small bits of organic matter produced many more fecal pellets than animals isolated in seawater with no macroscopic food source. It is assumed that animals primarily eat well decomposed detritus, since they generally ignored newly introduced food until it began to deteriorate. There was no evidence of cannibalism, but coprophagy was observed among animals with no other food source.

The gnathopods were used during feeding to grasp the decomposing material and push it directly to the mouthparts. The food was manipulated by the mouthparts and some particles were rejected. Animals were also observed trapping food particles on the setae of the antennae, and intermittently transferring these particles to the mouthparts.

SWIMMING AND BURROWING

Although _A_. _virginiana_ is considered an infaunal animal, its major mode of locomotion is by swimming, and the species is an abundant component of the intertidal plankton. Aided by its small size, body form, and rapid swimming speed, _A_. _virginiana_ was observed to dart rapidly into well liquefied sediments by pushing sand grains aside with the antennae and propelling itself with quick flexes of the abdomen. Both in the field and in the laboratory, _A_. _virginiana_ was observed remaining in the upper 2 cm of sediments and changing location by swimming along surface films of water, rather than by tunneling. Liquefied sand is necessary for burrowing; animals were never observed burrowing into partially dried sediments.

Swimming was accomplished either by sequential beating of the pleopods or by repeated, rapid flexures of the abdomen. Animals were observed swimming forward or upward. When descending through a water column, the animals sank slowly with dorsal surface down and the antennae and pereopods extended laterally.

REPRODUCTIVE BEHAVIOR

The reproductive behavior of most haustoriid amphipod species is essentially unknown. No pairs of *A.virginiana* in precopula were collected throughout the entire study (animals part when preserved), but field and laboratory observations of stages of the mating process were made. On several occasions, animals in precopula were observed swimming in the surface film of runoff over the beach. Occasionally females were observed with two males attached, a phenomenon not reported before for the Amphipoda.

On three occasions, living pairs in precopula were isolated and examined under a dissecting microscope. The male attached to the female's dorsum with the dactyl of gnathopod 2, and was oriented at a 90° angle to the anterior-posterior axis of the female. Although the male was situated in a position allowing potential transfer of sperm to the brood chamber, copulation was never observed since the animals quickly separated.

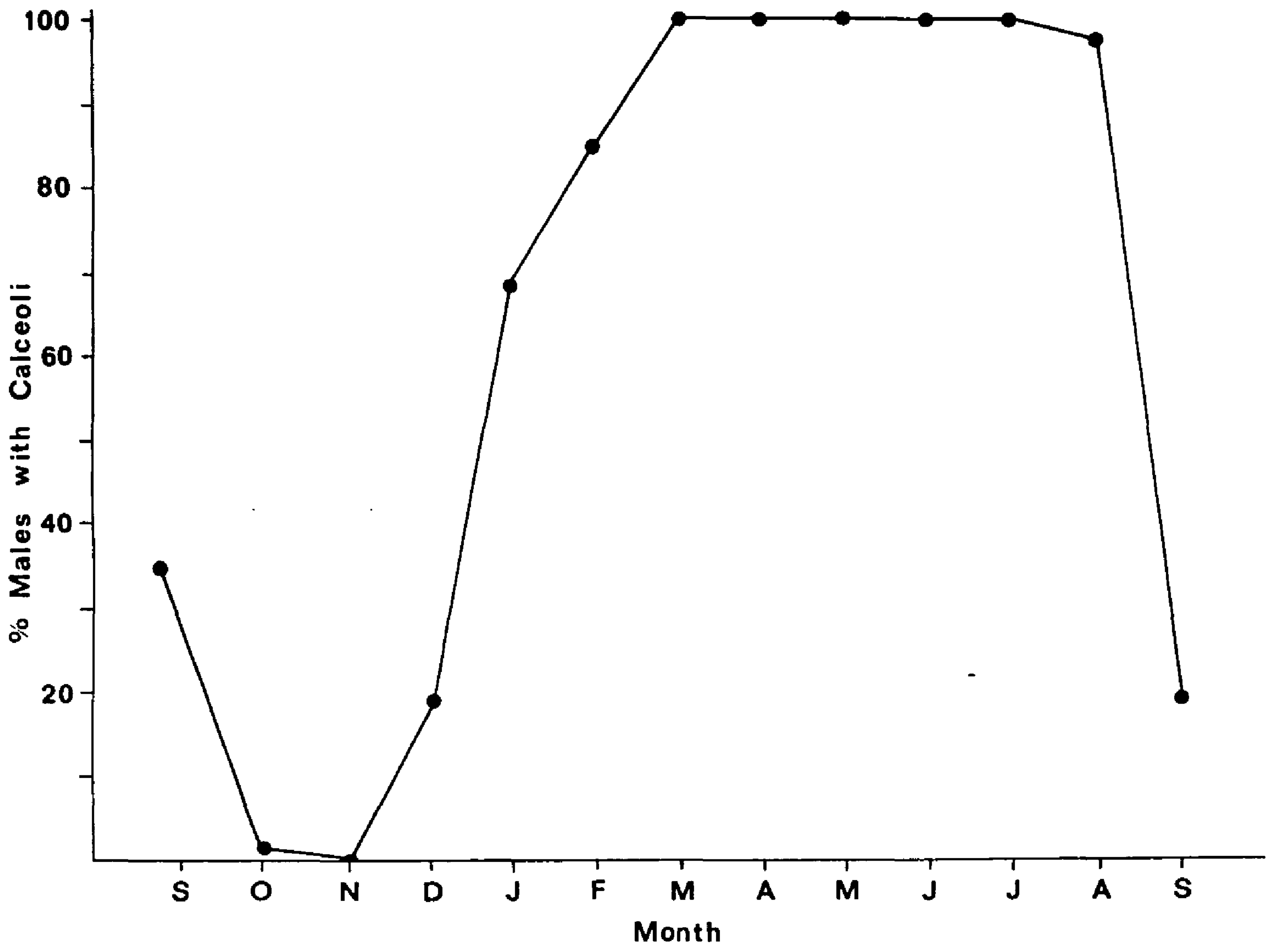
Since *A. virginiana* populations displayed within-habitat sex segregation, and since precopula was observed only in animals swimming along the sand surface, it is probable that mating occurs during brief encounters while the animals are swimming. The brief duration of precopula may explain the occurrence of two males per female, acting as additional insurance for mating.

Males of *A. virginiana* possess calceoli on antennae 2, but primarily only during the breeding season (Fig. 25). The occurrence of calceoli was unrelated to the size of the animal. Male specimens with damaged second antennae displayed calceoli on the first antennae, with occasional specimens bearing calceoli on both pairs of antennae. Dahl et al. (1970a, 1970b) presented evidence that calceoli in *Gammarus duebeni* were used as a pheremone receptor, aiding males in locating females. Calceoli on male *A. virginiana* may serve a similar function.

PREDATION

Specimens of *A. virginiana* were isolated for 72 hour periods with the following potential predators from the sand community: *Nephtys bucera*, *Nereis virens*, *Psammonyx nobilis*, and *Chiridotea tuftsi*. Predation was not evident in any of these runs.

Fig. 25. Percentage of male *A. virginiana* bearing calceoli at Ocean Park.


% Males with Calceoli
100
80
60
40
20
S
O
N
D
J
F
M
A
M
J
J
A
S
Month

Sandpipers frequently aggregate and feed in the backwash of waves at low tide, and sampling of their feeding areas demonstrated that A. virginiana was the only abundant invertebrate on which they could be feeding. Moran and Fishelson (1971) reported similar feeding behavior by plover birds on superficially burrowed mysids in the intertidal zone.

In addition to predation by shore birds, it is probable that fish migrating into the surf zone prey on the enormous numbers of A. virginiana found in the intertidal plankton. Other amphipod species may also prey on A. virginiana as Croker (pers. comm.) has observed Calliopius laeviusculus preying on live individuals in low tide pools.

PARASITISM

More than 6,000 preserved specimens used for measurements were also examined for any obvious internal parasites. An additional 500 freshly collected live animals were dissected and examined for internal parasites or larvae. None were found, an unusual finding considering the abundance of the species and the common use of amphipods in parasite life cycles.

DISCUSSION

Life history events of haustoriid amphipods are important to the community structure and stability of New England sand beaches where a relatively small number of these species frequently dominate the intertidal community (Croker et al., 1975). Haustoriid amphipod life cycles generally display one or two annual breeding generations, each composed of females that produce one brood (Croker, 1967; Dexter, 1971; Sameoto, 1969a, 1969b; Fincham, 1971). Timing and duration of reproductive periods are related to water temperature. Dexter (1971) reported a winter breeding generation in haustoriids from the Carolinas, while Sameoto (1969a, 1969b) found no breeding occurring during the cold months in Massachusetts. Although most New England amphipod species are eurythermal, Bousfield (1973) notes that boreal and subarctic species occurring in the area tend to be cold-stenothermal and confine reproductive activity to the coldest months, while warmer temperate and Virginian species found in New England are warm-stenothermal and breed only during the summer.

Species of Bathyporeia, the closest related genus to Amphiporeia (Bousfield, 1965), display bivoltine reproduction characterized by an overwintering generation producing young in early spring; these young mature rapidly and in turn produce the overwintering generation of the succeeding year (Fincham, 1971; Fish, 1975). Haustoriid species displaying bivoltine reproduction frequently show changes in the length of generation life span and the time of breeding over their geographic range (Salvat, 1967; Fincham, 1971). These variations in the timing of the bivoltine pattern are assumed to result from local temperature conditions.

Populations of *A. virginiana* from southern Maine display the bivoltine reproduction pattern. Winter temperatures remain too cold to permit winter breeding, but warmer water temperatures during spring, summer, and fall persist long enough to permit two generations to breed. It is probable that *A. virginiana* displays differing reproductive patterns over its extensive geographic range. The extended winter season in Nova Scotia may cause local populations to approach a univoltine situation, while the warm waters of the Carolinas may allow winter breeding.

Bousfield (1965) separated the family Haustoriidae into two subfamilies, the more primitive Pontoporeiinae (including *Amphiporeia*) and the more recently evolved Haustoriinae. Feeding type and general behavior are among the characteristics used by Bousfield (1970) in proposing the phylogeny of haustoriids. Members of the Haustoriinae are highly adapted to a more strict infaunal existence and frequently display intricate filter feeding mechanisms. The Pontoporeiinae have evolved from carnivorous Gammaridae, progressing through the genus *Amphiporeia* to the genus *Bathyporeia*, where a specialized epistrate feeding has evolved in the latter. *A. virginiana* is clearly an intermediate in this scheme with its loose affinity for the substratum and unspecialized feeding behavior.

SECTION III

DISTRIBUTIONAL ECOLOGY AND POPULATION FLUCTUATIONS

INTRODUCTION

Quantitative studies on the abundance and distribution of intertidal sand-burrowing amphipods of the western North Atlantic coast have generally interpreted population fluctuations with respect to life history phenomena (Croker, 1967a, 1967b; Dexter, 1967, 1971; and Sameoto, 1969a, 1969b). The haustoriid amphipod, _Amphiporeia virginiana_, displays considerably more swimming behavior and less affinity for the substratum than other infaunal amphipod species. Distributional patterns and population fluctuations of _A. virginiana_ are presumably dependent not only on life history phenomena, but also on the more mobile behavior of the species.

Recent studies have considered factors influencing the distribution and behavior of sand beach animals. Croker et al. (1975) showed that sand beach community structure and relative abundance of amphipod species is largely dependent on the physical nature of the beach; particularly wave exposure. The importance of behavioral and physiological cues in determining the intertidal distribution of mobile sand beach crustaceans was illustrated by the work of Enright (1961a), Cubit (1969), Jones and Naylor (1970) and Fish and

Fish (1972). The present study investigates the distributional patterns and population fluctuations of *A. virginiana* with respect to its life cycle, and its behavioral responses to the dynamic environment in which it lives.

MATERIALS AND METHODS

Quantitative collections were made during four related field studies: a general sampling of selected beaches over the geographical range of the species; four seasonal transects of the relatively stable Long Sands Beach, York, Maine; fifteen monthly transects of the high energy beach at Ocean Park, Maine; and two longshore collections on the coast of Saco Bay, Maine.

Geographical variation in distribution and abundance were investigated by taking duplicate 0.04 m^2 samples, as earlier described, from the lower, middle and upper foreshore of 85 selected beaches in New Brunswick, Nova Scotia, Maine, New Hampshire, Massachusetts, Rhode Island, Connecticut, New Jersey, North Carolina, and South Carolina. General inferences will be drawn from the voluminous data from these collections.

Fluctuations in the distribution and abundance of *A. virginiana* on a moderately exposed beach were studied by analyzing triplicate 0.04 m^2 samples from 5 levels over the beach foreshore at Long Sands in July and October, 1971, and January and May, 1972. Tidal levels were determined with the aid of a tidal staff and surveyor's transit after

Croker et al. (1975). Data on 31,810 specimens of A. virginiana were obtained from these collections.

The influence of a high energy beach environment on the distribution and abundance of A. virginiana was studied through 15 consecutive monthly transect collections taken from July, 1971 through September, 1972 from the beach at Ocean Park, Maine. Triplicate 0.04 m^2 samples were collected at 4 tidal levels on the beach foreshore. Beach profiles were measured and sand grain size parameters calculated to accompany these collections. Analysis of population fluctuations in relation to beach dynamics is based on data on 40,034 specimens of A. virginiana from these collections.

Longshore variations in the abundance of A. virginiana was determined by analyzing duplicate 0.04 m^2 samples from mean low water (0.0 m) at 7 stations along the shore of Saco Bay (Fig. 2). The collections of specimens and sediments were taken in March and August, 1972. In addition, complete transects (triplicate samples at 4 tidal levels) were taken at stations 3 and 6. These longshore collections produced data on 23,267 specimens of A. virginiana.

Data analysis was accomplished with the aid of an IBM/360 computer and appropriate programs. An additional 46,469 individuals representing 12 species of sand macroinfauna were collected during the Long Sands and Ocean Park studies and were also processed for their distribution and abundance. The data on the fauna associated with A. virginiana will be considered in general terms.

The salinity tolerance of A. virginiana was determined in the laboratory. Experimental solutions with salinities from 0 to 50 ^{o}/oo in 5 ^{o}/oo increments were made by diluting or boiling seawater, or by dissolving artificial sea salts ("Instant Ocean"). After 48 hours of acclimation to laboratory conditions, groups of 4 animals were placed in culture dishes containing 25 ml of test solution and kept in an Environair Systems Inc. Closed Environment Room with a constant 4^{o} C temperature. Experimental groups were maintained for 96 hours, with mortality recorded at 2 hour intervals. The experiments were repeated until a total of 48 animals were tested at each salinity increment.

To study desiccation tolerance, thirty-five 20 ml culture dishes were filled in the field with wet sand containing live specimens of A. virginiana. The vessels were returned to the laboratory, weighed, and placed in the environmental chamber at 30^{o} C and 20% humidity. At hourly intervals, two vessels were removed, weighed, and the percentage of dead A. virginiana calculated.

RESULTS

GEOGRAPHICAL DISTRIBUTION AND OCCURRENCE

Amphiporeia virginiana was present from eastern Nova Scotia to northern South Carolina on all beaches that had substantial wave activity and salinities of 27 ^{o}/oo or greater. It was frequently the numerically dominant macroinfaunal species on beaches exposed to strong surf action, and is the only intertidal amphipod present on northern New England high energy beaches.

The species was rare or absent on protected beaches with little wave action, and was absent from all estuarine sand habitats. In the field, _A_. _virginiana_ was found in a wide range of sediment textures from very coarse to very fine sand. Based on maximum field abundances, the species prefers fine sand with a mean diameter range of 2.0 ϕ to 2.5 ϕ.

INTERTIDAL COMMUNITY DISTRIBUTION

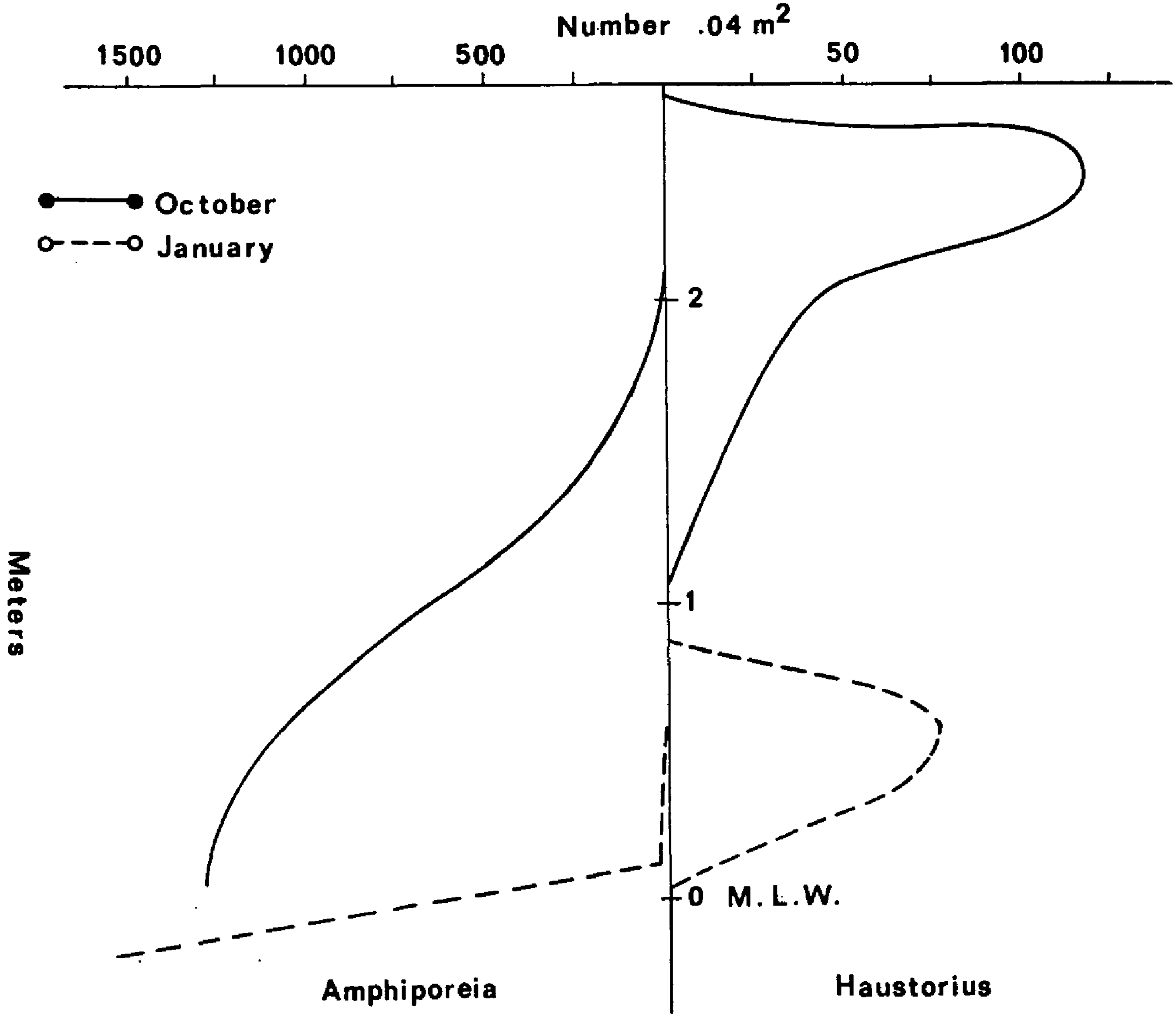
The two major study sites, Long Sands and Ocean Park, were selected for the contrast they provide. Both have direct exposure to surf action, but Long Sands maintains a stable profile and sediment texture, while Ocean Park displays constantly changing beach profiles and sediment characteristics. The steep slope and pronounced berm at Ocean Park result in a total drainage of the upper foreshore that is reflected in the lack of all sand macroinfauna at levels higher than 2 m above mean low water. Long Sands with its gentle slope, displayed macroinfaunal species up to levels 4 m above mean low water.

Amphiporeia _virginiana_ was the numerically dominant species at Long Sands and was typically aggregated on the lower foreshore (0.0 to 1 m tidal level), while upper foreshore sediments were dominated by the amphipod _Haustorius_ *canadensis*. Both species displayed a winter seaward migration of populations (Fig. 26), partly in avoidance of frozen sediments higher in the foreshore. On the other hand, Croker (pers. comm.) has evidence of migrations of *A. virginiana* populations to higher foreshore levels during mild winters.

Samples collected from 0.0 to -0.7 m below mean low water showed reduced abundances of *A. virginiana* at both Ocean Park and Long Sands, and at both subtidal locations the amphipod *Bathyporeia quoddyensis* and the cumacean *Mancocuma stellifera* were co-dominant species. Numerous 0.04 m^2 Shipek bottom samples taken seasonally, at depths of 5 to 7 m offshore from the *A. virginiana*-dominated beaches at Ocean Park and Goose Rocks Beach, Maine had a total absence of *A. virginiana*. Gnewuch and Croker (1973) earlier reported that *A. virginiana* was present in subtidal samples to depths of 3 m off New Hampshire beaches. It appears that the seaward abundance of *A. virginiana* is drastically reduced below mean low water levels.

Additional species that were typically found in the sand beach community both at Long Sands and Ocean Park were the polychaetes *Nephtys bucera*, *Scolelepis squamata*, and *Paraonis fulgens* and the gastropod *Polinices triseriata*. The amphipod *Acanthohaustorius millsi* was common from the lower foreshore of Long Sands, but was only occasionally present in Ocean Park collections. The isopod *Chiridotea caeca*, which is abundant and replaces *H. canadensis* on ocean

Fig. 26. Zonation and winter migration of A. *virginiana* and H. *canadensis* at Long Sands, October 2, 1971 and January 27, 1972.


Number .04 m^2
1500
1000
500
50
100
October
January
Meters
2
1
0 M.L.W.
Amphiporeia
Haustorius

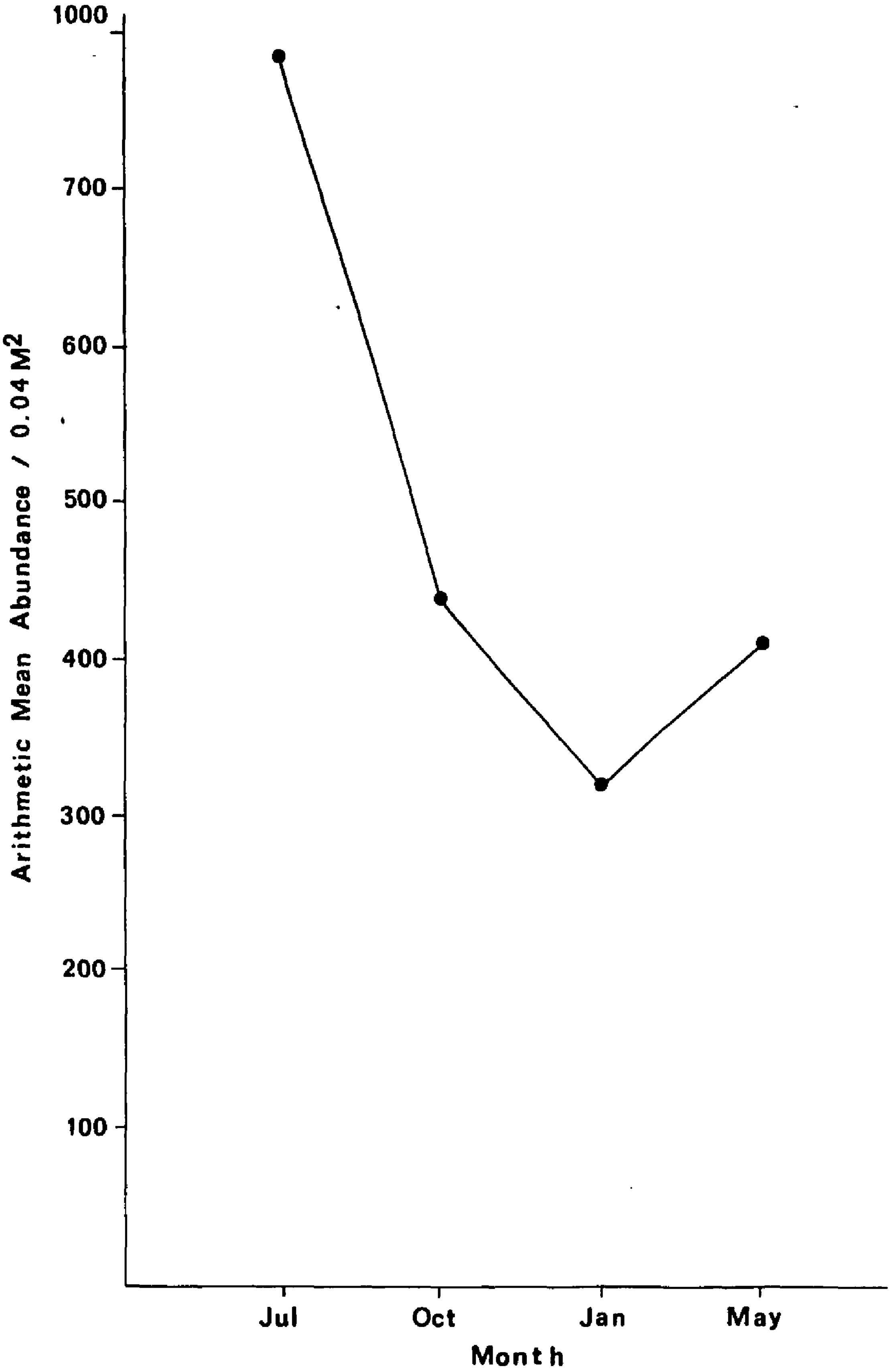
exposed beaches in Nova Scotia, was present in low abundance at Long Sands, but was never encountered at Ocean Park. Early spring collections at Long Sands and Ocean Park also included specimens of the amphipod Psammonyx nobilis.

POPULATION FLUCTUATIONS

A moderately exposed habitat like Long Sands has annual population fluctuations with maximum abundance of A. virginiana occurring during summer, and minimum abundance during winter (Fig. 27). The July, 1971 collection yielded a post-recruitment mean habitat abundance of 965 individuals per 0.04 m^2. In beach areas of maximum abundance, A. virginiana was present in excess of 5,000/0.04 m^2. The winter abundances decreased to 312/0.04 m^2. These seasonal changes in abundance are a regular progression of population increase and decrease in response to the life history events of the species already described.

Preliminary observations at Ocean Park indicated that population levels of A. virginiana fluctuated more rapidly than at Long Sands, necessitating more frequent sampling. For example, although a post-recruitment maximum abundance (September, 1971; 490/0.04 m^2) and a pre-recruitment minimum abundance (May, 1972; 39/0.04 m^2) were evident in the data, population levels between successive months varied widely. On the other hand, additional data from Long Sands (not shown) did not indicate erratic monthly fluctuations.

Fig. 27. Seasonal abundance of *A. virginiana* at Long Sands, 1971-72.


1000
700
600
500
400
300
200
100
Arithmetic Mean Abundance / 0.04 M2
Jul
Oct
Jan
May
Month

Monthly variations in abundance of A. virginiana at Ocean Park will be shown to be dependent on the species' ability to disperse and utilize maximum potential habitat space during beach cycles. But, to eliminate these dispersal effects and to generate an annual abundance pattern reflecting life history events, it was necessary to consider the mean abundance of A. virginiana only in its area of maximum abundance. Figure 28 depicts mean monthly maximum abundance of the species at Ocean Park. Summer and fall abundances were relatively stable (500 to 680/0.04 m^2), but declined during winter months to a pre-recruitment minimum abundance of 110/0.04 m^2. The release of young by the winter generation resulted in the strong increase in June abundance (927/0.04 m^2), followed by the return to typical summer abundance levels in July as the overwintering adults were presumably eliminated from the population. Fall recruitment and death of the summer generation adults was evident in the September through November fluctuations.

In the analysis of the monthly fluctuations over the entire beach foreshore at Ocean Park, the data were expressed as derived (geometric) means (Fig. 29). These data show an annual fluctuation of 14 fold for this high energy beach in contrast to the 4 fold fluctuations in amphipod populations (A. virginiana comprised 85% of these populations) reported by Croker (in press) for the moderately exposed Long Sands habitat over a 4 year period.

The geometric mean is not only a useful indicator of

Fig. 28. Mean monthly abundance of _A_. _virginiana_ in the zone of maximum population abundance at Ocean Park, 1971-72.

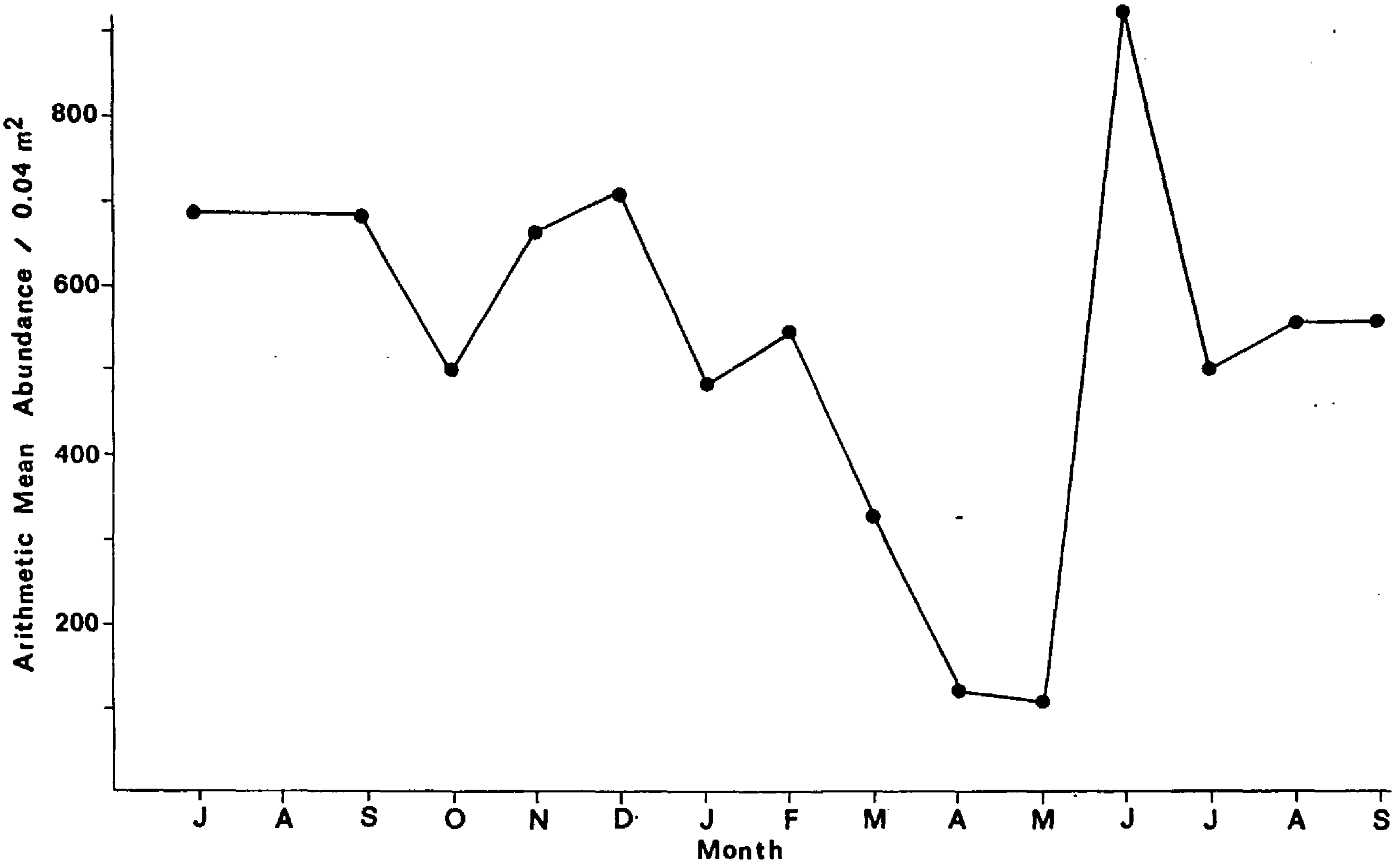
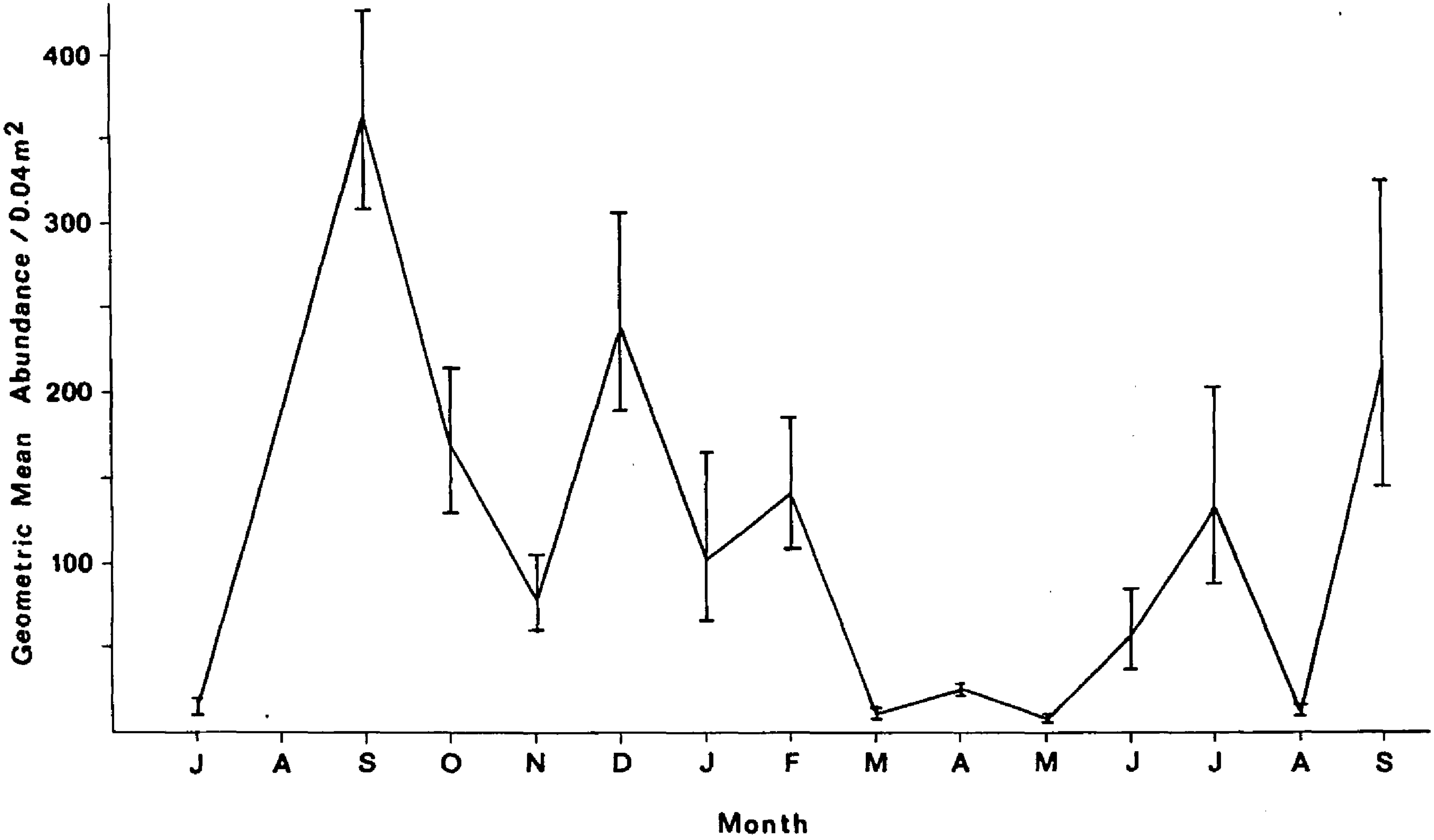

Arithmetic Mean Abundance / 0.04 m^2
800
600
400
200
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
Month

Fig. 29. Monthly abundance of A. *virginiana* at Ocean Park, 1971-72, expressed as derived (geometric) means ± 95% confidence intervals.


400
300
200
100
Geometric Mean Abundance / 0.04m2
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
Month

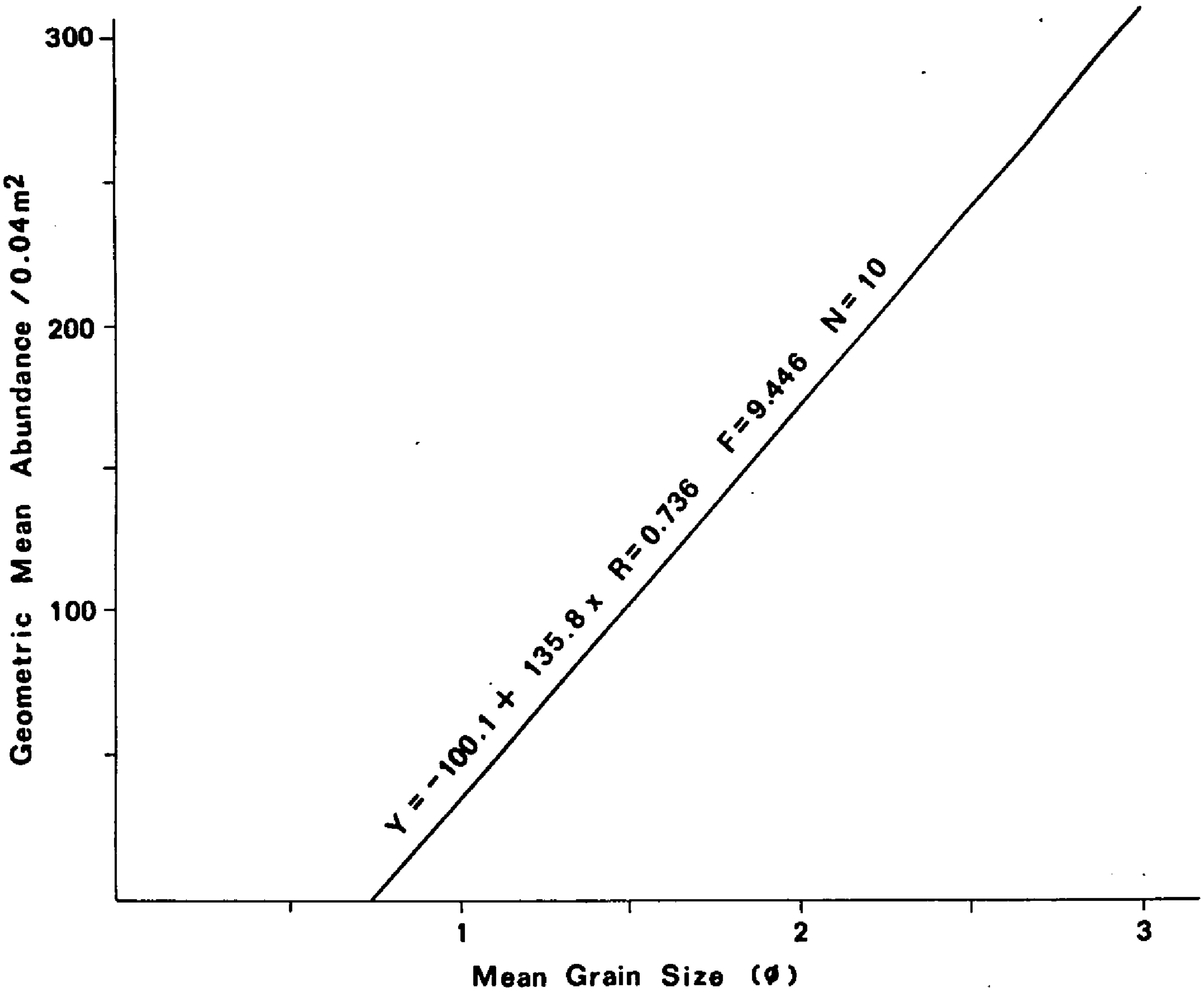
relative abundance, but also indirectly expresses dispersal since monthly data that generated high geometric means were characterized by high, relatively uniform abundances over the entire foreshore, while monthly data that generated low geometric means reflected lower, more erratic abundances with extreme aggregation in the lower foreshore. Although spring and late summer recruitment are evident in Figure 29, the significantly different overall abundances between some successive months is difficult to explain in terms of life cycle events exclusively.

It was noted during the Ocean Park collections that the absence of A. virginiana from the upper foreshore coincided with periods of active beach deposition, when coarse grained sand bars were migrating landward across the upper foreshore toward the berm. The relationship between mean grain size of upper foreshore sediments and the monthly geometric mean abundance of A. virginiana was examined and found to be significantly correlated; $p<0.01$ (Fig. 30). It is apparent that populations of A. virginiana evacuate foreshore areas as mean grain size of the sediments increases, and then repopulate the foreshore when finer sediments are re-deposited.

STORM EFFECTS - BEACH REPOPULATION

The severe storm of February 19, 1972 presented an opportunity to measure beach evacuation and recolonization by A. virginiana. Using pre-storm abundance data collected

Fig. 30. Relationship between mean grain size of upper foreshore sediments and abundance of A. *virginiana* on the Ocean Park foreshore. *Regression line* based on monthly data from 10 consecutive months.


Y = -100.1 + 135.8 x R=0.736 F=9.446 N=10
Geometric Mean Abundance / 0.04 m²
300
200
100
1
2
3
Mean Grain Size (ø)

on February 15, 1972 as a baseline, supplementary transect collections were taken 1,3,7, and 21 days after the storm (Fig. 31). The foreshore abundance of A. virginiana was drastically reduced from a pre-storm abundance of 245/0.04 m^2 to a post-storm abundance of 7/0.04 m^2. An abundance of 98/0.04 m^2 was evident three weeks after the storm, with low abundances persisting at the Ocean Park habitat until recruitment in June.

For several weeks following the storm, coarse grained sand bars were evident in the foreshore. The population of A. virginiana remained aggregated near the low water mark and was not common in upper foreshore sediments until 60 days after the storm.

Croker (1968) noted negligible disruption of the amphipod fauna of Georgia beaches following hurricanes. However, a number of these southern species burrow deeper into the sediments and rarely swim. Shortly after spring storms and beach erosion, Lemire (1968) found little change in sand-burrowing amphipod abundance, with the exception of a post-storm absence of A. virginiana along her study transect. It is evident that A. virginiana avoids the altered conditions created along a depositional beach area following storm erosion.

LONGSHORE DISTRIBUTION

Longshore population abundances of A. virginiana at mean low water on two separate days are tabulated in Figure 32 (station locations are shown in Fig. 2). The distribution

Fig. 31. Arithmetic mean abundance of *A. virginiana* at Ocean Park following a severe storm on February 19, 1972. Pre-storm data collected on February 15, 1972.

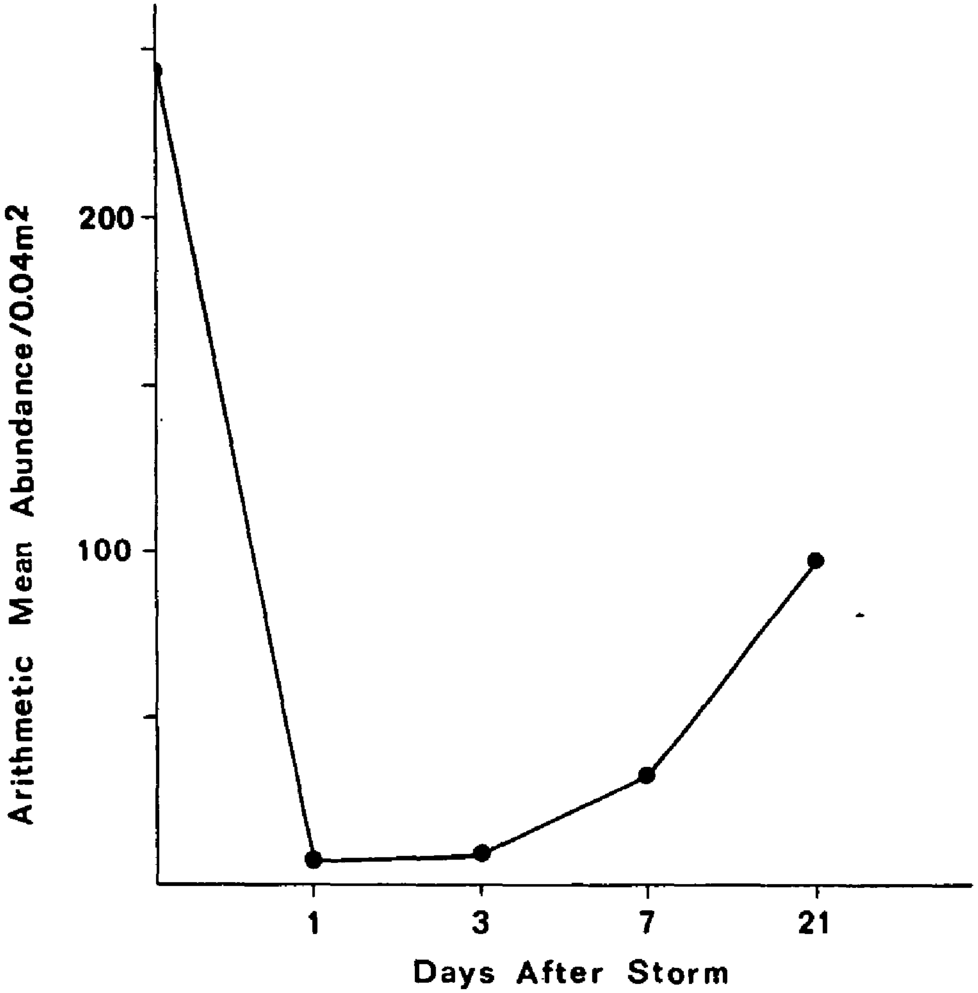
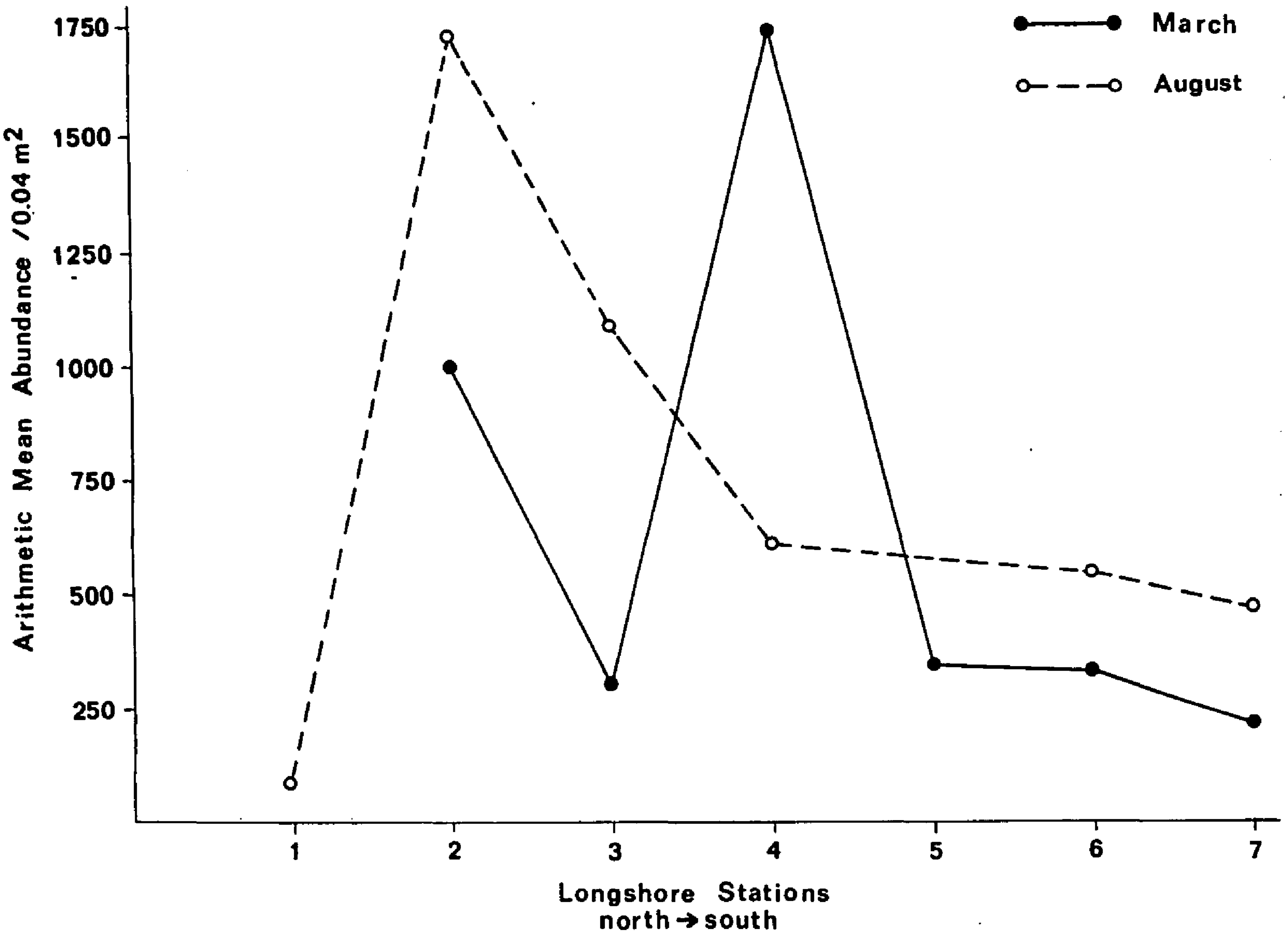

Arithmetic Mean Abundance/0.04m2
200
100
1
3
7
21
Days After Storm

Fig. 32. Abundance of A. *virginiana* at Saco Bay longshore stations (mean low water) on March 20, 1972 and August 27, 1972.


1750
1500
1250
1000
750
500
250
Arithmetic Mean Abundance /0.04 m^2
1
2
3
4
5
6
7
Longshore Stations
north → south
March
August

of _A_. _virginiana_ along the shore of Saco Bay was not uniform. Population abundance was higher along the northern beaches of Saco Bay than on the central and southern beaches.

The number of species in the macroinfaunal community was also variable. Croker et al. (1975) have recorded 17 species on the protected beaches at Prout's Neck, to the east of the present station 1. During the current transect studies, the northern beaches (example - station 3) revealed 9 species of sand macroinfauna, while the central beaches (example - station 6) rarely had more than 6 species. Although _A_. _virginiana_ numerically comprises more than 95% of the fauna on most Saco Bay beaches, it was rare at station 1 and was absent from the protected beach at Prout's Neck.

Beach stability, relative wave action, and sediment texture control both the longshore distribution of _A_. _virginiana_ and macroinfaunal community structure. Sedimentary data from both the present study and the work of Farrell (1972) indicate that mean sediment size changes drastically along the shore of Saco Bay between stations 4 and 5 (Fig. 10). Northern beaches typically have mean grain sizes of approximately 2 ϕ, while central and southerly beaches are composed of 1 ϕ sediments (Farrell, 1972). Population abundances of _A_. _virginiana_ are reduced by 50% or more on these coarse sand beaches (Fig. 32, stations 1 and 2).

The reduction in the number of species from Prout's

Neck to Ocean Park is related to the corresponding increase in wave action and beach dynamics. Monthly collections at Ocean Park yielded reduced numbers of species during periods of active beach accretion or erosion, and during rapid beach changes, *A. virginiana* was frequently the only macroinfaunal species present.

The ability of *A. virginiana* to leave the upper foreshore in response to unfavorable sedimentary conditions implies population migration to either shallow subtidal sands or adjacent intertidal areas. It was expected that August collections at longshore stations would show increased population abundances compared to the March collections as a result of the intervening June recruitment. Increased abundance was evident at all longshore stations except at station 4, where a 64% reduction from March to August was apparent (Fig. 32). Station 4 had unusually high March population abundances, while adjacent areas of the beach to the south were still at low population abundances following the February, 1972 storm. It is possible that the high abundance of *A. virginiana* at station 4 in March resulted from a migration of the species from the depositional areas further south. The low summer abundance could have been due to dispersal of animals to areas where appropriate sediments had returned during the intervening months.

SALINITY TOLERANCE

The exposure time causing 50% mortality in populations of A. virginiana in $4^{\circ}C$ seawater with varying salt concentrations is presented in Figure 33. Similar experiments were conducted in late spring at environmental ambient temperatures ($15^{\circ}C$) with similar results. It is evident that A. virginiana has a good short term (< 24 hours) tolerance to most salinities. Long term survival (> 4 days) requires a narrow range of salinity between 25 and 35 $^{o}/oo$. There were no discernible differences in salinity tolerance according to sex or size.

Salinity is probably an important limiting factor in habitat selection by A. virginiana, prohibiting the species from penetrating into estuarine habitats. With the exception of heavy rains and fresh water runoff, salinity would not be an important factor in determining within-habitat intertidal distribution, since the species is capable of tolerating any potential salinity changes on marine sand beaches during a twelve hour tidal cycle. Collections and observations during, and after heavy rains however, showed that A. virginiana evacuated the upper foreshore, and swam seaward in surface runoff. Many animals were noted under stress, or moribund in surface runoff with salinities as low as 2 to 4 $^{o}/oo$ (Croker, unpublished).

DESICCATION TOLERANCE

Amphiporeia virginiana is generally found in sediments containing 15-25% water by weight. Mortality increases drastically when the water content drops below 11% (Fig. 34). This poor tolerance to desiccation may account

Fig. 33. Time to 50% mortality in populations of *A. virginiana* exposed to 4°C water at various salinities. N=48 animals per salinity test.

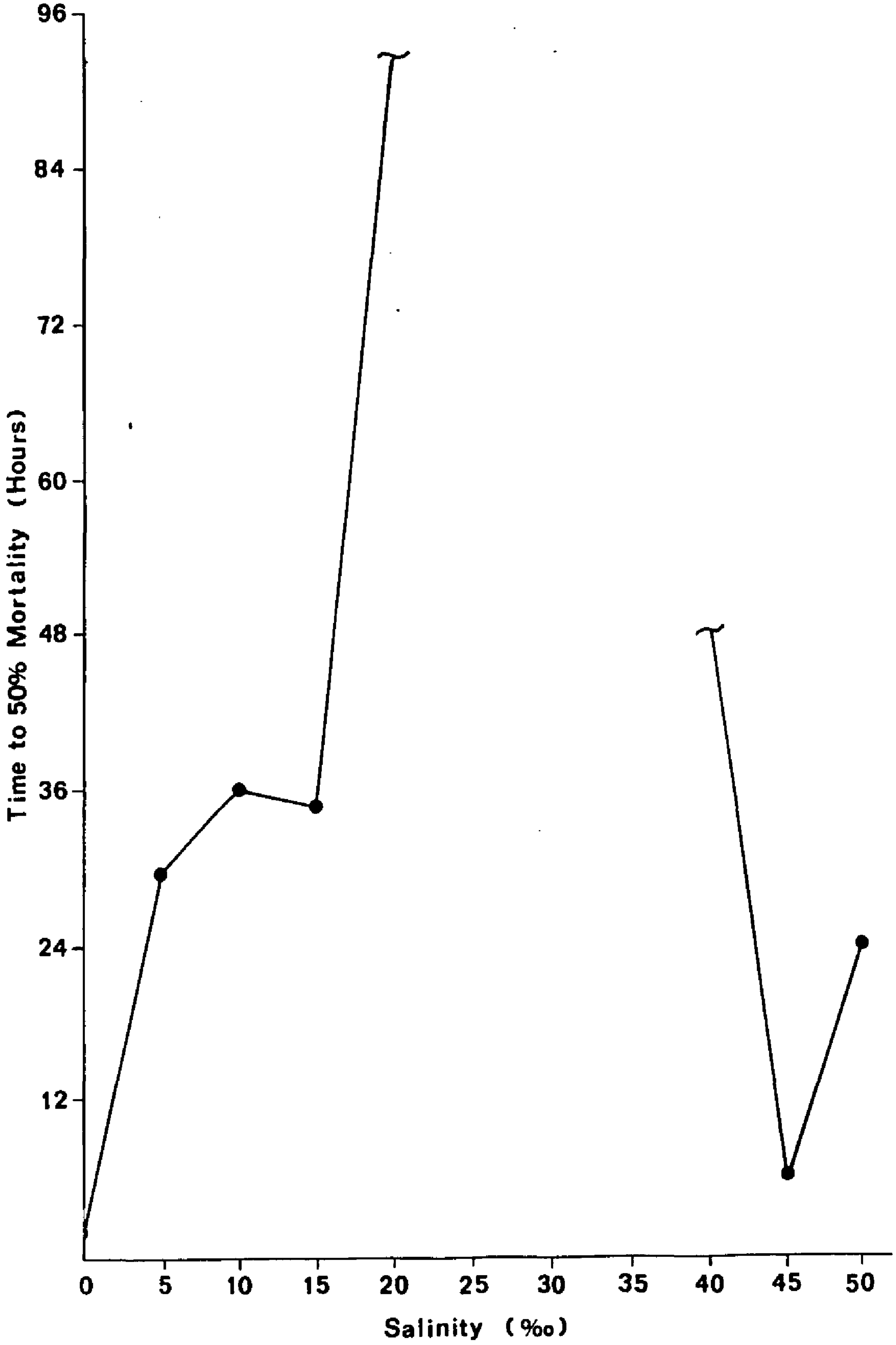
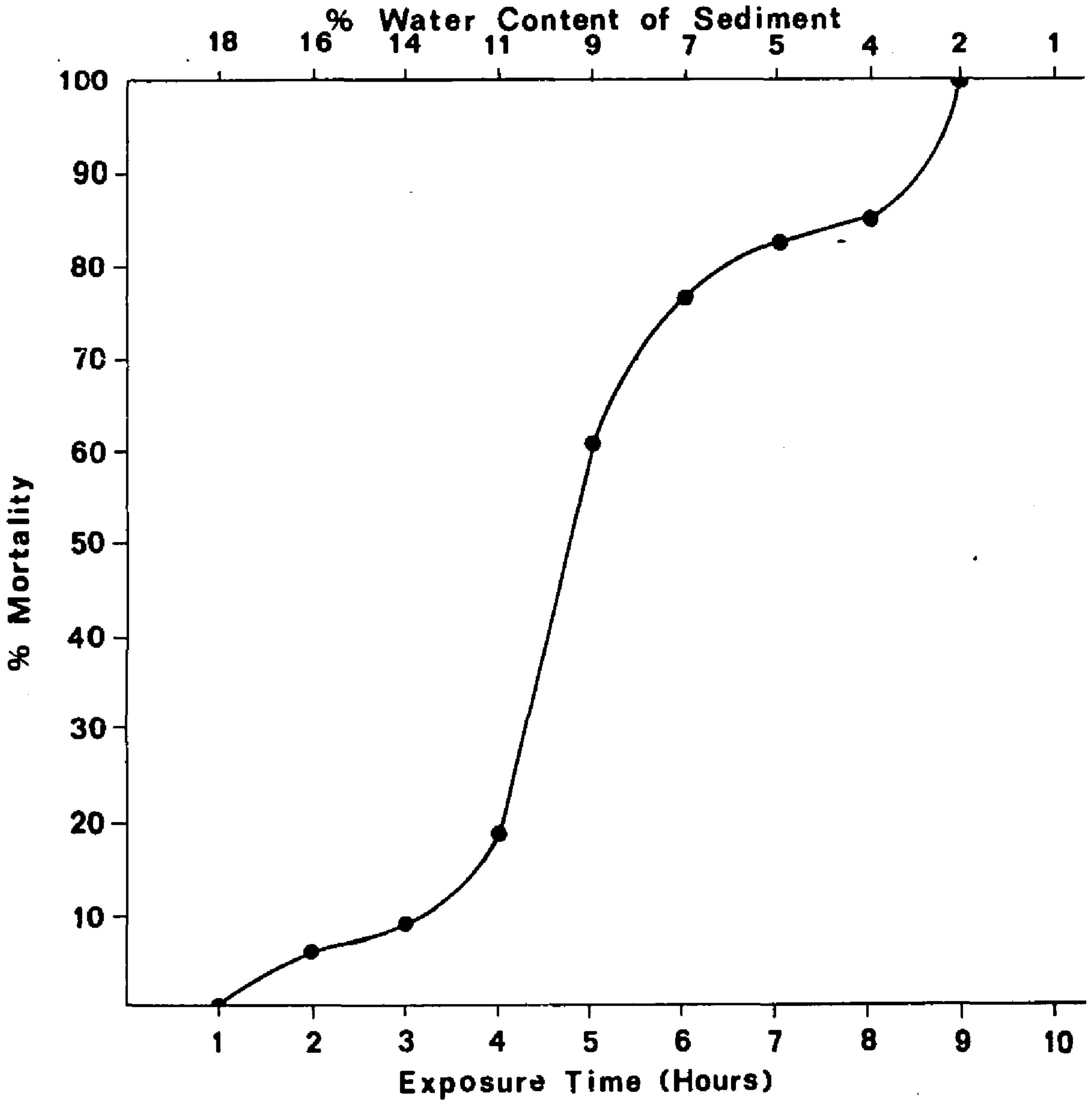

Time to 50% Mortality (Hours)
96
84
72
60
48
36
24
12
0
5
10
15
20
25
30
35
40
45
50
Salinity (‰)

Fig. 34. Percent mortality of *A. virginiana* in response to sediment desiccation at 30° C and 20% humidity. N=291 animals.


% Water Content of Sediment
18
16
14
11
9
7
5
4
2
1
100
90
80
70
60
50
40
30
20
10
% Mortality
1
2
3
4
5
6
7
8
9
10
Exposure Time (Hours)

for the confinement of the species to areas of the beach that experience minimal water loss. A depositional beach, with migrating sand bars that increase the desiccation rate of foreshore sediments, presents a potentially dangerous habitat for *A. virginiana*. Desiccation may also account for increased mortality found in collections of animals from the upper foreshore.

DISCUSSION

The studies of Watkin (1939a, 1939b, 1941), Colman and Segrove (1955), and Fincham (1970a) considered the swimming behavior displayed by several sand beach amphipods, and concluded that the species investigated undertook only brief excursions into the water column, producing minimal effects on their horizontal distributional patterns in beach sediments. Other sand beach crustaceans, e. g. *Emerita analoga*, are known to perform daily migrations with resultant daily changes in distribution (Efford, 1965; Barnes and Wenner, 1968; Cubit, 1969; Dillery and Knapp, 1970). Distributional changes on sand beaches due to daily migrations were also suggested for populations of the amphipod *Synchelidium* sp. (Enright, 1961a), the isopod *Eurydice pulchra* (Fish and Fish, 1972) and the shrimp *Crangon crangon* (Al-Adhub and Naylor, 1975).

Daily migrations of *A. virginiana* over the beach foreshore account for the short term fluctuations in distribution and abundance displayed by this species. The distributional changes are minimal on a stable beach, but are more pronounced on a dynamic beach where the species avoids areas undergoing drastic changes in sediment texture. The success of any animal in a physically controlled community requires certain morphological, physiological, and behavioral adaptations. The swimming behavior of *A. virginiana* allows the species to disperse and constantly redistribute itself into appropriate habitats along the beach, in both longshore and landward-seaward directions. This mobility appears to be the behavioral mechanism allowing *A. virginiana* to achieve its dominance on high energy beaches.

Considerable literature is available concerning the suggested relationships between species diversity and the relative physical stability of habitats. Although Johnson (1970) and Jackson (1972) have observed variations in faunal diversity within relatively homogeneous environments and concluded that diversity was the result of the relative physical stability of any given area within the habitat, Gray (1974) pointed out that changes in sediment structural complexity have not been considered when viewing environmental stress gradients and intertidal sand communities. The present longshore data from Saco Bay, including the data of Croker et al. (1975) and Farrell (1972), provide preliminary evidence of changes in community structure and sedimentary structure along an environmental stress gradient, thus supporting Johnson's (1970) suggestions that small scale changes in diversity are related to small scale changes in habitat stability.

SECTION IV

PELAGIC BEHAVIOR IN THE SURF PLANKTON

INTRODUCTION

The tidal plankton over sand beaches is a relatively unexplored subject, although the few investigations made to date have revealed a dynamic association, undergoing daily and seasonal changes. Earlier, Watkin (1939a, 1939b, 1941) showed that the macrofaunal plankton is composed primarily of peracaridean crustaceans, including an intertidal sand-dwelling component undergoing a vertical migration into the surf, and a component of migrants that venture to shore from adjacent rocky areas or the sublittoral benthos. Watkin further noted that both components were decidedly nocturnal and possibly were responsive to the lunar cycle.

Subsequent studies (Colman and Segrove, 1955; Fincham, 1970a) confirmed many of Watkin's observations. The surf plankton is markedly nocturnal with the migrant component distributed in surface waters throughout the tidal zone, and with the sand-dwelling component distributed in bottom waters over the location of the benthic abundance. It has also been shown that a given species may have differing planktonic and infaunal sex ratios, and that population abundances vary with time of day, tidal level, and lunar phase.

Enright (1961a) demonstrated the ability of the sand beach amphipod, _Synchelidium_ sp. to enter the tidal plankton and undergo daily intertidal migrations. Enright (1961b) also provided evidence that this species entered the plankton in response to minute changes in the pressure exerted on the substratum. Fincham (1970b) and Fish and Fish (1972) found that sand-burrowing crustaceans displayed endogenous rhythms of swimming behavior coincident with tidal phenomena. The available literature on tidal rhythms was reviewed recently by Palmer (1973, 1974).

Since the majority of the studies on the composition and dynamics of the surf plankton are confined to European shores, the current study was undertaken to survey the tidal plankton over a temperate western Atlantic sand beach, and disclose the dynamics of the various components. The dynamics and behavior of _Amphiporeia virginiana_ populations in the surf plankton is given particular attention to determine the effect swimming behavior may have on infaunal distribution.

MATERIALS AND METHODS

Tidal plankton collections were made at the Ocean Park transect site in Saco Bay, Maine (Fig. 2). Duplicate tows were taken every two hours for a 24 hour period on April 18, and April 25, 1971, and every two hours for a 12 hour period on May 2, May 9, September 7, and December 8, 1971. Individual samples were taken by slowly towing a

0.25 m, 0.569 mm mesh plankton net in waters one meter deep; thus various tidal levels were sampled as the tides rose and fell. The net was kept 15 cm below the surface of the water by means of two floats attached to both ends of the net. The net was towed 3 m behind the collector, to avoid capturing animals from disrupted sediments, in a direction parallel to the shore. The position on the beach of each sample was determined by measuring from a fixed reference point established in the dunes, and locating the exact elevation on a beach profile diagram constructed from surveying data measured at low water on the days of collection. Animals were preserved in the field in 5% formalin and returned to the laboratory for identification and counting. At the time of each collection, water temperature and salinity were recorded and observations were made on wave height, weather conditions, and illumination.

Observations on swimming activity of A. virginiana were made in late November, 1973. Six 2 gallon aquaria were filled in the field with seawater and 5 cm of sediments containing live specimens of A. virginiana. The aquaria were transported to an unheated, glass enclosed room close to the beach, where temperature and lighting conditions closely paralleled beach conditions. At hourly intervals for a 48 hour period, the number of A. virginiana swimming in the aquaria were recorded. The procedure was repeated for a second 48 hour period one week later to see if swimming behavior was related to the neap-spring tidal cycle.

During this second experiment, 2 aquaria were exposed to natural lighting, 2 aquaria were maintained in constant darkness, and 2 aquaria were maintained in constant artificial light.

RESULTS

PLANKTON COMPOSITION AND FLUCTUATIONS

A macrofaunal assemblage of 43,601 animals representing 16 species was identified during the study. An abundant microfaunal component composed of barnacle nauplii, calanoid copepods, polychaete and fish larvae was evident in the spring collections, but the present study will focus on macrofaunal species exclusively.

The composition and relative abundance of species for the entire study is summarized in Table 1. The large majority of the surf plankton was composed of amphipods and cumaceans with four species: *Amphiporeia virginiana*, *Mancocuma stellifera*, *Bathyporeia quoddyensis*, and *Gammarus lawrencianus*: numerically comprising over 99% of the macroplankton. The first three species are infaunal residents of intertidal sediments, while *G. lawrencianus* occurs on deeper subtidal sediments or on subtidal algae (Steele and Steele, 1970). *Gammarus lawrencianus* frequently drifts into the night tidal plankton clinging to floating algae. *Amphiporeia virginiana* was numerically the dominant species, accounting for 65% of all animals collected and comprising from 60 to 100% of individual samples.

TABLE 1

OCEAN PARK SURF PLANKTON - SPECIES COMPOSITION AND FREQUENCY OF OCCURRENCE

	Total Numbers	%Frequency+
*Amphiporeia virginiana	28,242	94
*Mancocuma stellifera	11,792	73
*Bathyporeia quoddyensis	2,252	58
Gammarus lawrencianus	1,263	94
*Psammonyx nobilis	11	14
Idotea baltica	11	17
Idotea phosphorea	10	5
*Scolelepis squamata	5	8
Photis sp.	4	11
*Chiridotea tuftsi	3	8
*Chiridotea coeca	2	5
Gammarus oceanicus	1	2
Jassa falcata	1	2
Calliopius laeviusculus	1	2
Corophium sp.	1	2

*Members of macroinfauna of coastal sand communities

+Percent frequency of occurrence in a total of 50 samples

Variability in the relative abundance of the four principal species was more pronounced on a short-term scale, reflecting the influence of tidal level of capture and the day-night cycle, as compared with long-term variability that would have implied lunar or seasonal effects. Since these diurnal events appeared most important, the parameters influencing the planktonic occurrence of the animals can be most clearly seen through analysis of data collected over a single 24 hour period (April 18, 1971).

Daily variations in the abundance of the three principal amphipod species are shown in Figures 35 and 36. Amphiporeia virginiana displayed several periods of peak abundance during both day and night, while B. quoddyensis and G. lawrencianus displayed peak abundance at night. The daytime abundance of B. quoddyensis is severely reduced, but not as dramatically as that of G. lawrencianus, because daylight samples taken at mean low water or below were over the normal infaunal location of B. quoddyensis. Gammarus lawrencianus occurs further offshore. Jansson and Kollander (1968) demonstrated that certain algal dwelling amphipods swam in response to decreasing light intensity and were less active with increasing light activity. The absence of G. lawrencianus from daylight samples suggests that this species displays this type of behavior.

The cumacean M. stellifera was abundant in samples taken over its usual benthic location, i.e. low water and below. It was rare in waters over areas of the beach it did

Fig. 35. Mean number of A. *virginiana* collected at two hour intervals from the surf plankton over various beach elevations at Ocean Park, Maine on April 18, 1971.

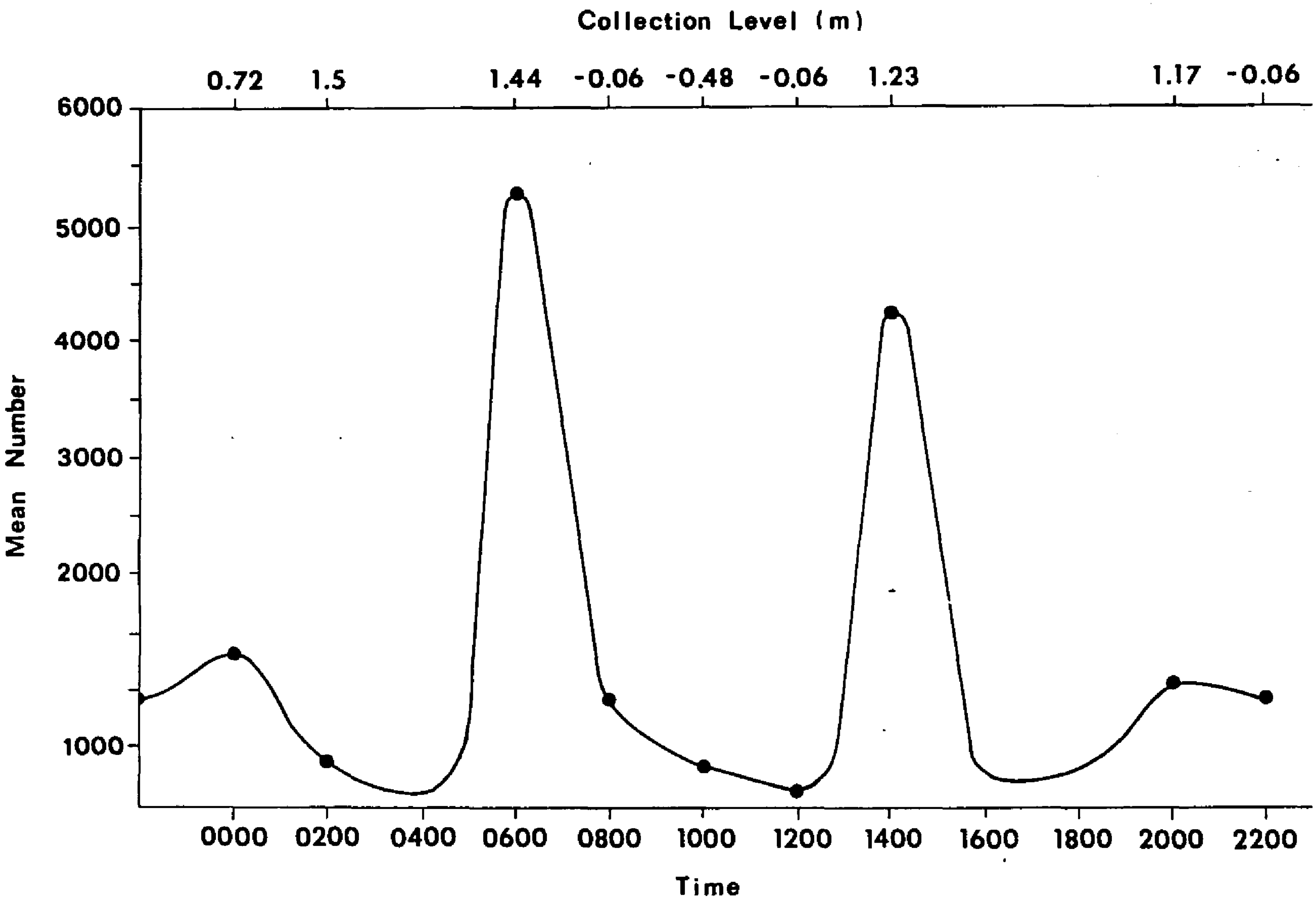
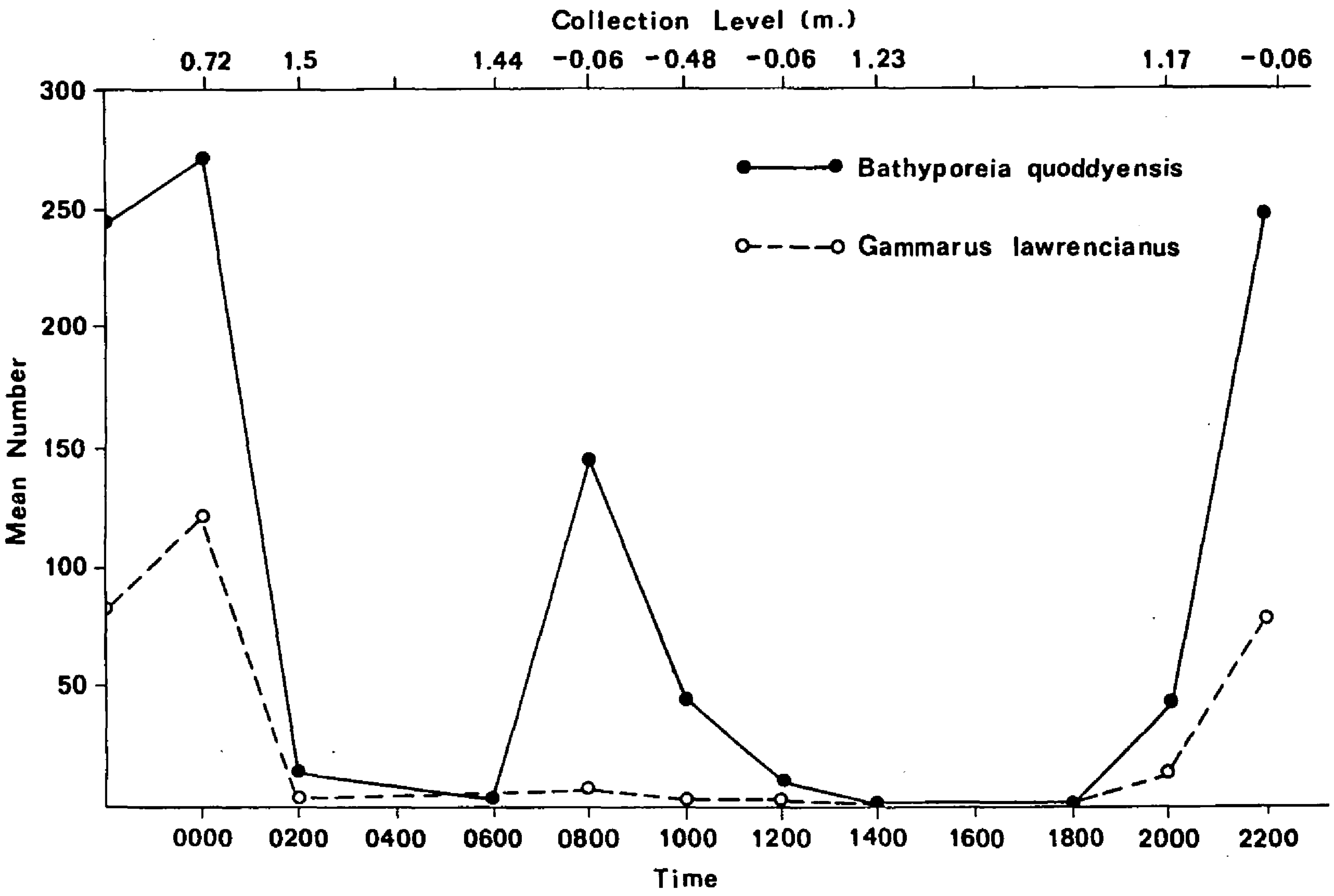

Collection Level (m)
0.72
1.5
1.44
-0.06
-0.48
-0.06
1.23
1.17
-0.06
6000
5000
4000
3000
2000
1000
Mean Number
0000
0200
0400
0600
0800
1000
1200
1400
1600
1800
2000
2200
Time

Fig. 36. Mean numbers of *B. quoddyensis* and *G. lawrencianus* collected at two hour intervals from the surf plankton over various beach elevations at Ocean Park, Maine on April 18, 1971.


Collection Level (m.)
0.72
1.5
1.44
-0.06
-0.48
-0.06
1.23
1.17
-0.06
300
250
200
150
100
50
Mean Number
Bathyporeia quoddyensis
Gammarus lawrencianus
0000
0200
0400
0600
0800
1000
1200
1400
1600
1800
2000
2200
Time

not normally occupy, and no differences were evident between day and night samples.

PELAGIC POPULATIONS OF *A. VIRGINIANA*

The planktonic occurrence of *A. virginiana* lacked a day-night pattern, rather abundance was related to collection location on the beach. Samples collected from waters overlying beach elevations of 1 to 1.7 m generally yielded maximum numbers of *A. virginiana*. Although *B. quoddyensis*' occurrence was partially related to beach level, that species was typically more abundant in waters over its preferred habitat zone. *Amphiporeia virginiana* generally inhabits lower foreshore sediments with maximum infaunal abundance occurring from 0.0 to 0.7 m above mean low water. The landward shift of the pelagic distribution relative to the infaunal distribution indicates that *A. virginiana* undertakes a diurnal migration over the beach foreshore, rather than the brief, primarily nocturnal vertical excursions taken by *B. quoddyensis* into waters directly over its usual benthic habitat zone.

Subsamples of *A. virginiana* were taken from collections representing various levels on the beach, and a total of 624 specimens were sexed and measured. Sex zonation of *A. virginiana* in the tidal plankton closely paralleled the infaunal sex zonation where males predominated on the lower foreshore, and females predominated on the upper foreshore.

By plotting abundance values of *A. virginiana* in relation to tidal level of collection, and connecting the data points in a time sequence, a daily distribution pattern emerged (Fig. 37). The abundance of *A. virginiana* in the water overlying the beach steadily increased from a minimum below mean low water level to a maximum near 1.5 m above mean low water. The abundance of the species rapidly declined above the 1.5 m level. The abundance of *A. virginiana* was also markedly greater in ebb tide collections than in flood tide collections at comparable tidal levels.

The hypothetical distribution of *A. virginiana* in the surf plankton over a single tidal cycle is presented in Figure 38, based on inferences from field data. Animals leave the sediments shortly after they are covered with water during the flood tide. A landward migration over the foreshore accompanies the rising tide, resulting in maximum pelagic abundances of *A. virginiana* in waters near the 1.5 m level shortly after high water. The steep beach slope at Ocean Park begins at approximately 1.7 m creating a physical barrier preventing further landward migrations. Animals that have either burrowed into upper foreshore sediments, or remain swimming in the water column eventually migrate in a seaward direction during the ensuing ebb flow and ultimately burrow into lower foreshore sediments. Animals that are momentarily stranded on the upper foreshore as the tide recedes were observed to swim in a seaward direction in surface films as far as possible before burrowing into the sand.

Bathyporeia quoddyensis and *Gammarus lawrencianus*

Fig. 37. Mean number of A. *virginiana* collected from waters over various beach elevations at Ocean Park, Maine on April 18, 1971. Data points are connected in the time sequence of collection.

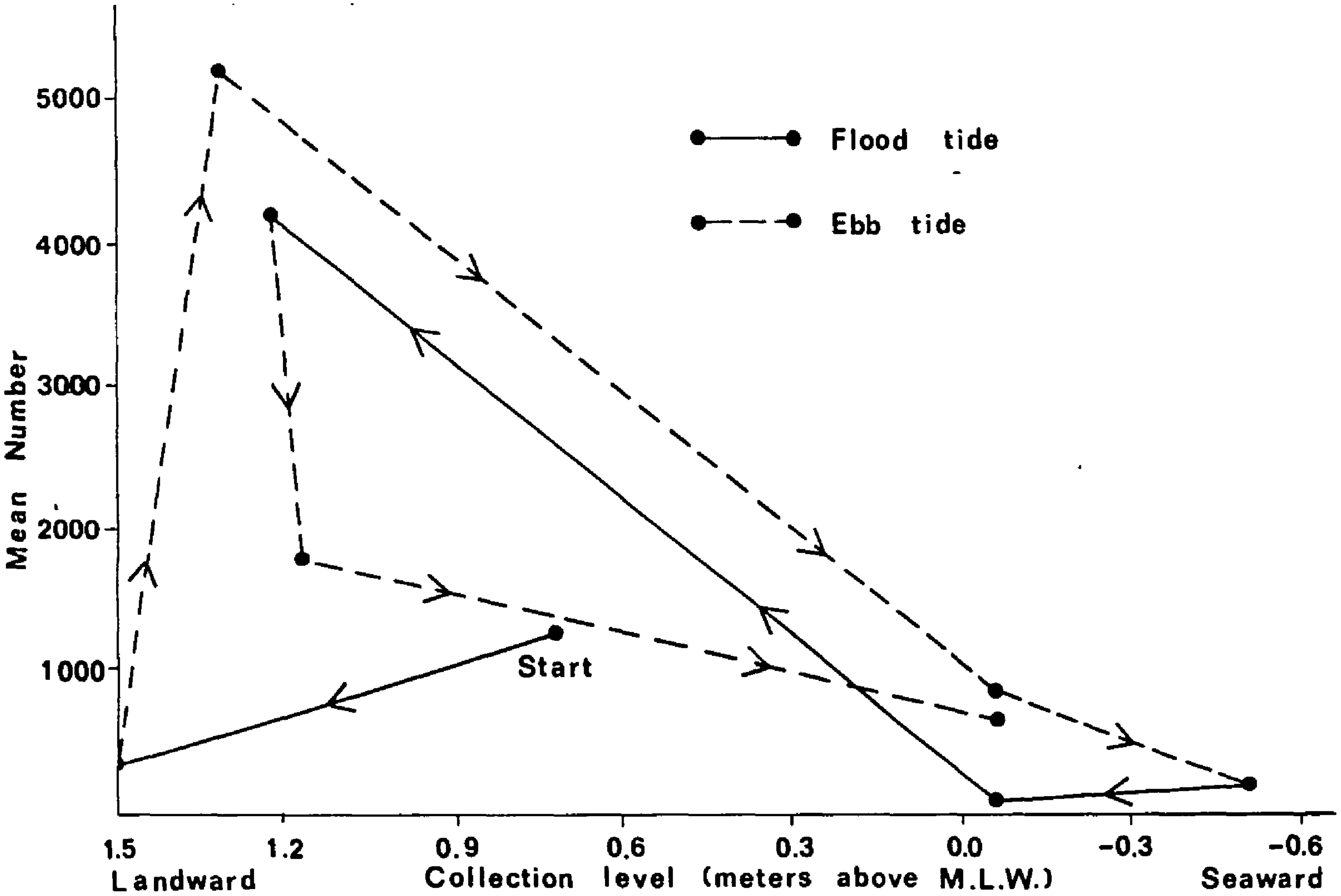
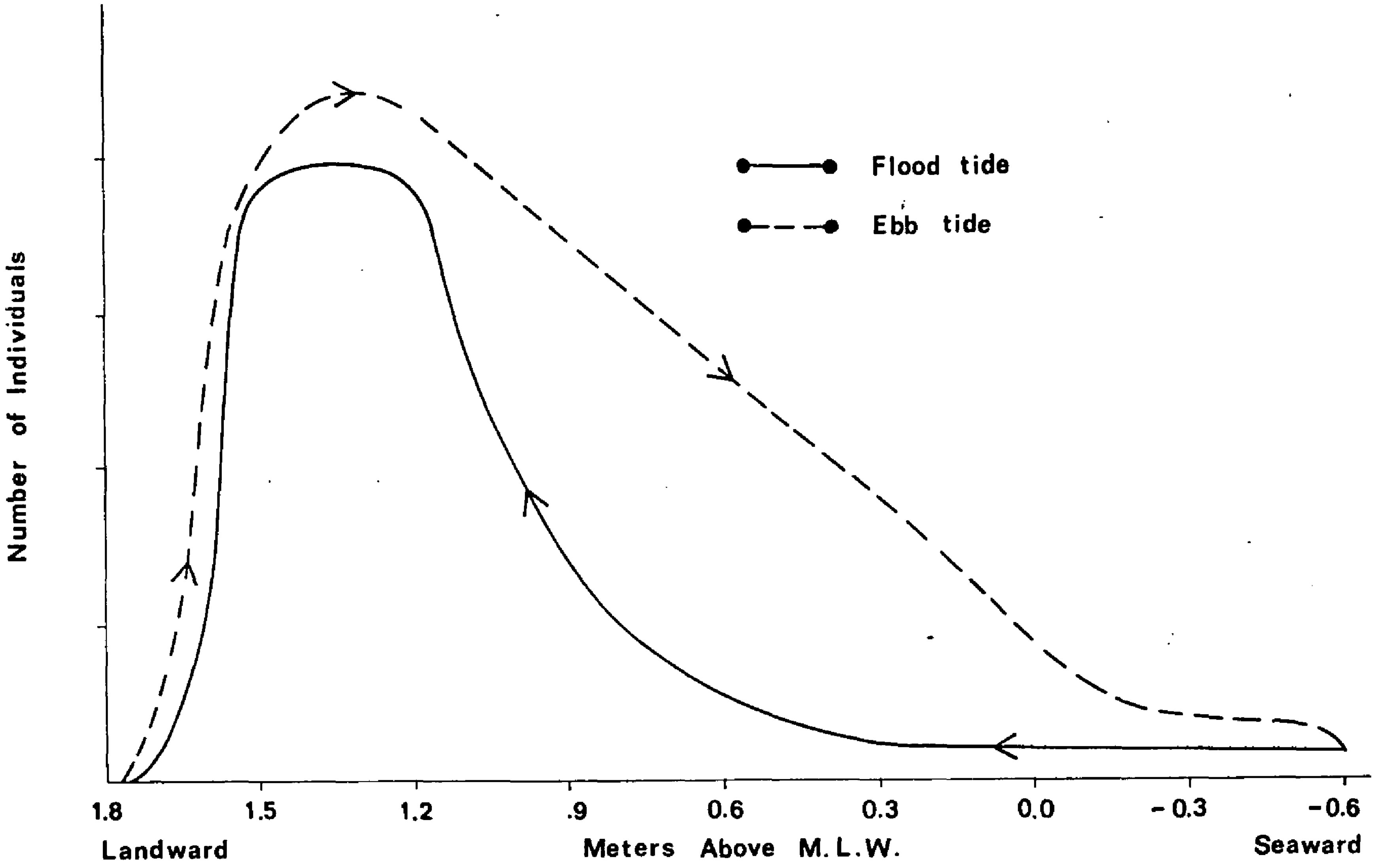

Mean Number
5000
4000
3000
2000
1000
Flood tide
Ebb tide
Start
1.5
1.2
0.9
0.6
0.3
0.0
-0.3
-0.6
Landward
Collection level (meters above M.L.W.)
Seaward

Fig. 38. Hypothetical pelagic distribution of *A. virginiana* at Ocean Park, Maine during a 12 hour tidal cycle.


Flood tide
Ebb tide
Number of Individuals
1.8
1.5
1.2
.9
0.6
0.3
0.0
- 0.3
-0.6
Landward
Meters Above M.L.W.
Seaward

evidently enter the plankton in response to reduced light intensity, but this stimulus for swimming activity is not apparent for A. virginiana. It was observed, for example, that numbers of A. virginiana varied widely between replicate samples taken at each scheduled collection time, while the numbers of other species remained similar (Table 2). The only factor observed to vary between the two samples was the increase of intensity of surf action. It is quite probable that A. virginiana swims in response to either increased pressure or the liquification and disturbance of sand produced by waves.

SWIMMING BEHAVIOR

Laboratory observations on the swimming behavior of A. virginiana provided support for field findings (Figs. 39 and 40). Although the animals were presented no stimuli other than light, rhythmic swimming activity occurred with maximum activity occurring at the time of the ebbing tide on the shore. Swimming activity ceased at the time of low tide, and did not resume until shortly before the time of high water. Swimming behavior synchronous with the tidal cycle was found in all aquaria and no significant discrepencies were noted between aquaria, regardless of lighting conditions. In the absence of natural tidal cues, the swimming rhythm rapidly degenerated after the first 24 hour period.

TABLE 2

VARIATION BETWEEN REPLICATE PLANKTON SAMPLES

Sample #12 April 18, 1971 2200 hours -0.05 m below MLW

	Replicate Samples	
Species	A	B
Amphiporeia virginiana	483	902
Bathyporeia quoddyensis	249	235
Gammarus lawrencianus	41	121
Mancocuma stellifera	176	124

Note: Samples were taken ten minutes apart, but sample B was taken in heavier surf than sample A. Sample B contained a greater amount of floating algae, associated with the increased abundance of *G. lawrencianus*.

Fig. 39. Percentage of A. *virginiana* swimming in aquaria in relation to tidal cycle over a 48 hour period: November 19 through 21, 1973. N=523 animals.

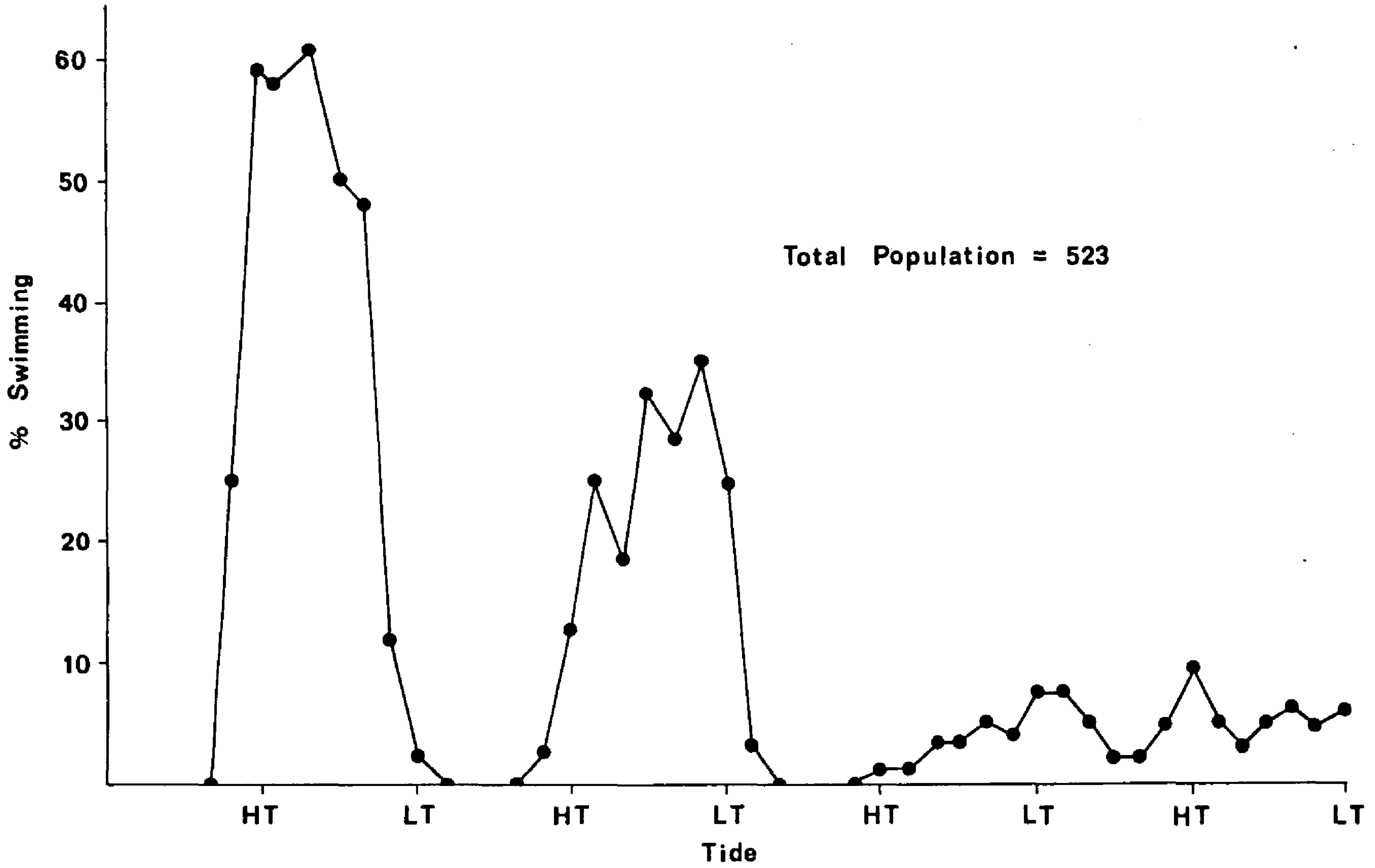
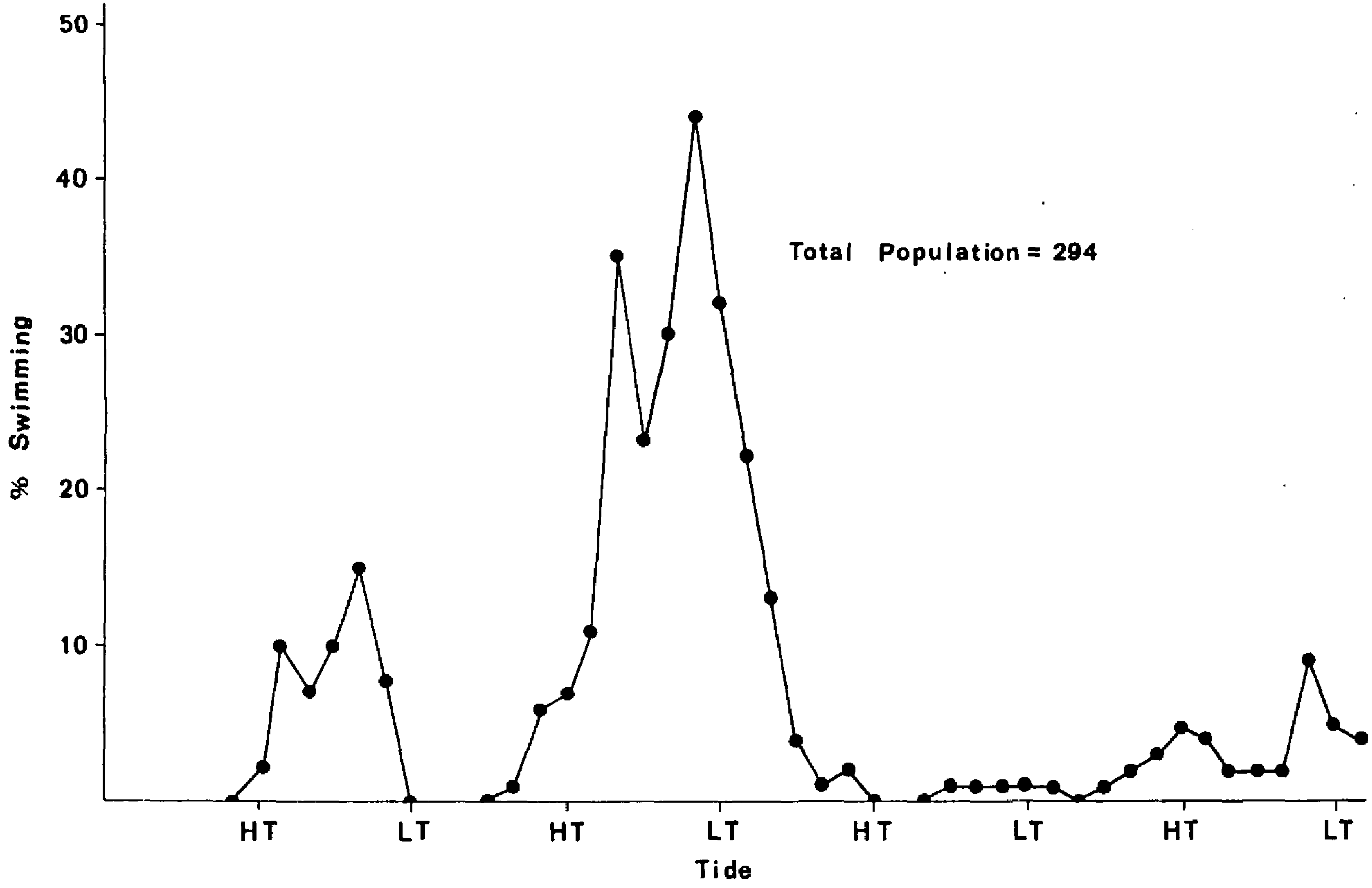

% Swimming
60
50
40
30
20
10
Total Population = 523
HT
LT
HT
LT
HT
LT
HT
LT
Tide

Fig. 40. Percentage of *A. virginiana* swimming in aquaria in relation to tidal cycle over a 48 hour period: November 27 through 29, 1973. N=294 animals.


% Swimming
50
40
30
20
10
Total Population = 294
HT
LT
HT
LT
HT
LT
HT
LT
Tide

DISCUSSION

Watkin's (1939a, 1939b, 1941) division of the tidal plankton into infaunal residents performing vertical migrations, and tidal migrants from subtidal habitats is applicable to the surf plankton at Ocean Park. Vertical migrants are *A. virginiana*, *B. quoddyensis*, and *M. stellifera*, while *G. lawrencianus* and other less commonly encountered amphipods and isopods are tidal migrants.

The maintenance of infaunal zonation patterns by sand beach crustaceans vertically migrating into the tidal plankton is well documented by Watkin (1941), Colman and Segrove (1955), and Fincham (1970a). In the present study, the intertidal sand-dwelling species *B. quoddyensis* and *M. stellifera* remained accurately zoned, while *A. virginiana* established a pelagic distribution skewed in the landward direction from its infaunal distribution. Enright (1961a) showed that the sand beach amphipod *Synchelidium* sp. performed a diurnal migration over the beach; it appears that the behavior of *A. virginiana* more closely parallels the behavior of *Synchelidium* than its familial relation, *B. quoddyensis*.

The endogenous rhythmic swimming behavior of *A. virginiana* is similar to that reported for *Bathyporeia pelagica* (Fincham, 1970b) and for *Eurydice pulchra* (Fish and Fish, 1972); all three species displayed peak swimming activity synchronous to times of ebbing tides. In sharp contrast to the latter two species, _A_. _virginiana_ showed no suppression of swimming activity in response to light or lunar cycle. Persistence of the endogenous rhythm in _A_. _virginiana_ is substantially briefer than that noted for most intertidal marine crustaceans (Palmer, 1973, 1974). Enright (1972) demonstrated endogenous tidal rhythms that were evident longer than 60 days in the laboratory.

Enright (1961b) demonstrated swimming behavior in _Synchelidium_ sp. in response to pressure changes, and later entrained a sand beach isopod, _Exicirolana chiltoni_, to a tidal swimming rhythm by simulating wave action on sediments (1965). Since light appears unrelated to swimming behavior in _A_. _virginiana_, it is probable that wave action on sediments serves as the major stimulus to initiate the vertical migrations of the species. For example, repeated observations showed that the mere pressure and resultant liquification of sand by a footstep stimulated _A_. _virginiana_ to leave the sediment and swim in beach surface water films.

Swimming activity in _A_. _virginiana_ presumably enhances opportunities for mating contacts as was suggested for the haustoriid _B_. _pelagica_ (Fincham, 1970b). The mobility and intertidal migrations of _A_. _virginiana_ has further adaptive significance by allowing the species to occupy extremely unstable habitats, or temporarily utilize habitat space that may become unsuitable during some portion of the tidal cycle.

Although pelagic occurrence is known for several species of haustoriid amphipods, the species undertaking substantial vertical migrations from the sand are all members of the subfamily Pontoporiinae. For the other haustoriid subfamily, the Haustoriinae, a significant pelagic phase has never been noted. Conspicuous in their absence from surf plankton collections were *Acanthohaustorius millsi* and *Haustorius canadensis*, both members of the Haustoriinae and both common in the sediments at the Ocean Park study area. Bousfield (1970) noted that the subfamily Haustoriinae is more recent, and more highly adapted to a sand-burrowing existence than the Pontoporeiinae. The loose affinity with the substratum and the daily migrations displayed by many species within the Pontoporeiinae, lends behavioral support to current views of evolutionary trends in haustoriid amphipods.

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