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PATTERNS OF SUCCESSION IN BENTHIC INFAUNAL COMMUNITIES FOLLOWIN--ETC(U)

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DREDGED MATERIAL RESEARCH PROGRAM

TECHNICAL REPORT D-77-27

PATTERNS OF SUCCESSION IN BENTHIC INFAUNAL COMMUNITIES FOLLOWING DREDGING AND DREDGED MATERIAL DISPOSAL IN MONTEREY BAY

by

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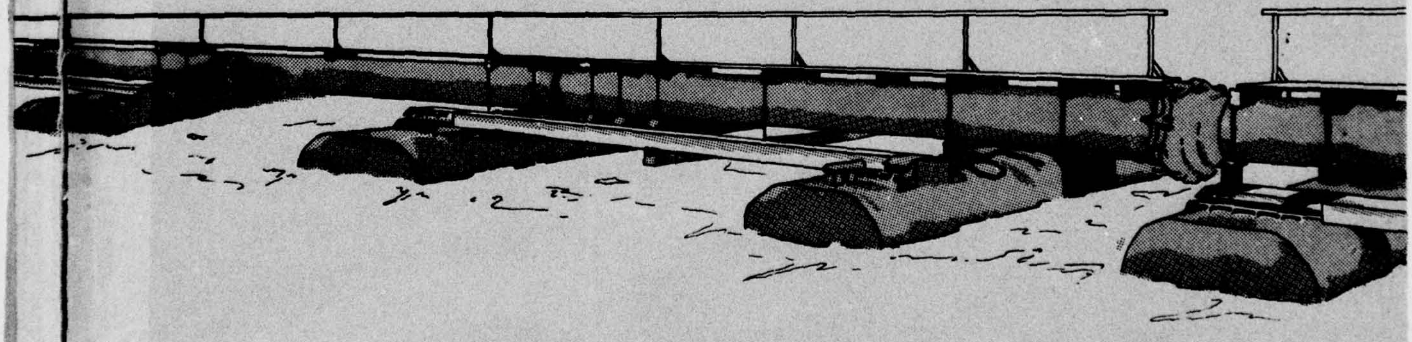
Final Report



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1. The technical report transmitted herewith represents the results of a study undertaken as Work Unit 1D10 of Task 1D, Effects of Dredging and Disposal on Aquatic Organisms, of the Corps of Engineers' Dredged Material Research Program (DMRP). Task 1D is a part of the Environmental Impacts and Criteria Development Project (EICDP), which has the general objective of determining on a regional basis the direct and indirect effects on aquatic organisms due to dredging and disposal operations. The study reported herein was part of a series of research contracts developed to achieve the EICDP general objective.

2. The objective of this work was to define and evaluate the patterns of benthic community development in sandy bottom marine communities and the mechanisms that control them. These patterns of community succession are discussed in relation to the ecological impacts of dredged material disposal. The study was a large-scale controlled field experiment, with barge loads of sedimentologically defined dredged material deposited at precisely the time and place desired for study. The disposal sites were sampled prior to, immediately after, and periodically for several years after disposal. The species and number of individuals present were recorded and species diversity indices were calculated at each sampling time.

3. It was found that the general pattern of community development following a perturbation, here referred to as community recovery or succession, was highly dependent upon the nature of the physical environment and the structure of surrounding communities. Succession was divided into an early and a late phase. The early phase was characterized by the immigration of crustaceans and the settlement of the larvae of relatively opportunistic species of polychaetes. The latter have relatively short generation times, small size, low fecundity, and high larval availability (frequency and abundance of larvae in the water). These opportunists were uncommon in the natural, undisturbed bottom community. The later phase of succession was characterized by the gradual re-establishment of the less mobile crustaceans and less opportunistic polychaetes that inhabited the areas prior to the experimental disturbances. The opportunistic or early polychaete colonists

were, in general, the same species at both the dredged material and disposal sites, but the polychaetes that characterized the later phase of succession, and crustacean and mollusk colonists when present, were dependent upon the composition of the adjacent undisturbed bottom communities.

4. Temporal and spatial variations in the near-offshore fauna were strongly influenced by wave-induced substrate motion. There is a unidirectional gradient in environmental variability related to increasing substrate motion along a shoaling bottom. Shallow areas are physically more variable and disruptive and the community is also more variable there. Since many of these species are adapted to a high level of natural disturbance, they were also characteristic of the early phase of recovery following the experimental disturbances. In general, the zonation of animals along this depth-dependent gradient of natural substrate instability was similar to the sequence of succession observed at the experimental disturbance sites. A positive relationship was determined between community resilience (rate of recovery or succession) and environmental and community variability. Communities inhabiting naturally highly variable and frequently disrupted physical environments (e.g., shallow water in offshore areas and the variable salinity back harbor) rebounded or recovered more quickly from the experimental disturbances (dredging and disposal) than those found in less variable and more benign conditions (e.g., deeper water offshore and outer harbor areas bathed by more marine water). Community resilience was correspondingly lower in the more complex communities of deeper water.

5. It was concluded that the management of benthic marine resources and dredging operations should involve an analysis of the natural disturbance regime at the potential dredging or disposal site and its relation to the associated bottom communities. For example, one disposal scheme might be to utilize natural sedimentary cycles where sediments are reworked by waves or currents and bottom communities are thus adapted to relatively high levels of natural disturbance.

6. The information and data published in this report are contributions to the further understanding of the complex nature of sediment water and biological interaction that govern the ecological recovery of aquatic dredged material deposits and establish a baseline from which to develop meaningful evaluations for the selection of an environmentally compatible disposal alternative. It is expected that the methodology employed in

this study and the resulting interpretation of the biological interactions will be of significant value to those persons concerned with CE dredged material permit programs.

JOHN L. CANNON
Colonel, Corps of Engineers
Commander and Director

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This report deals with the patterns of benthic succession in soft-bottom marine communities. The primary study objective was to elucidate and evaluate the mechanisms that control these patterns. Benthic succession is the pattern of community recovery following a perturbation. Controlled perturbations of bottom communities were effected by the dredging of locations in Moss Landing Harbor and by the disposal of dredged material in Monterey Bay, California.

The general pattern of succession was highly dependent upon the nature of the physical environment and the structure of surrounding communities. The open coast communities of Monterey Bay are numerically dominated by small crustaceans and polychaetes. Succession was divided into an early and a late phase. The early phase was characterized by the immigration of peracarid crustaceans and the settlement

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20. ABSTRACT (Continued).

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of the larvae of relatively opportunistic species of polychaetes. The latter have relatively short generation times, small size, low fecundity and high larval availability (frequency and abundance of larvae in the water). These opportunists are uncommon in the natural, undisturbed bottom community. The later phase of succession was characterized by the gradual reestablishment of the less mobile crustaceans and less opportunistic polychaetes that inhabited the areas prior to the experimental disturbances. Succession in this offshore environment was studied after the controlled mass deposition of sediment on well-defined bottom sites.

Faunal recovery after dredging in the Moss Landing Harbor involved primarily the early and late polychaete colonists. Crustaceans were uncommon. A large, dense patch of a tube-building phoronid worm was established and maintained during the succession at one harbor station. This patch was a "stable plateau" in succession which prolonged the rate of recovery of the predredging fauna but was eventually destroyed by a nudibranch predator.

The opportunistic or early polychaete colonists were, in general, the same species at all the disturbed locations (dredged and disposal sites) but the polychaetes that characterized the later phase of succession, and crustacean and mollusk colonists when present, were dependent upon the composition of the adjacent undisturbed bottom communities.

The temporal consistency of successional patterns was examined by dredging a harbor area in August 1974 very close to one dredged in August 1971 and by dumping dredged material on an offshore area during the same month in 1974 and 1971. In general, the patterns of succession were similar. The one significant and outstanding difference was the establishment of a phoronid patch in the harbor area in 1971, while none was established in 1974.

Temporal and spatial variations in the offshore fauna are strongly influenced by wave-induced substrate motion. There is a unidirectional gradient in environmental variability related to increasing substrate motion along a shoaling bottom. Shallow areas are physically more variable and disruptive and the community is also more variable there. Since many of these species are adapted to a high level of natural disturbance, they were also characteristic of the early phase of recovery following the experimental disturbances. In general, the zonation of animals along this depth-dependent gradient was similar to the sequence of successions observed.

A positive relationship was determined between community resilience (rate of recovery or succession) and environmental and community variability. Communities inhabiting highly variable and disruptive environments (e.g., shallow water in offshore areas and the back harbor) rebounded or recovered more quickly from the experimental disturbances (dredging and disposal) than those found in less variable and more benign conditions (e.g., deeper water offshore and outer harbor areas bathed by more marine water). Community resilience was correspondingly lower in the more complex communities of deeper water.

It was concluded that the management of benthic marine resources and dredging operations should involve an analysis of the natural disturbance regime at a potential dredging or disposal site and its relation to the associated bottom communities. For example, one disposal scheme might be to utilize natural sedimentary cycles where sediments are channelized or reworked by waves or currents and bottom communities are thus adapted to relatively high levels of natural disturbance.

PREFACE

This report is the final product of a two-year study conducted for the Office, Chief of Engineers, by the Moss Landing Marine Laboratories, Moss Landing, California, under Contract No. DACW39-74-C-0151 with the Environmental Effects Laboratory (EEL), U. S. Army Engineer Waterways Experiment Station (WES), Vicksburg, Mississippi.

The study, which forms part of the EEL Dredged Material Research Program (DMRP), was done in cooperation with the Moss Landing Harbor District, the San Francisco District of the Corps of Engineers and the Smith Rice Company.

Some of the work performed prior to the present contract was partially funded by the San Francisco District, the Moss Landing Harbor District and the Coastal Engineering Research Center.

The principal investigators and authors of the report were John S. Oliver, Peter N. Slattery, Larry W. Hulberg and James W. Nybakken.

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The following EEL personnel were involved with the study: Drs. R. H. Plumb, Jr., Environmental Impacts and Criteria Development Project (EICDP), Contract Manager, and R. M. Engler, EICDP Project Manager. The study was under the general supervision of Dr. John Harrison, Chief, EEL.

The Directors of WES during conduct of the study and preparation of the report were COL G. H. Hilt, CE, and COL J. L. Cannon, CE. Technical Director was Mr. F. R. Brown.

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CONVERSION FACTORS, U.S. CUSTOMARY TO SI UNITS OF MEASUREMENT

U.S. customary units of measurement can be converted to SI units as follows:

Multiply	By	To Obtain
Feet	0.3048	Metres
Miles (U.S. nautical)	1852	Metres
Fathoms	1.8288	Metres
Cubic yards	0.7645549	Cubic Metres
Gallons (U.S. liquid)	0.003785412	Cubic Metres

CHAPTER ONE

GENERAL INTRODUCTION

Man's activities have caused numerous local changes in estuarine and marine coastal environments. Among these, dredging to maintain harbor and ship channels and the disposal of dredged material disrupt marine bottom communities. Most field studies designed to determine the effects of dredging operations have been qualitative or quantitative descriptive surveys. The only significant generalization that seems to have emerged from this work is that benthic recovery from a particular disturbance occurs within one to three years. Collecting large amounts of descriptive data and subjecting these to the most sophisticated mathematical analyses has not been a productive method for evaluating man's "effect." This is the result of at least two facts; it is difficult to generalize from a purely descriptive study in one locale to another, and descriptive data per se are rarely explanatory. Without an understanding of what causes and maintains community boundaries, patches and gradients, reasonable predictions of the effect of a human activity like dredged material disposal cannot be made.

The authors do not mean to imply that descriptive data are worthless. On the contrary, they are essential in identifying patterns. However, they contribute little to the understanding of patterns and, therefore, to the construction of a predictive model. Such a model is probably mathematically intractable because most of the important biological factors are undoubtedly non-linear and dependent on many parameters which cannot be accurately estimated. But such a conceptual model can be developed from a reductionistic approach to community ecology.

This study employs a hypothetico-deductive method which is rarely used or considered appropriate in situations that demand (sometimes by law) monitoring or determining the effect of man's activities on biological communities. Specific hypotheses are generated from previous descriptive work and are tested experimentally. This approach will lead much more quickly to a realistic explanatory understanding of communities. The level of this understanding will determine the ability to make meaningful predictions concerning the effect of man.

Realizing the limitations of a purely descriptive approach, the main objective of this study is to elucidate and evaluate the mechanisms controlling benthic recovery following dredging and disposal of dredged material. In this report, recovery from disturbance is called succession. The results of previous work enabled the development and evaluation of several hypotheses concerning these controlling factors and the relation between succession and natural perturbations of these communities. In particular, the importance of dispersal or mobility of various life cycle stages, larval substrate selectivity, animal interactions and the life history patterns of potential colonists as ecological factors controlling succession were examined. Several larger scale field experiments were also performed to document the temporal consistency of observed recovery patterns: to determine the relationship between community resilience, community complexity and physical environmental stress; and to examine the variations in succession along experimental disturbance gradients. Bottom sampling also continued along a permanent transect in Monterey Bay (Figures 1 and 2) established in 1971 to document the

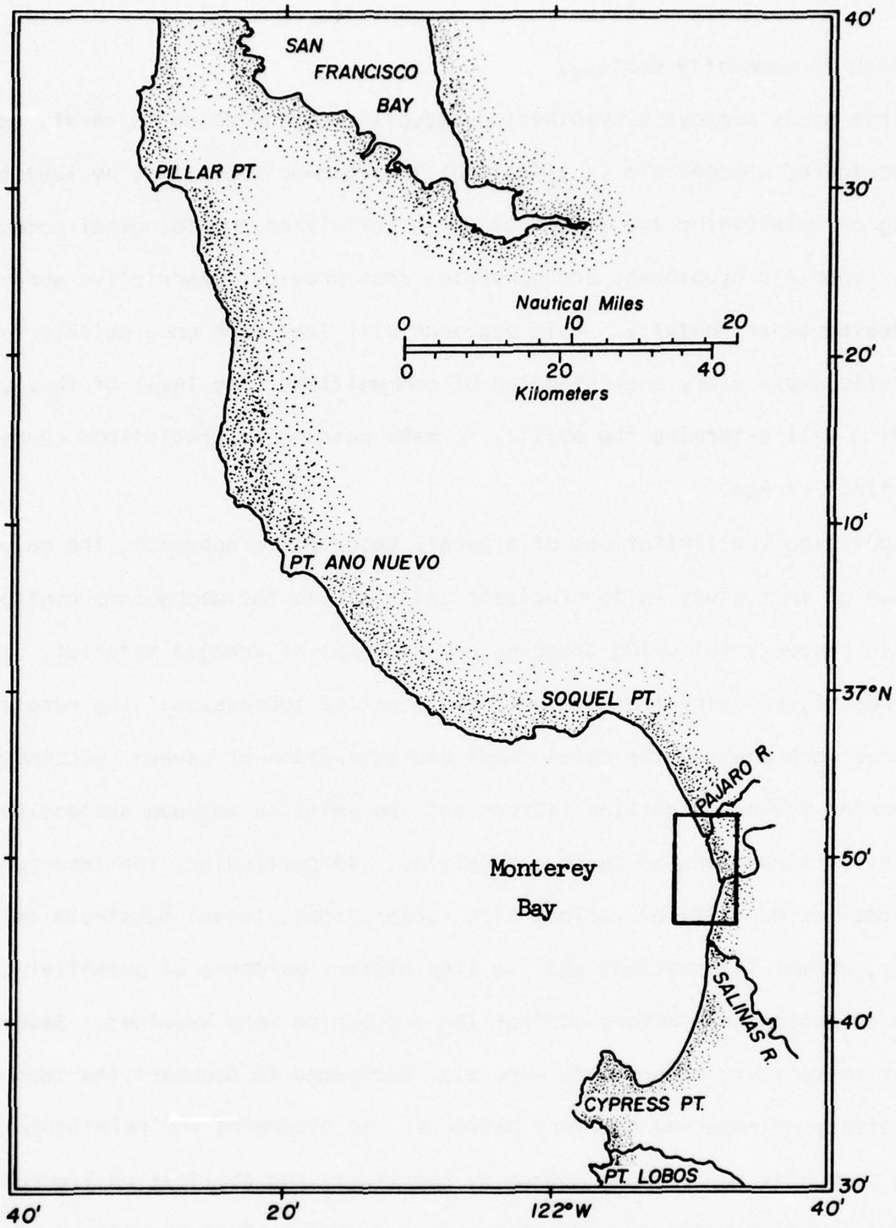

Figure 1. Monterey Bay, California. Rectangular region is enlarged in Figure 2.

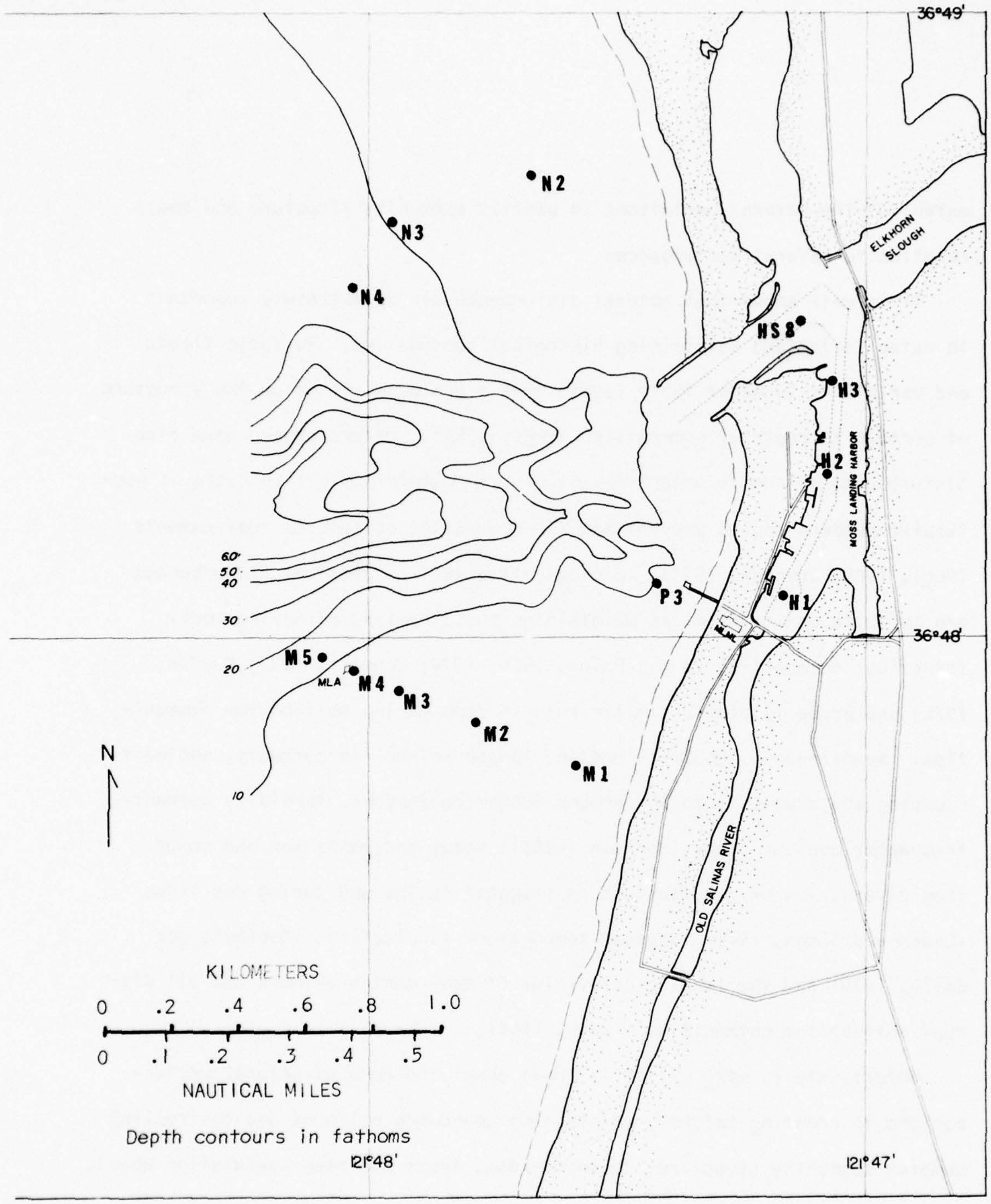

Figure 2. Central Monterey Bay. Solid circles indicate the location of benthic stations.

extent of the natural variations in benthic community structure and their relation to natural disturbances.

It is well known that natural disturbance can be extremely important in establishing and maintaining biological communities. Periodic floods and variations in water table levels have a profound effect on the structure of certain terrestrial communities (Vogl, 1969). Others depend upon fire disturbances to remove understory debris, to complete the life cycle of particular members and to prevent species monopolies or species replacements (Vogl, 1969; Dryness, 1973). Biological as well as physical disturbances are known to be important in maintaining the structure of marine rocky intertidal communities (e.g., Paine, 1966, 1974; Connell, 1972; Dayton, 1971) and probably play a similar role in some marine soft-bottom communities. Wave-induced substrate motion, longshore and rip currents, sediment slumping and movements in and around submarine canyons, turbidity currents, freshwater aquifer seeps (Hartman, 1963), heavy sedimentation and scour from rivers, low oxygen tensions in stagnant basins and during red tides (Dauer and Simon, 1976), unusual temperature fluctuations (Dahlberg and Smith, 1970) and the feeding activities of many marine animals can all disrupt soft-bottom communities (Fager, 1964).

Unfortunately, very little is known about the role of natural perturbations in creating patches, maintaining abundance patterns and controlling complex community structure. Nevertheless, there has been speculation about, and some data supporting, a relationship between natural disturbances, succession (i.e., recovery from disturbance) and variations in community structure (e.g., Johnson, 1970; Sutherland, 1974; Horn, 1975; Grassle and Grassle, 1974). The general hypothesis is that a community is a collection of patches which have different disturbance histories and, therefore, are in different states of succession. In other words, a community is envisioned as a mosaic of local successional states that are out of phase. If this hypothesis is true, then the description of benthic successional patterns will be helpful in explaining variations in benthic community structure. Moreover, the factors that control these patterns probably contribute significantly to the maintenance of these communities. Regardless of the validity of the hypothesis, marine bottom communities are often perturbed and subsequently recover in nature.

Little is known about the effect of natural disturbances on the bottom communities in the study area. There is a distinct unidirectional gradient in substrate motion (i.e., disturbance) related to increasing wave activity along a shoaling bottom. The zonation of the fauna along this gradient has been described (Oliver et al., M.S.), and it has been demonstrated that the pattern is primarily controlled by substrate stability (Oliver and Slattery, M.S.). In this report, an attempt is made to relate some of the natural variations in community structure to, among other factors, seasonal variations in wave activity (Chapter 2). Unfortunately, this is basically all that is known about the possible role of natural disturbance in maintaining the structure of local communties. Most of this report concerns the description of benthic successional patterns and the elucidation and evaluation of factors that control these patterns (Chapters 3, 4 and 5). At the end of this report, the general descriptive and experimental results are discussed and a conceptual ecological model is proposed that begins to incorporate the nature of marine bottom communities into a management process. It should be emphasized that the report and the model introduced are only *preliminary* contributions to that process. The primary objective is to increase the understanding of benthic succession: a phenomenon that must be understood to manage the disturbance activities of our civilization and insure that future generations inherit a healthy environment.

CHAPTER TWO

NATURAL VARIATIONS IN BENTHIC COMMUNITY STRUCTURE

Little is known about the natural temporal variations in benthic community structure and especially about their relation to natural disturbances. Sampling of the benthic infauna was conducted along a transect to document temporal and spatial variations in community structure. An attempt is made to relate these variations, in a very qualitative manner, to substrate disturbance caused by wave activity and to compare the amplitude of natural variations along the depth gradient to the changes caused by experimental dredged material disposal. The depth zonation of the benthos is primarily determined by wave-induced substrate motion (Oliver et al., M.S.), and it is argued here that periodic temporal variations in wave activity also have a distinct effect on the community.

Methods

Benthic infaunal cores (area = 0.018 m^2; height = 15 cm) were taken along a transect from June 1971 to April 1975 ('M' stations, Figure 2) and periodically along a similar transect at the head of the Monterey Submarine Canyon (P station, Figure 2). Usually, a total of eight replicate cores was taken from each station (depth) at each sampling interval. Cores were washed over a 0.5-mm-square mesh, fixed in 10% formalin and sorted to 70% ethanol. At least one smaller core was also taken for measuring the physical properties of the sediment. Median grain diameter, sorting coefficient (Folk and Ward, 1957) and percent sand and silt/clay were estimated from a modified Emery tube analysis (Emery, 1938). Percent by weight of organic carbon in the sediment was measured with a Leco Carbon Analyzer after acid treatment to remove inorganic carbon residues. The Appendix contains a discussion of the methods used to obtain many ancillary data.

Environmental Setting

The most distinct bathymetric feature of Monterey Bay is the large Monterey Submarine Canyon which heads at Moss Landing (Figures 1 and 2). Temperature (Figure 3), river runoff (Figure 4) and the influx of organic carbon (Figure 5) all exhibited marked seasonal patterns. In regard to temperature and river runoff, the short-term variations (i.e., several days) were often nearly as great as that during the entire year.

The seasonal trend in average wind speed reflects the relatively strong and consistent winds that blow during the spring upwelling period, but the average values are not indicative of the magnitude of bottom disturbance caused by wave activity. The most important bottom disturbances are associated with the few, relatively intense periods of rough seas (personal observation). Southern winds are often related to the largest local storms and are more frequent during the winter. This seasonal pattern of winter roughness was more evident by considering the number of days during the month that the average daily wind speed was greater than 5 cm/sec. (Figure 6).

Wave gauge data from northern Monterey Bay also showed a marked increase in wave height during the winter. These wave data, the strongest southerly winds and extensive observations by the authors of the seasonal trends in sea state and bottom disturbance by waves all indicate that the period of most intense wave disturbance of the bottom is during the winter.

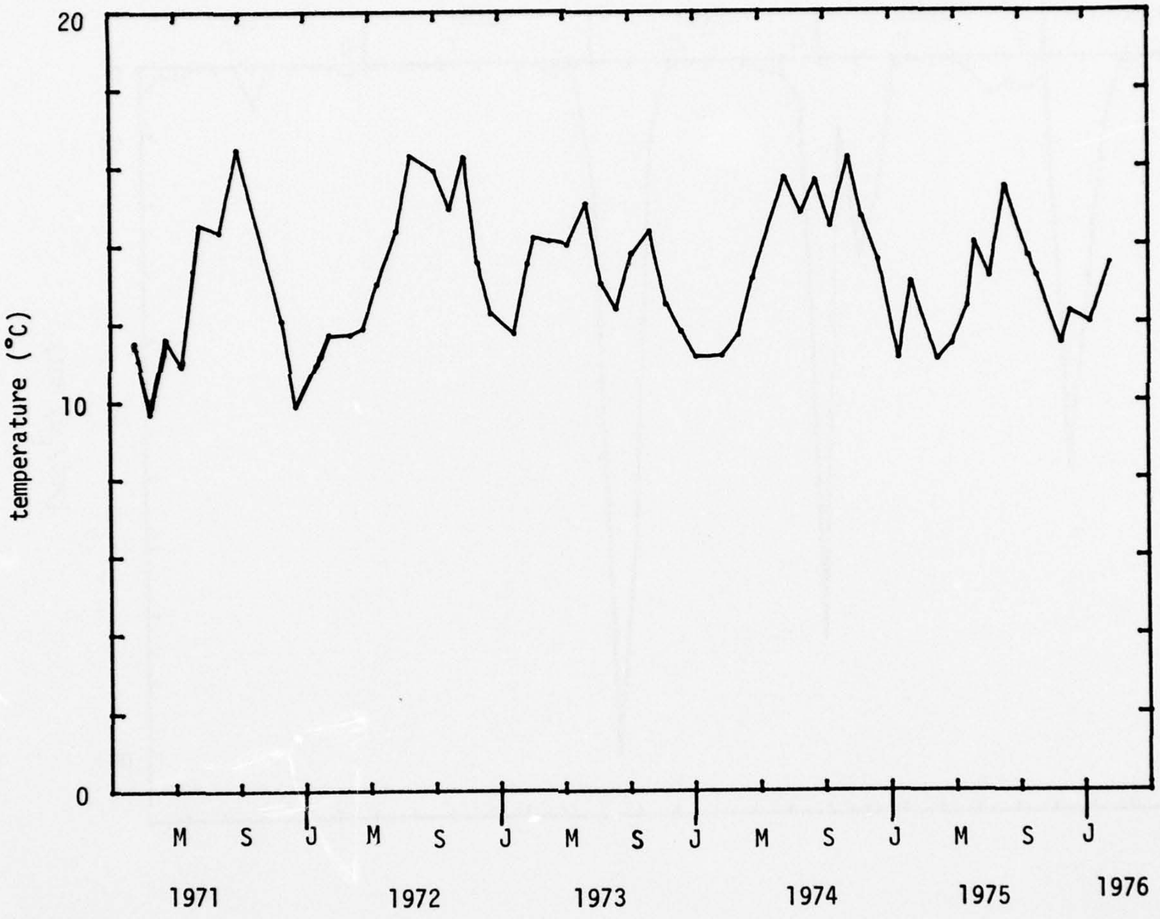

Figure 3. Average monthly water temperature.

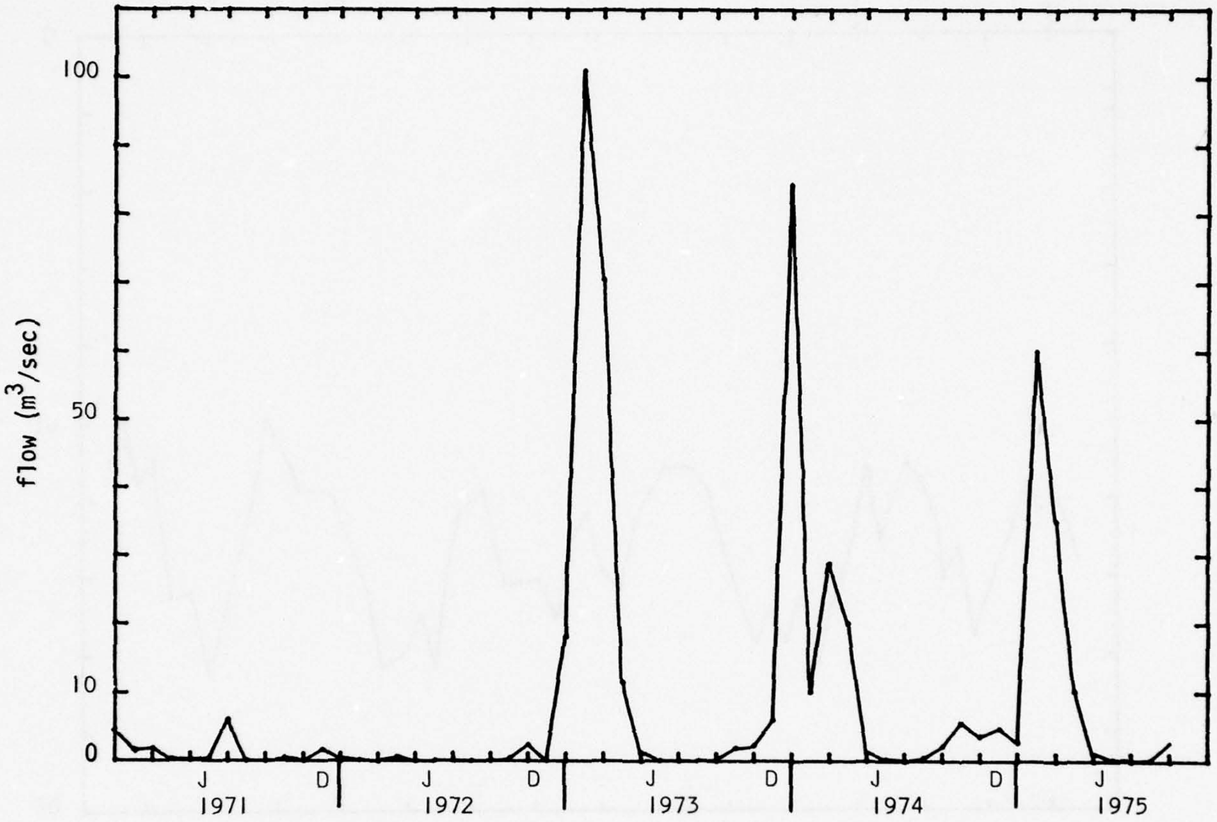

Figure 4. Mean monthly flow of the Salinas River.

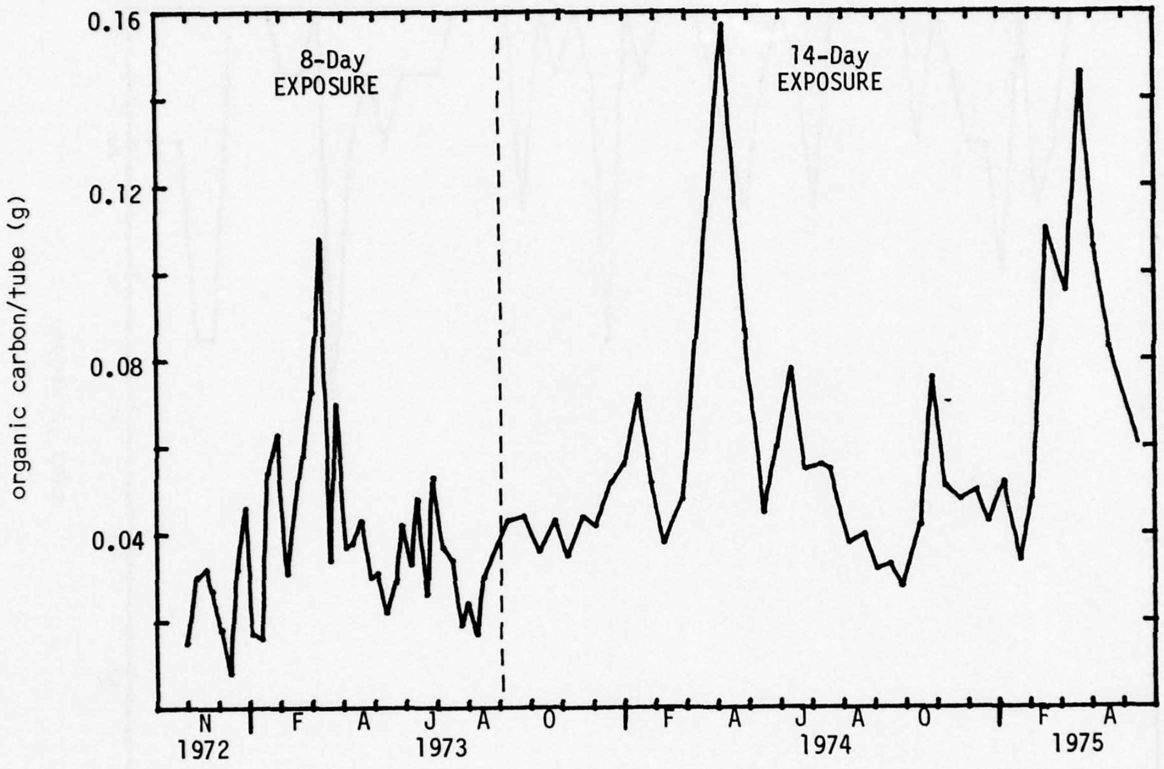

Figure 5. Total organic carbon collected in settling tubes (diam. 3.4 cm, ht. 30 cm) positioned 1 m above the bottom at station M-4. These were collected and replaced every 8 days until August 1973 and every 14 days thereafter.

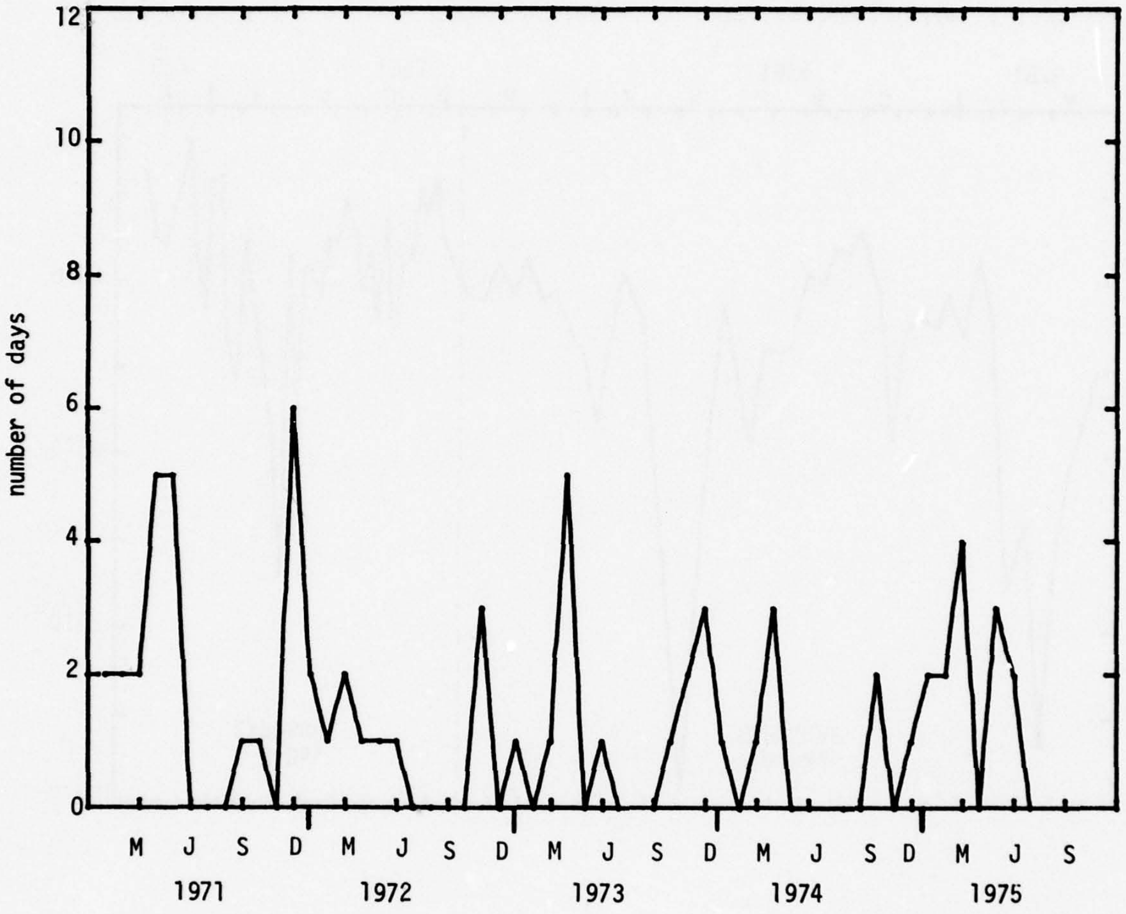

Figure 6. Number of days the daily average wind speeds attained 5 m/sec or greater.

Temporal Variations in the Fauna

Temporal variations in the benthic fauna can be divided into four main categories which more or less overlap. Short-term variations concern periodic migrations of animals that result in detectable changes in abundance patterns. Seasonal variations are of two kinds. There are changes related to seasonal breeding cycles and changes related to seasonal variations in the environment. Obviously, these two categories can potentially overlap completely. Finally, there are longer term changes that are not seasonal in nature and occur sporadically.

1. Short-Term Variations

The most dramatic short-term variation in abundance was that associated with the movement of the sand dollar, Dendraster excentricus. During rough seas, the entire sand dollar bed migrated offshore and covered M-1, and during calmer seas, it moved inshore from this station. Several species of amphipods probably exhibited a similar behavior. Eohaustorius sencillus was most abundant at M-2 (9 m), and E. sawyeri was most abundant shallower (personal data) than the shallowest station (M-1, 6 m); however, the distribution of both species overlapped at M-1. The changes in their relative abundance at M-1 were complementary (Figure 7). This suggests that both species made seaward and shoreward migrations in concert. This relation is further illustrated by the density changes of E. sencillus at both M-1 and M-2 (Figure 8), where abundances were roughly inversely related. The abundance of Paraphoxus obtusidens showed a similar trend at these stations. There were no direct measurements of wave activity that allow a quantitative correlation between the movements of these crustaceans and bottom disturbances. How-

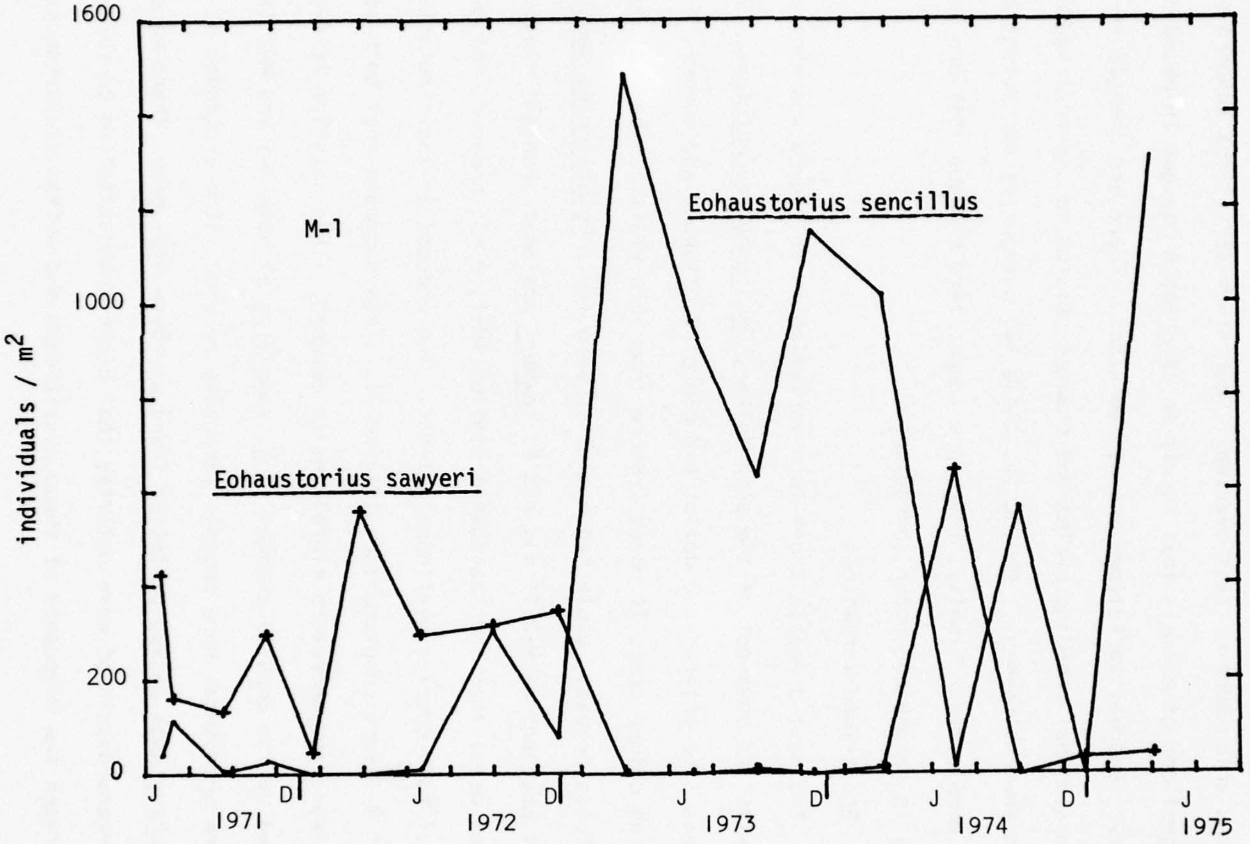

Figure 7 . Variation in abundance of _Eohaustorius sencillus_ and _Eohaustorius sawyeri_ at M-1.

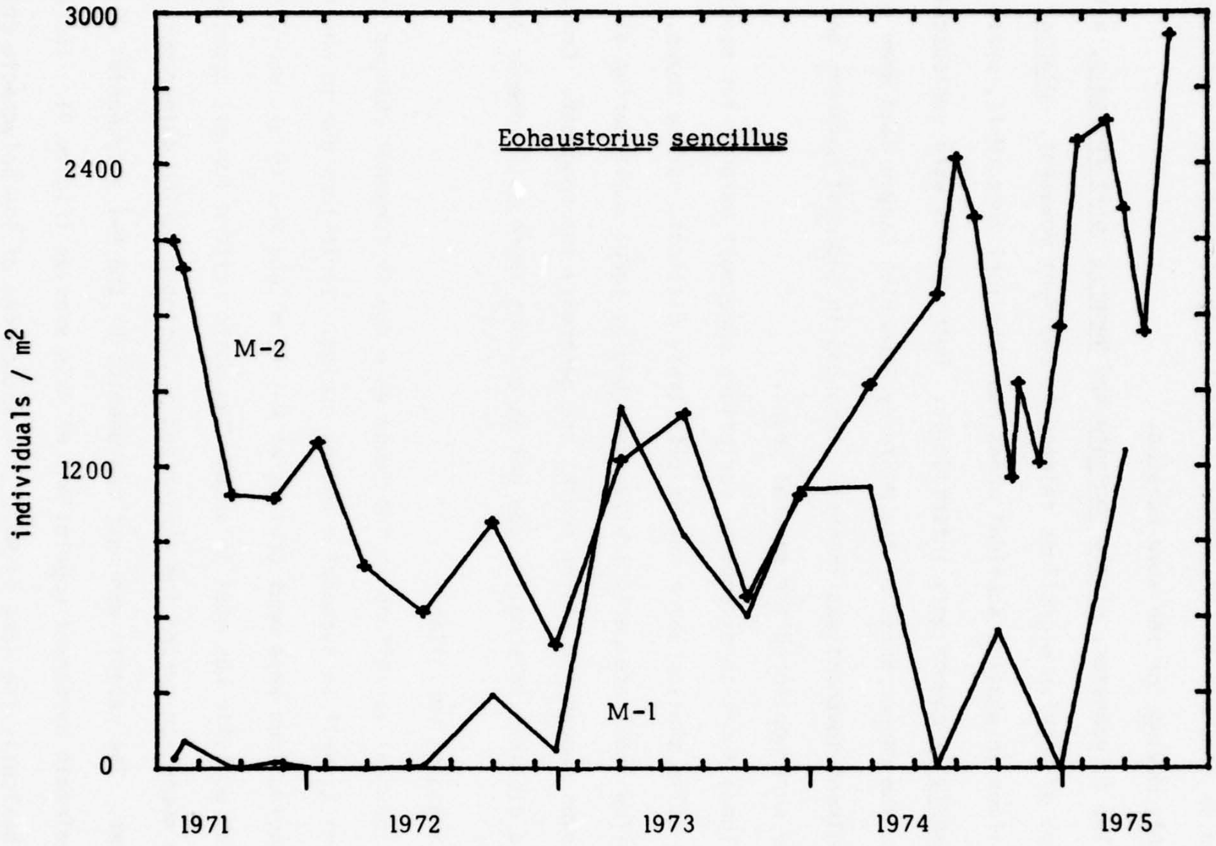

Figure 8. Temporal variations in Eohaustorius sencillus at M-1 and M-2.

ever, personal observations and numerous measurements of sand dollar migrations in response to variations in swell suggest that the crustaceans are probably moving for the same reasons.

Two polychaetes, _Dispio uncinata_ and _Nephtys californiensis_, also made active or passive migrations related to sediment movement. _Dispio uncinata_ lives in shallow subtidal areas near the surf zone (M-1), while _N. californiensis_ is common only intertidally. Both species were periodically swept into the deeper areas of the Monterey Submarine Canyon Head when down-canyon sediment movement was intense. (Changes in sediment movement and topography were monitored for several years.)

These short-term temporal variations were most evident for species living in quite shallow water and in relatively distinct, narrow zones. These shallow areas are periodically disturbed by large swell during all seasons, even though the winter months are generally the roughest. Consequently, a distinct seasonality was not as evident there as in deeper areas.

2. Seasonal Variations

Seasonal variations in the fauna were due to seasonal changes in the environment as well as seasonal breeding cycles. Variations due to environmental fluctuations were most obvious at M-1 (6 m) and M-2 (9 m), where seasonal storm activity was most intense. The basic pattern for all species was a low abundance during the winter and an increase during calmer portions of the year. The pattern was best represented by the M-1 polychaetes which did not maintain permanent populations at this station (Figure 9). The pattern was basically the same at M-2. The abundances of the polychaete _Priono-_

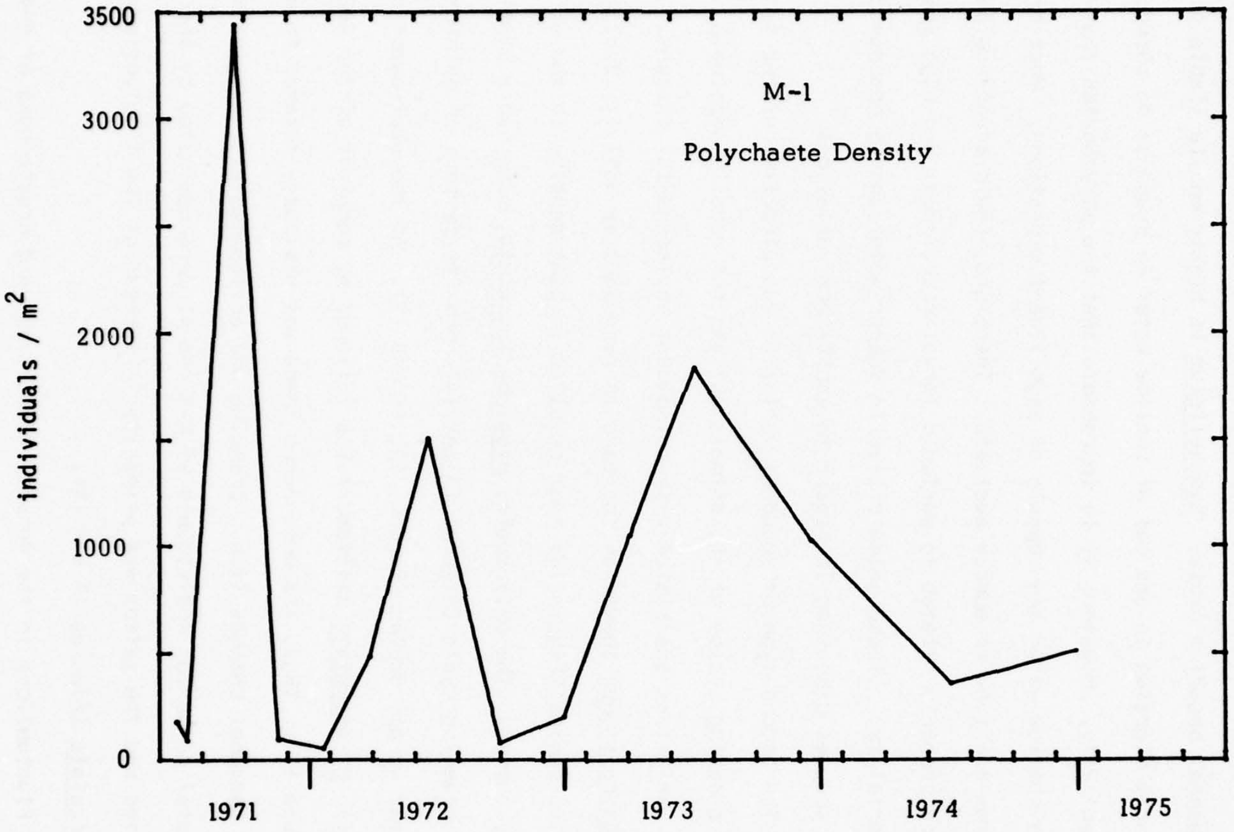

Figure 9. Temporal variations in polychaete density at M-1.

spio pygmaea (Figure 10) and the amphipod Synchelidium spp. (Figure 11) were particularly illustrative since neither of these species have a distinct seasonal breeding cycle. Synchelidium is highly mobile (Table 1) and probably migrates in and out of shallow water in response to changes in wave activity. However, it is improbable that the polychaetes that settle in shallow water are capable of significant migrations. Most of these forms are tube or burrow dwellers. Therefore, their abundance patterns were probably related to periodic larval recruitment and high post-larval mortality. These animals live in deeper water and in broader zones than the species discussed in regard to short-term variations.

The second type of seasonal variation was directly related to seasonal breeding cycles of the animals but was not readily separable from the variations associated with coincident environmental changes. Paraphoxus epistomus showed an increase in reproductive activity during the calm spring months (Figure 12) that resulted in peak density in the spring and early summer. The polychaete, Magelona sacculata, also had a distinct seasonal breeding cycle (Figures 13 and 14), and its pattern of settlement was similar at all depths (Figures 15, 16 and 17). At the shallowest station (M-1), M. sacculata settlement was followed by complete winter mortality (Figure 15). Thus, its occurrence there was obviously related to both kinds of seasonal changes (i.e., breeding and environmental). Variations in the total number of individuals at M-4 (18 m) were dominated by the polychaetes and the latter was primarily influenced by the fluctuations of M. sacculata (Figures 17 and 18).

Fluctuations in the density of molluscs and crustaceans at M-4

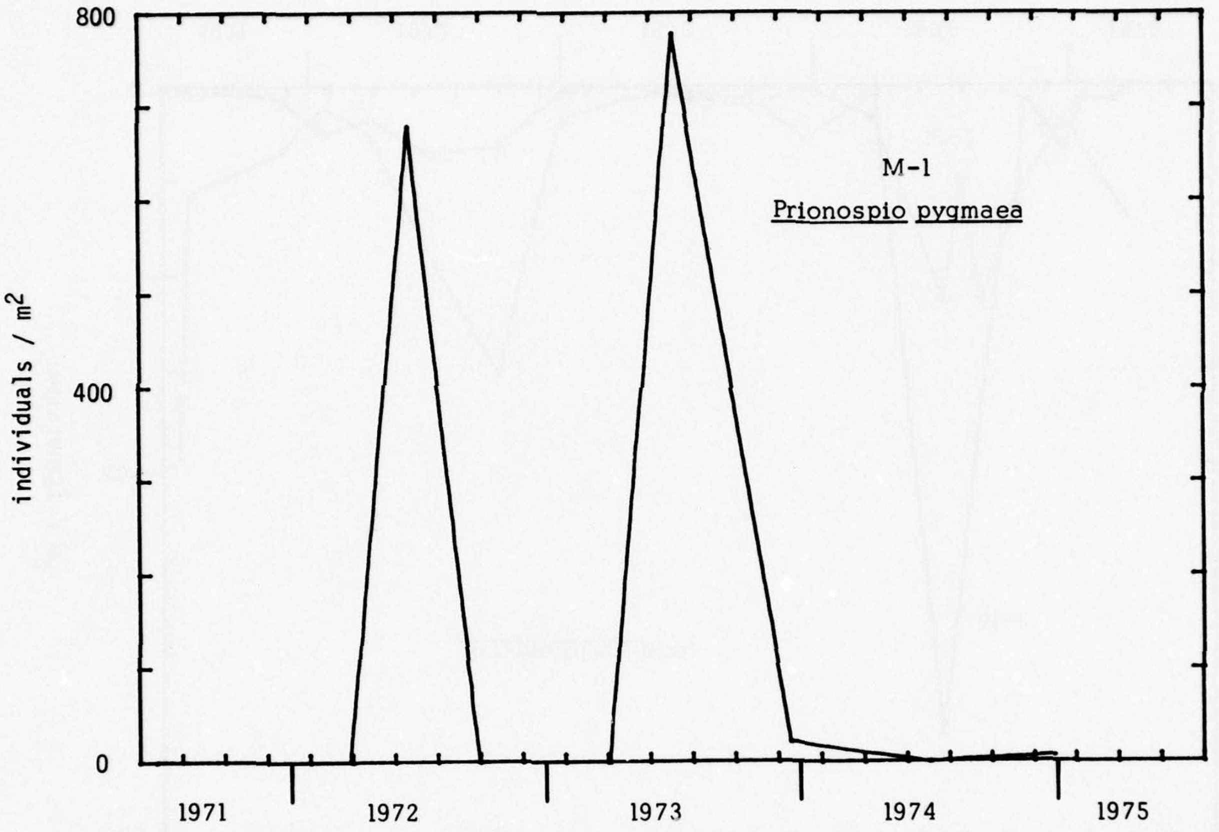

Figure 10. Temporal variations in Prionospio pygmaea at M-1.

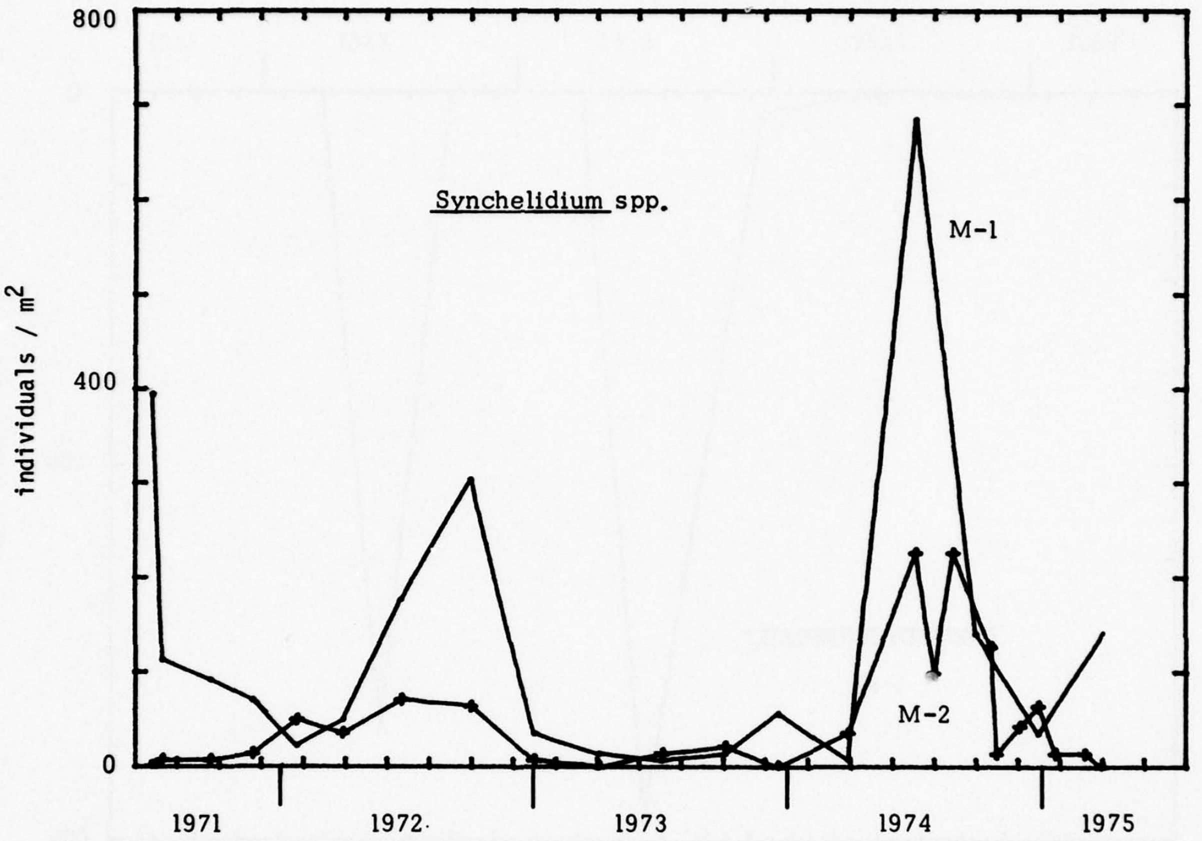

Figure 11. Temporal variations in Synchelidium spp. at M-1 and M-2.

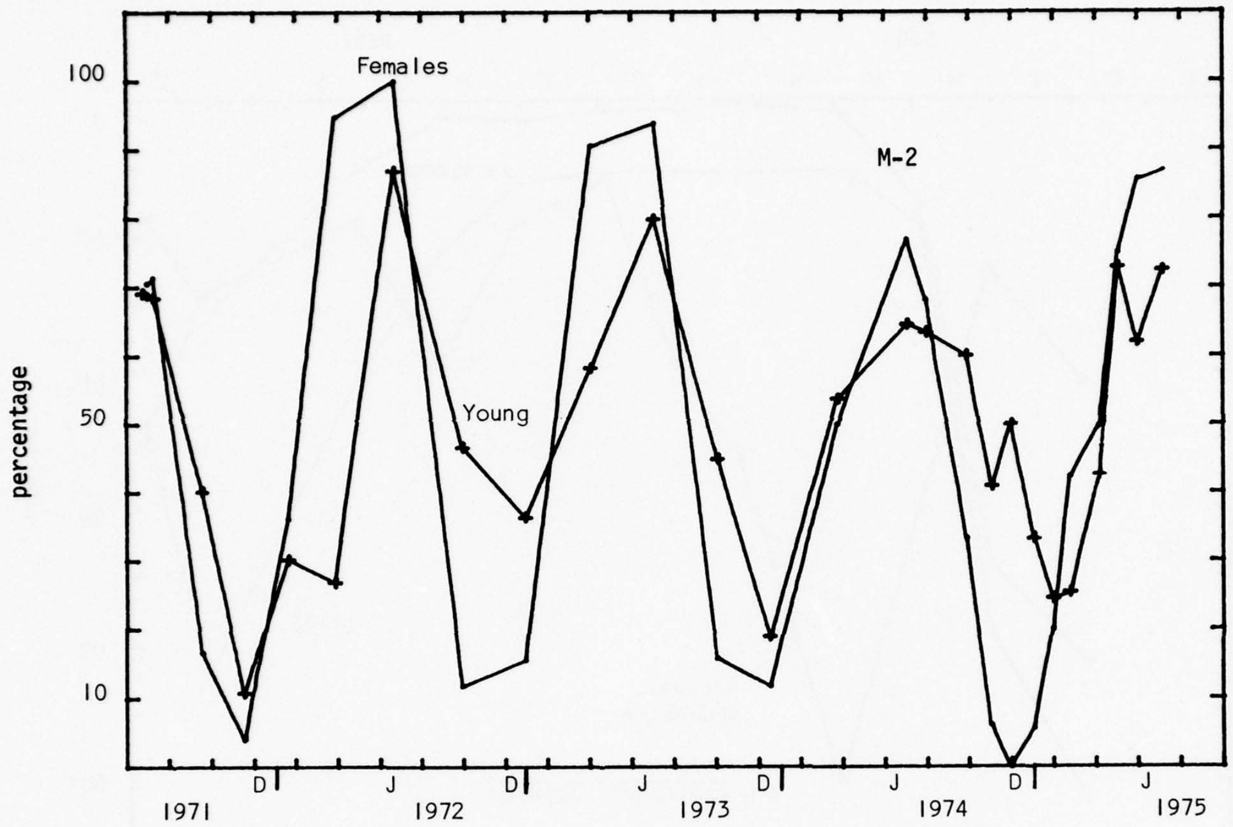

Figure 12. Seasonal variation in the life cycle of Paraphoxus epistomus at M-2: percentages of ovigerous females and young.

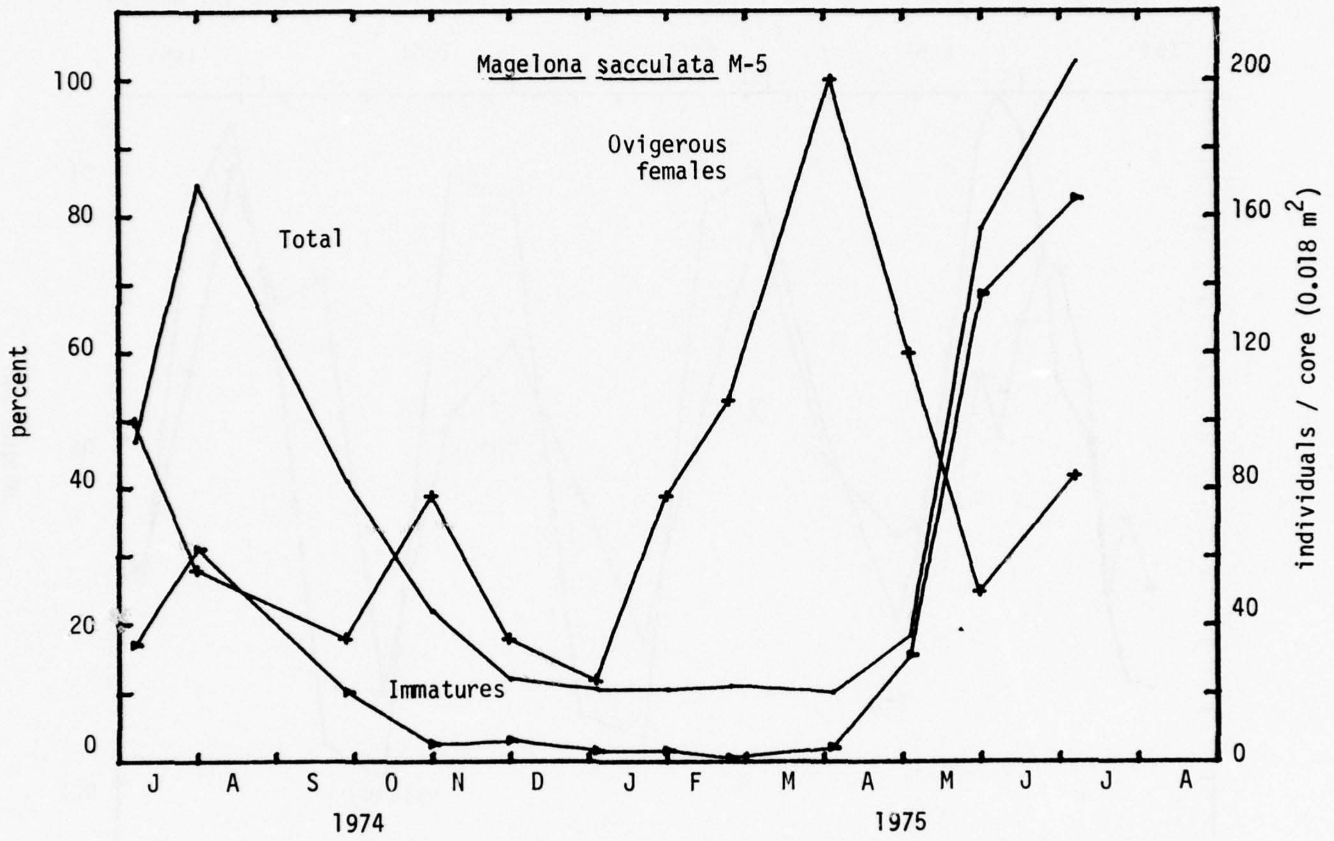

Figure 13. Total number of Magelona sacculata per sample, number of immatures and percent ovigerous females at M-5.

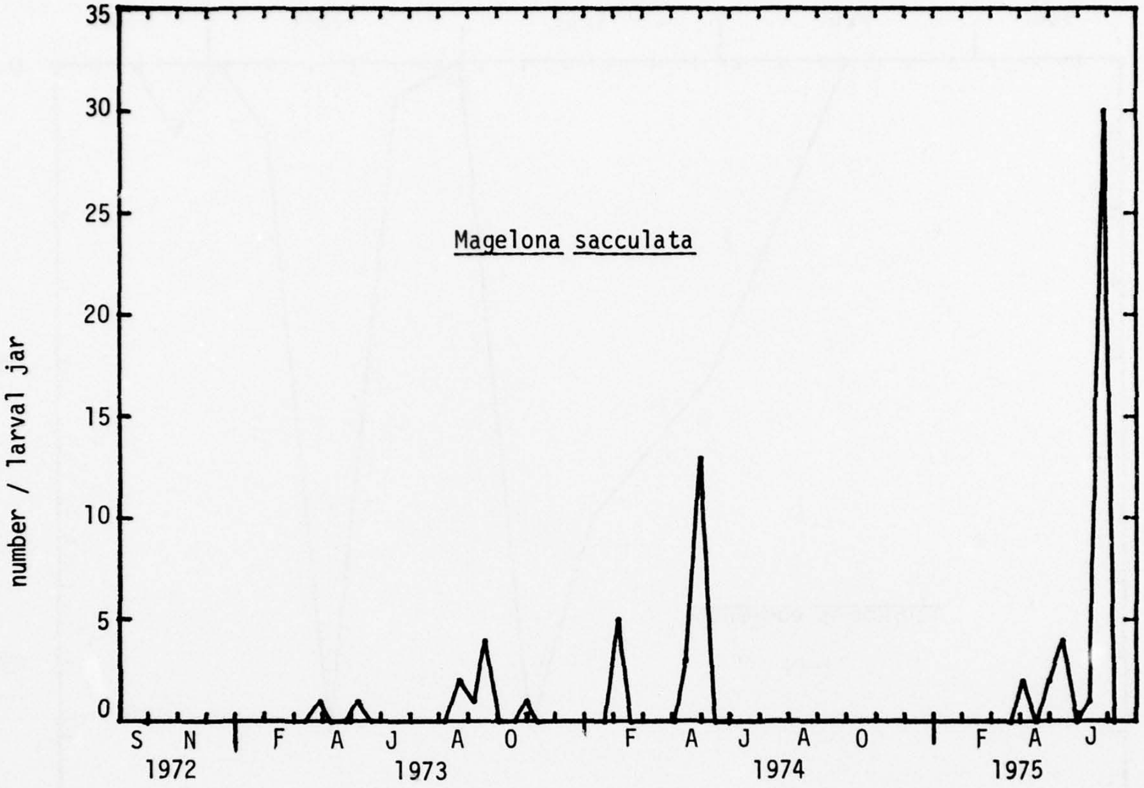

Figure 14. Total number of post-larval Magelona sacculata collected in larval settling jars per 14-day exposure (see Appendix).

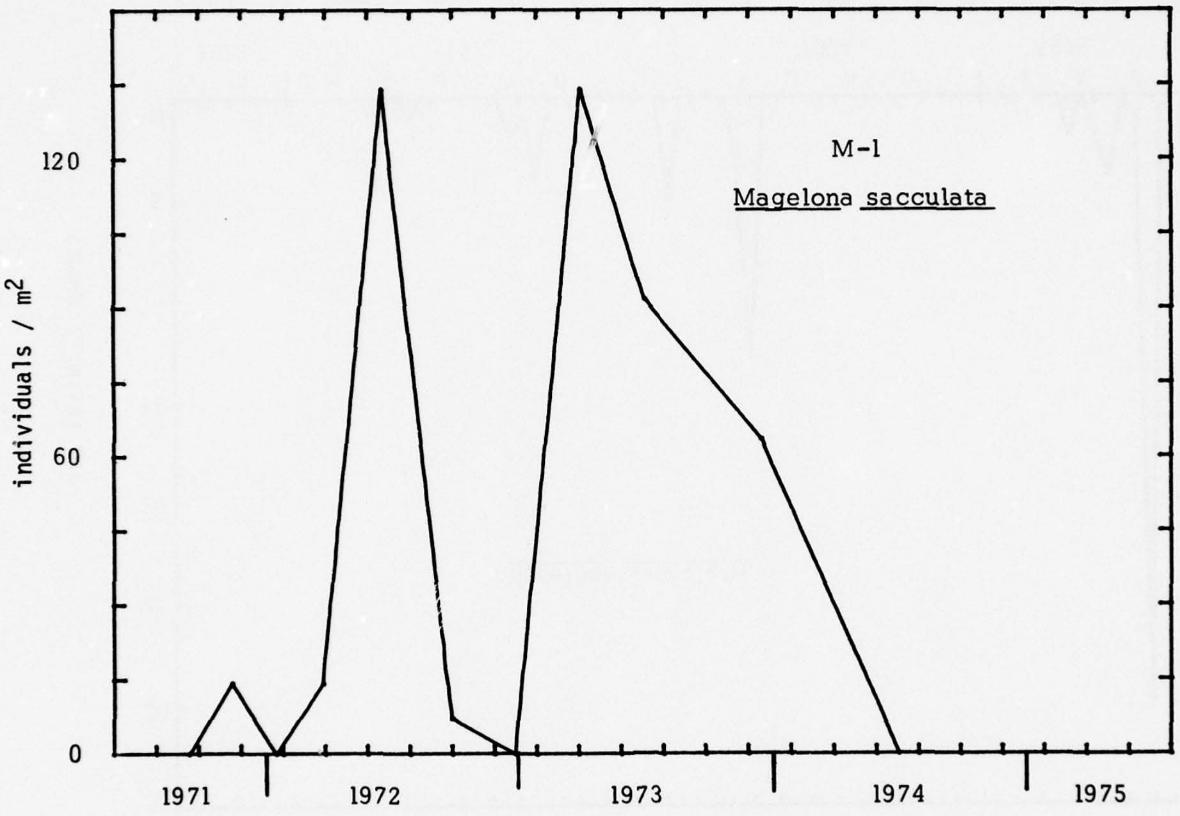

Figure 15. Temporal variations in *Magelona sacculata* at M-1 (6 m).

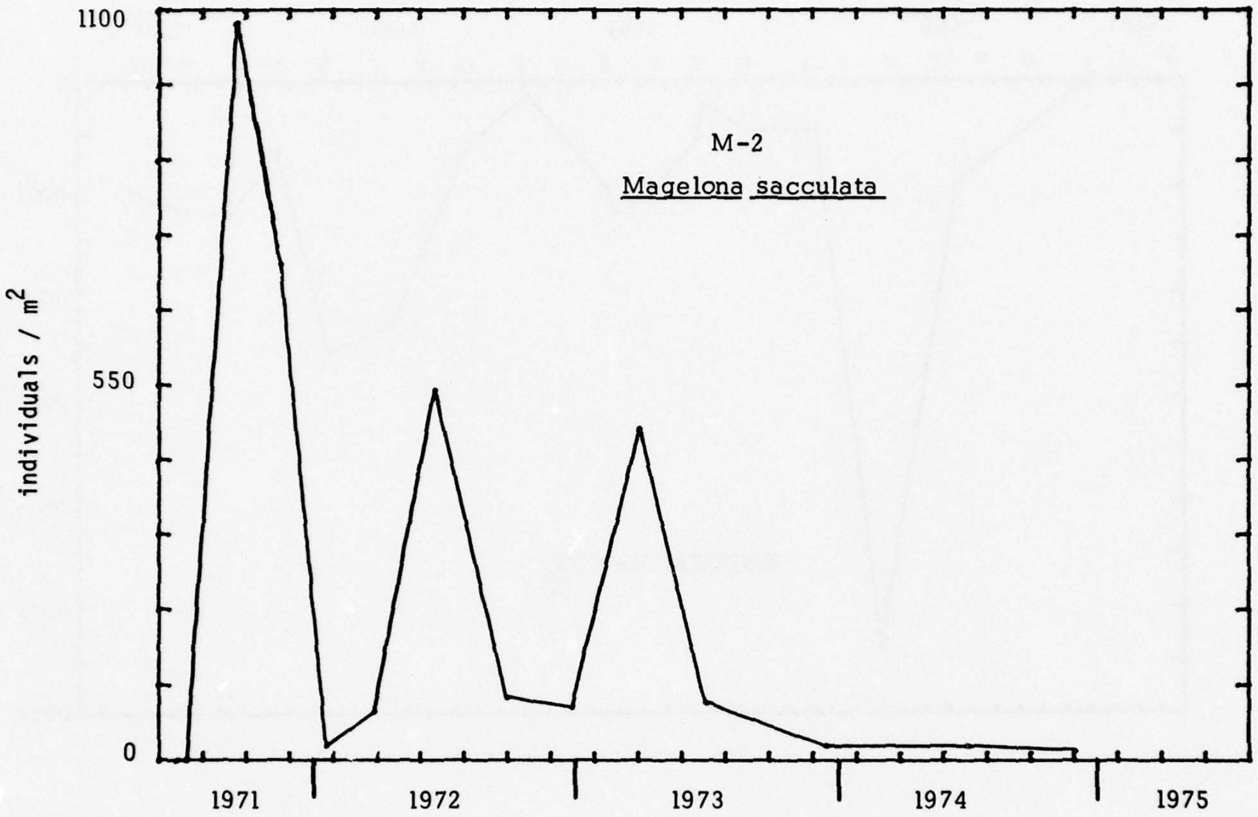

Figure 16. Temporal variations in _Magelona_ _sacculata_ at M-2 (9 m).

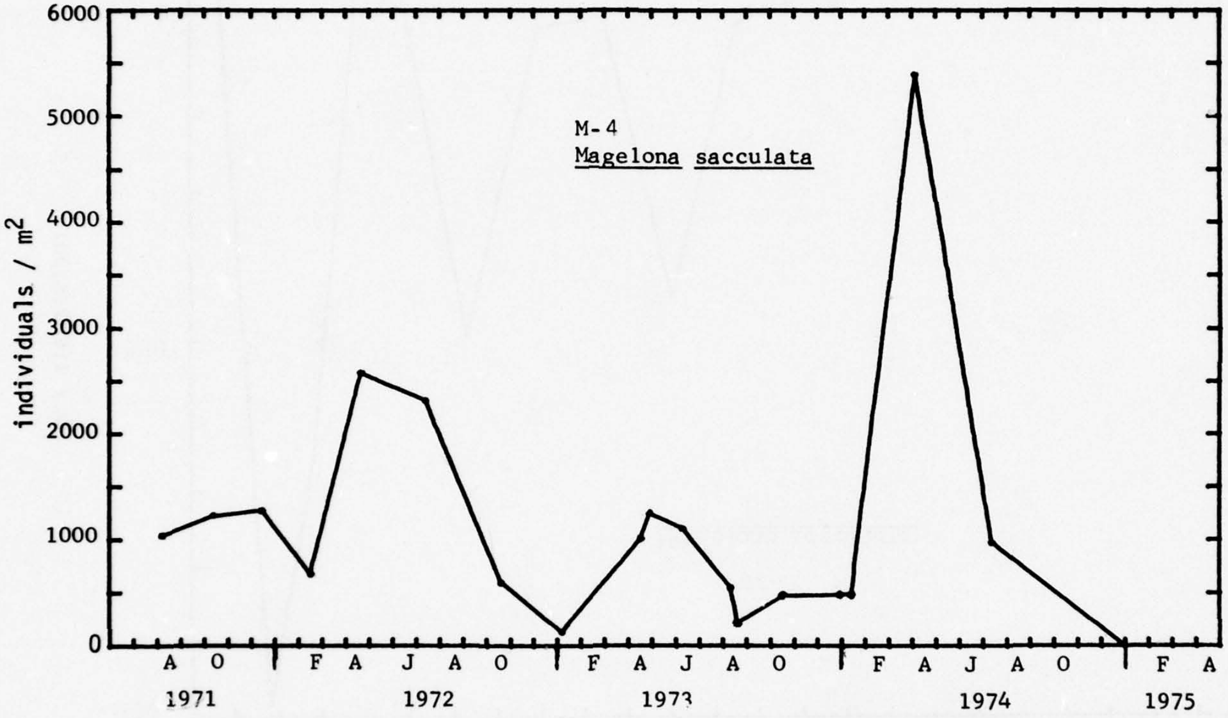

Figure 17. Temporal variations in Magelona sacculata at M-4 (18 m).

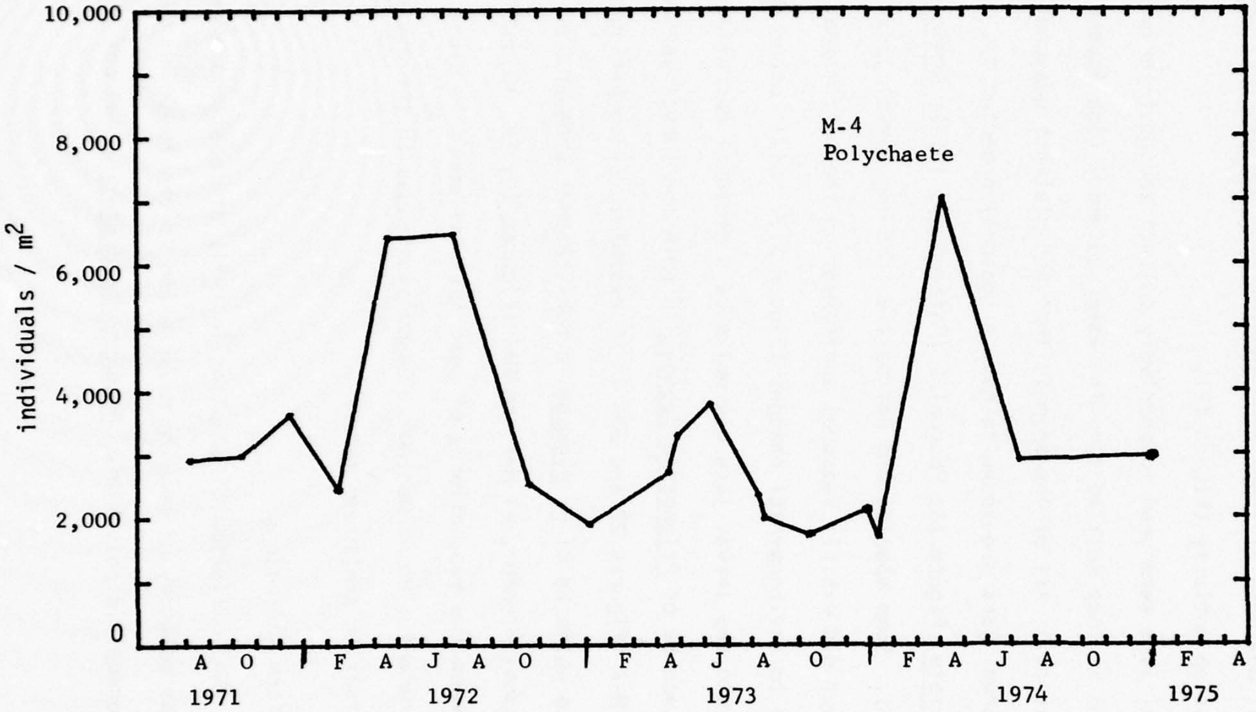

Figure 18. Temporal variations in polychaete density at M-4 (18 m).

were not markedly seasonal (Figures 19 and 20). The crustaceans had more distinct trends in seasonal abundance at the shallower stations (M-1 and M-2, Figure 8), and many of these same species also had distinct seasonal trends in breeding activity (Figure 12).

Larval jars were used to passively collect the post-larval stages of bottom forms as they settled from the water column. (See Appendix for methods discussion.) All of the animals that had distinct seasonal settlement in the larval jars are known to have a seasonal breeding cycle: e.g., *Magelona sacculata*, Figure 13; Phoronids (Rattenbury, 1953); *Armandia brevis* (Hermans, 1966). Some species did not settle into the larval jars in significant numbers but did exhibit seasonal settlement on the bottom that could not be related to environmental changes (Figure 21). Still other species that settled into the larval jars did not show a seasonal recruitment pattern. The abundance of *Prionospio pygmaea* in both the larval jars and on the bottom at M-4 (Figures 22 and 23) is an example. By comparing the temporal abundance patterns of *P. pygmaea*, a non-seasonal breeder, and *M. sacculata*, a seasonal breeder, at M-1 and M-4 (Figures 10, 22, 15 and 17), the difference between the two patterns of seasonal settlement is clear (i.e., seasonal environmental vs. breeding). Seasonal changes in the environment are most important in shallower water.

3. Long-Term Variations

Since the initiation of sampling in 1971, at least one event which clearly fits the category of long-term variation in the fauna has been observed. The terebellid polychaete, *Amaeana occidentalis*, was not present

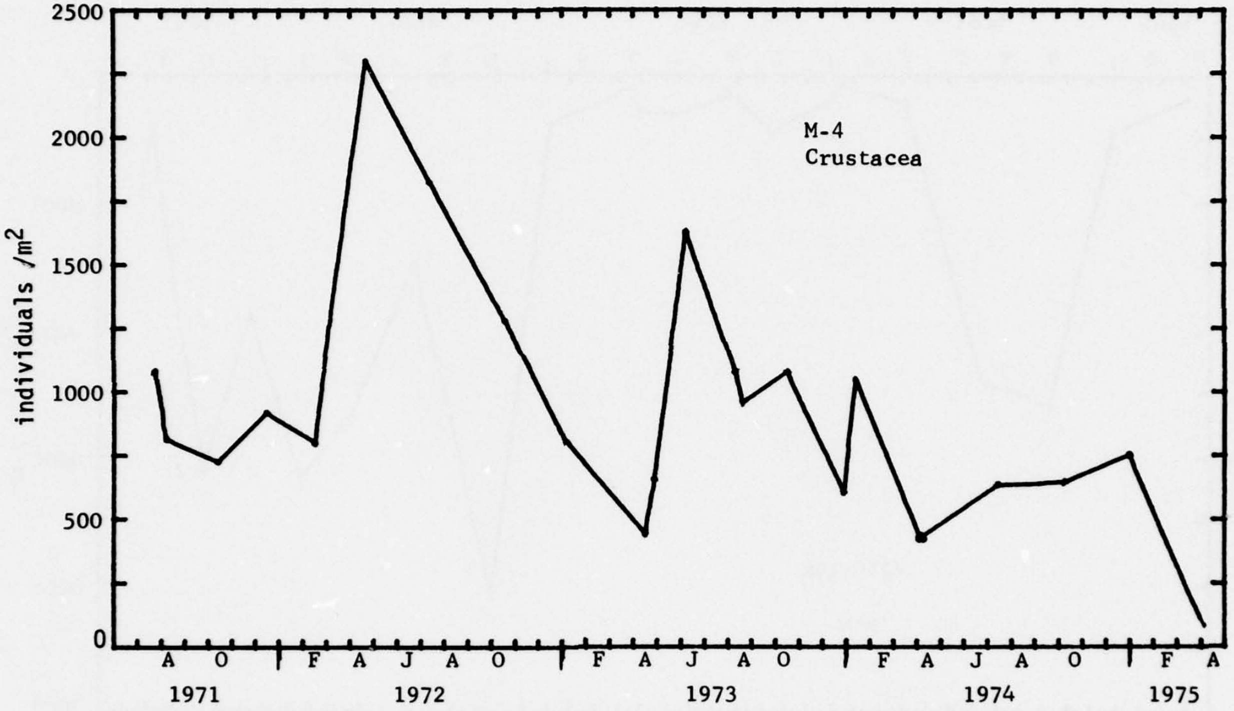

Figure 19. Temporal variations in crustacean density at M-4 (18 m).

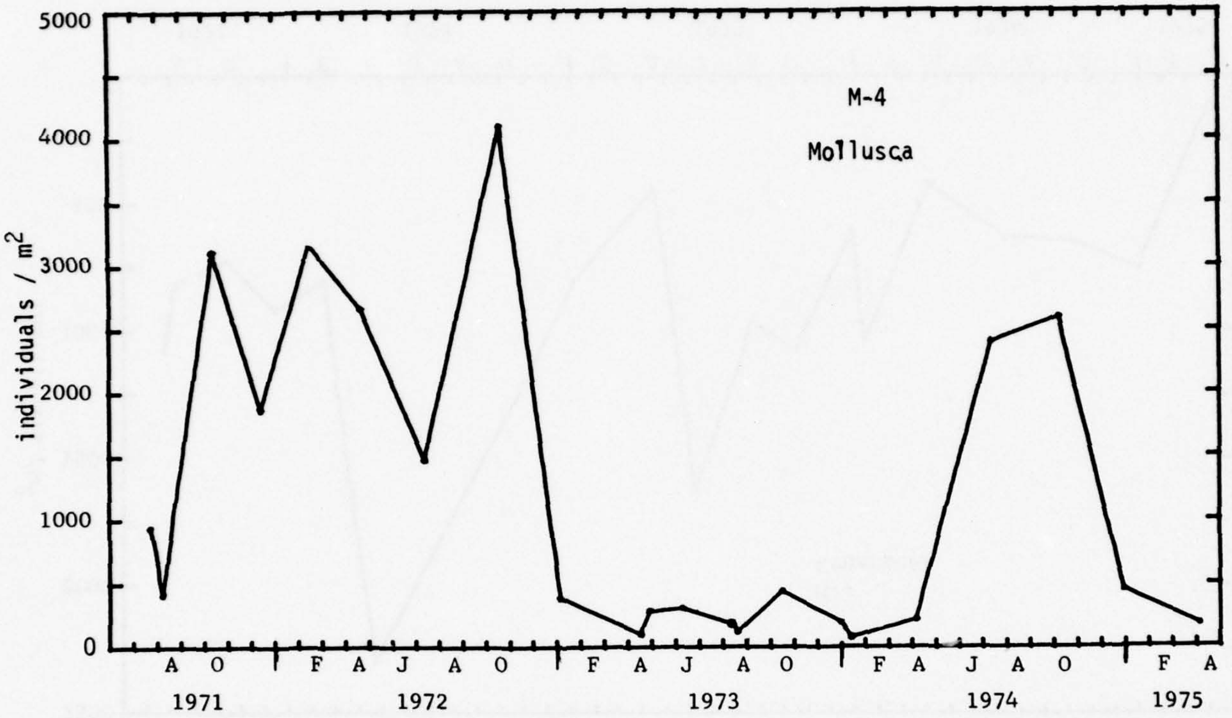

Figure 20. Temporal variations in molluscan density at M-4 (18 m).

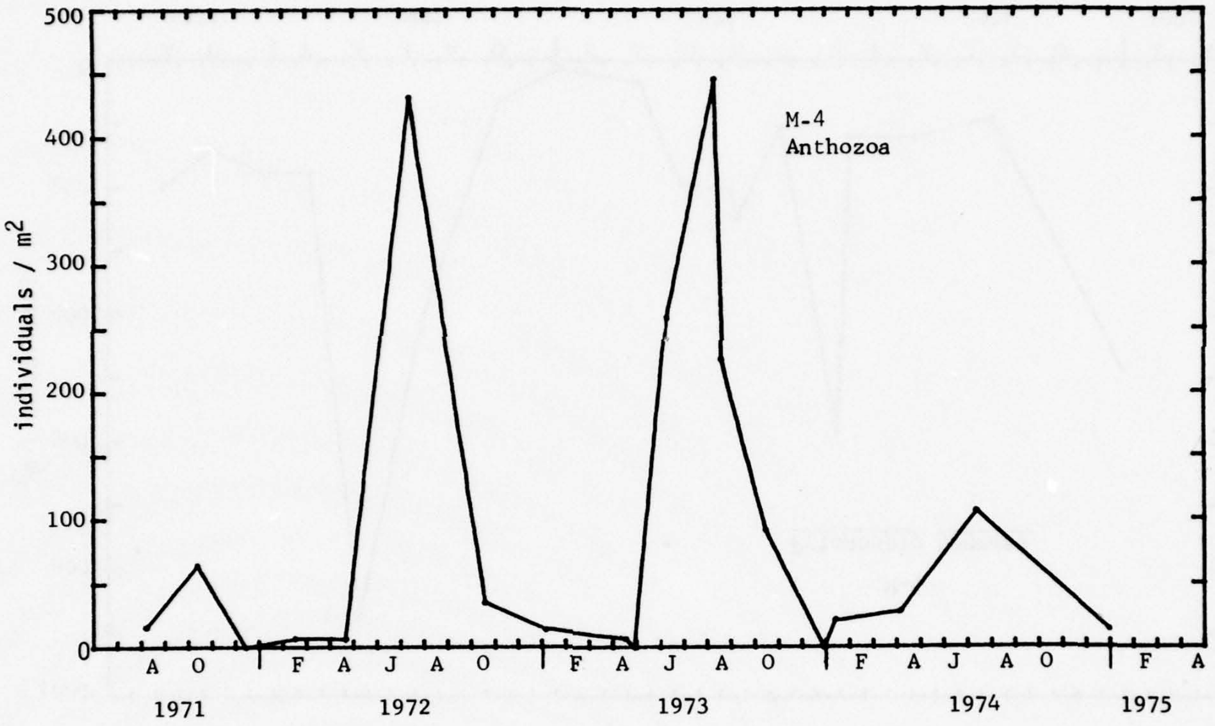

Figure 21. Temporal variation in an anthozoan at M-4 (18 m).

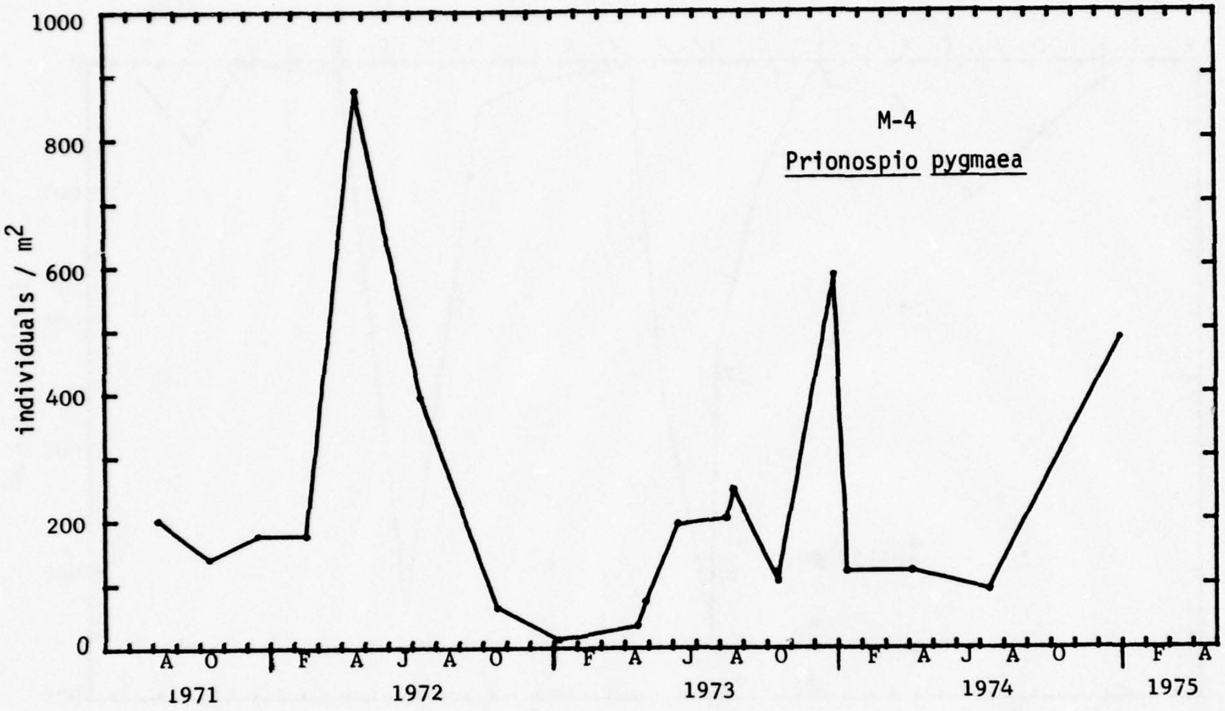

Figure 22. Temporal variations in Prionospio pygmaea at M-4 (18 m).

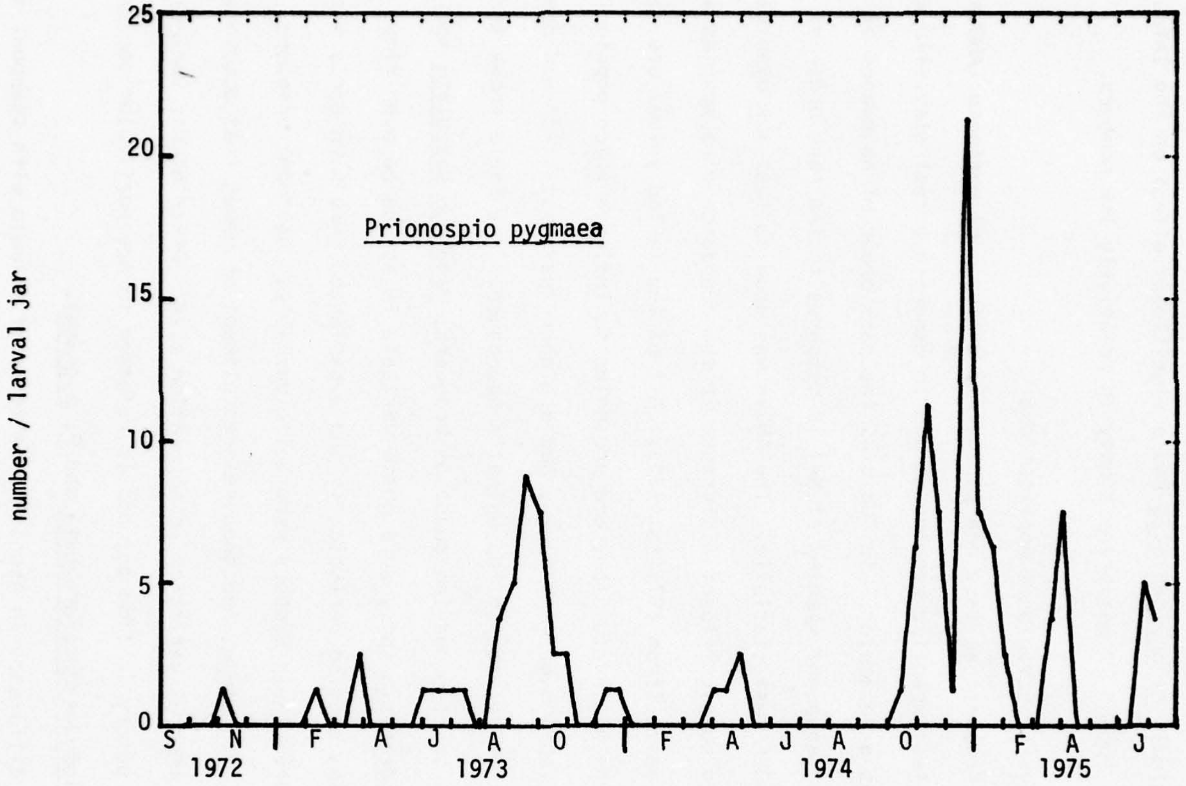

Figure 23. Number of post-larval <u>Prionospio pygmaea</u> collected in settling jars per 14-day exposure.

at any station along the depth transect until it suddenly appeared in March 1972 and has since been a common member of the assemblage (Figure 24). As a large animal, A. occidentalis had a significant effect on the infaunal biomass, even though it was present only in relatively low numbers.

4. Analysis of Variance Applications

The Kruskall-Wallace non-parametric analysis of variance (ANOVA) was used both to test specific hypotheses and to generate a test statistic which was treated as a parameter. In Table 2, the rank order of abundance of the seventeen most abundant species at M-4 is compared to the rank order of species by ANOVA test statistic. The ANOVA was used to test the hypothesis that there was no significant difference in the abundance of a species among the sampling dates (from 1971 to 1975). All of the tabled values are significant at the 5% level. They are presented to indicate which populations were most variable over time (i.e., had a higher test statistic) and how that variability relates to the animal's abundance. The table shows that the three bivalve species and the seasonal breeders, Magelona sacculata and the anthozoans, Edwardsia spp., were quite variable in abundance over time. All bivalve species settled periodically and experienced very high early mortality. Therefore, their numbers were quite variable. Seasonal breeders, especially M. sacculata, had seasonal recruitment of young that accounted for much of the temporal variation in population size. Other highly variable animals were patchy in time but not in relation to any particular season (e.g., Euphilomedes carcharodonta and P. pygmaea).

The difference in abundance patterns of animals with seasonal and

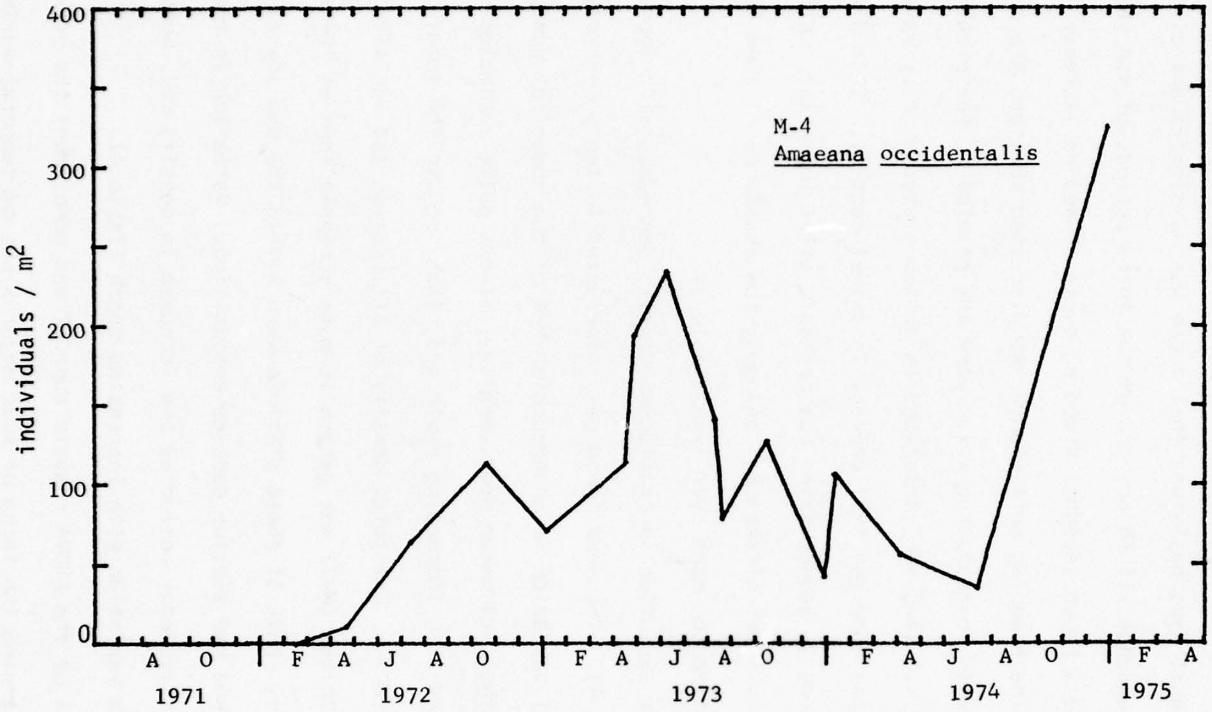

Figure 24. Temporal variations in _Amaeana occidentalis_ at M-4 (18 m).

relatively aseasonal breeding cycles is further illustrated in Table 3. Abundances during winter (December, January, February), spring (March, April, May) and summer (June, July, August) were treated separately in this ANOVA. The null hypothesis was that there was no significant difference in a species abundance within any one of the three periods of the year. Animals that had a known seasonal breeding cycle showed an increase in variation during the breeding settlement. As discussed earlier, there were also seasonal changes in abundance which were not related to the breeding cycles of the animals. Seasonal variations in bottom disturbance by wave activity probably caused some seasonal changes in animal density. This disturbance was less severe in deeper water but probably still important. Although there were two types of seasonal changes, the abundance of some species still did not change much over time (Table 3).

The variation in crustacean density decreased with increasing depth (Table 4). The same trend was interrupted in the polychaetes by the high seasonal variation in abundance at M-4 of the numerical dominant, Magelona sacculata. Molluscan settlement was always quite variable, but settlement increased with increasing depth and, thus, so did the total variation in density (Table 4). The total density of all species and individuals at the shallowest station (M-1) was generally more variable than at the next deeper station (M-2). Both of these stations were within the shallow water crustacean zone and had similar species composition. Variation in the Shannon-Weaver diversity index reflected the increase in density and, hence, dominance and its variation with increasing depth (Table 4).

All of the ANOVA results support and complement the previous discussion concerning the three or four major kinds of temporal variations in the animal assemblages along the depth transect. Seasonal and aseasonal short-term migrations of animals were observed in shallow water that were probably related to periods of large swell. There was clearly an increase in wave-induced substrate movement during the winter months. At all depths, animal density was lowest during winter. This was not the result of the termination of annual life cycles. Peaks in ovigerous females of the numerically dominant crustaceans and polychaetes did not occur prior to or during the winter but were in early spring. Thus, the low winter densities probably resulted (directly or indirectly) from increased mortality due to physical disturbance. Winter recruitment was much lower in shallow water and was probably restricted by highly variable and intense sediment movement.

Crustaceans dominate the shallow water zone and are replaced by polychaetes in deeper water (Oliver et al., M.S.). This pattern is primarily controlled by sediment movement (Oliver and Slattery, M.S.). It is, therefore, not surprising to find that, during the calm period of the year, these zones shift toward shallow water (i.e., polychaete recruitment is high) and that the opposite holds during the rough period (i.e., crustaceans migrate out of very shallow water and polychaete recruitment is low).

CHAPTER THREE

OFFSHORE DISTURBANCE GRADIENTS

An obvious gradient of physical disturbance caused by wave-generated substrate motion exists along the offshore transects. In shallow water, organisms are subjected to extreme fluctuations in sediment movement that decrease with increasing water depth. The fauna is dominated by mobile, deposit-feeding crustaceans. With increasing water depth, the substrate stability allows the establishment and maintenance of more permanent tubes and burrows. As a result, the number of sessile and semi-sessile forms, commensal animals and suspension and selective surface deposit feeders increases in the deeper polychaete zone (Oliver et al., M.S.).

Previous descriptive studies along the coast of western North America have documented the basic structure of relatively shallow shelf communities (Barnard, 1963; Carey, 1965, 1972; Lie and others, 1969, 1970a, 1970b); however, the effects of natural or experimental perturbations of these communities are unknown. This chapter presents the results of a set of field experiments conducted along the northern sandflat (Figure 2; N stations) that were designed to test two major hypotheses:

<u>Hypothesis No. 1</u>: The ability of animal assemblages to rebound from a simulated natural disturbance is related to the magnitude of natural disruption and variability of the environment. Assemblages subjected to high and variable natural physical stress rebound or recover from perturbation more quickly than those associated with a more benign (less variable) environment.

Hypothesis No. 2: The pattern of benthic succession following a simulated natural disturbance is similar to the zonation of animals along a related physical stress gradient. Animals that characterize the most disturbed end of the natural gradient will appear first in a related succession.

In addition to these hypotheses, the experiments were designed to evaluate other specific questions about factors suspected to control benthic successional patterns.

Methods

Experimental disturbances were created by mass deposition of sandy sediment. Sediment dredged from the entrance channel to the Moss Landing Harbor was loaded into a 1000-cubic yard* scow and deposited over reference grids laid on the bottom and marked by surface buoys. Each grid was a square, 30 m on a side, formed of metal stakes protruding a meter above the bottom and connected by metered line. One barge load of coarse, sandy sediment was dumped at each of three grids in 9 (N-2), 18 (N-3) and 24 (N-4) m of water on the northern sandflat (Figure 2). The physical characteristics of the translocated sediments are shown in Table 5 (November 1974: N-2C, N-3C, N-4C).

Divers surveyed the bottom, measured the precise amount of deposition and established well-defined disturbance (deposition) gradients immediately after dumping. Four permanent stations (A, B, C, D) were established along each disturbance gradient running parallel to the shoreline (i.e., water depth was constant). Station A was to the north and was undisturbed. Station D was located at the disturbance center; i.e., at maximum deposition. The

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*A table of factors for converting U.S. customary units of measurement to SI can be found on page 9.

length of each gradient transect was approximately 30 m. Stations D and C were combined after a large storm in October 1974, when samples indicated no significant difference between the two stations.

The three grid sites were sampled prior to the experimental disturbance in late August 1974 and were observed and sampled at various intervals thereafter. Infaunal and sediment samples were collected and processed as described in Chapter 2. It is important to emphasize the highly controlled nature of the dumping and the establishment of well-defined depositional gradients. The tug boat operator was able to maneuver the scow to the center of the grid (buoyed at each corner) and maintain that position until the dumping was completed. As a result, the position of the nearest colonizing source relative to areas of differential disturbance was well known. Deposition over a larger area would have been more difficult to control.

Physical Environment

A conical pile of coarse, sandy sediment that was approximately 2 m high was deposited at station D at each depth. About 30 cm of sediment accumulated on the C stations and less than 10 cm on the B stations. The undisturbed control areas were located to the north of the disturbance grid because the strongest longshore currents trended south. Finer particles were resuspended and the relatively coarse sand that remained was quickly worked into large ripple marks whose characteristics varied with depth. The coarse sediment was physically reworked into the bottom and was thus covered by finer sands. The shallowest pile (N-2) was dispersed the quickest; however, in late October 1974, a large storm obliterated the main piles at all depths. The storm moved the deposits to such a degree that no physical or biological differences were detected between stations D and C at each depth. Thus, stations C and D were combined after September 1975 and called station C. Sectioned vertical sediment cores taken in January 1975 revealed a homogeneous sediment at N-2 (Table 5), a layer of fine sediment covering the coarse foreign deposit at N-3 and a thin layer of coarse introduced sediment covering the natural deposit at N-4. This pattern was undoubtedly caused by a decrease in physical reworking of the bottom sediments with increasing water depth. As expected, ripple marks of coarse sediment persisted longest at the deepest station (N-4). The coarse sediment was physically reworked into at least the natural surface deposit at all depths by April 1975 (Table 5).

Shallow Disturbance Gradient (N-2, 9 m)

The assemblage at N-2, 9 m, was characterized by few polychaetes and a relatively large number of mobile crustaceans that tolerate extensive substrate movement. The mass deposition of 2 m of sediment destroyed essentially all of the fauna at the center of the disturbance. The less mobile infaunal crustaceans were present in the disturbed areas only in very low numbers until after the following winter. These included species of the amphipod genera Paraphoxus (Figure 25) and Eohaustorius (Figure 26), the ostracod genus Euphilomedes (Figure 27) and the crab Pinnixa franciscana. In contrast, the more mobile crustaceans were present in relatively large numbers along the entire disturbance gradient only a short time after disposal. Several cumaceans (Figure 28) and the amphipods Monoculodes spinipes, Synche-

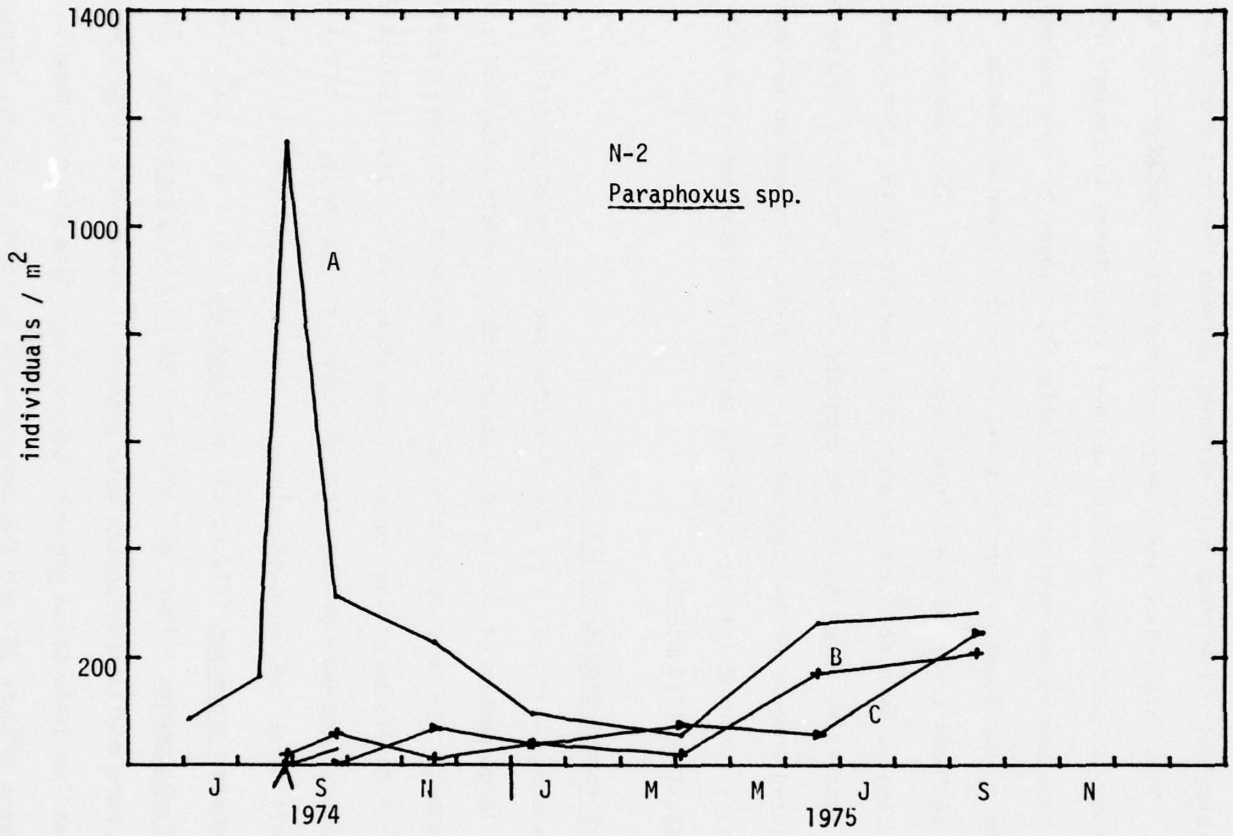

Figure 25. Variations in <u>Paraphoxus</u> spp. along the N-2 disturbance gradient (means). Arrow indicates disturbance.

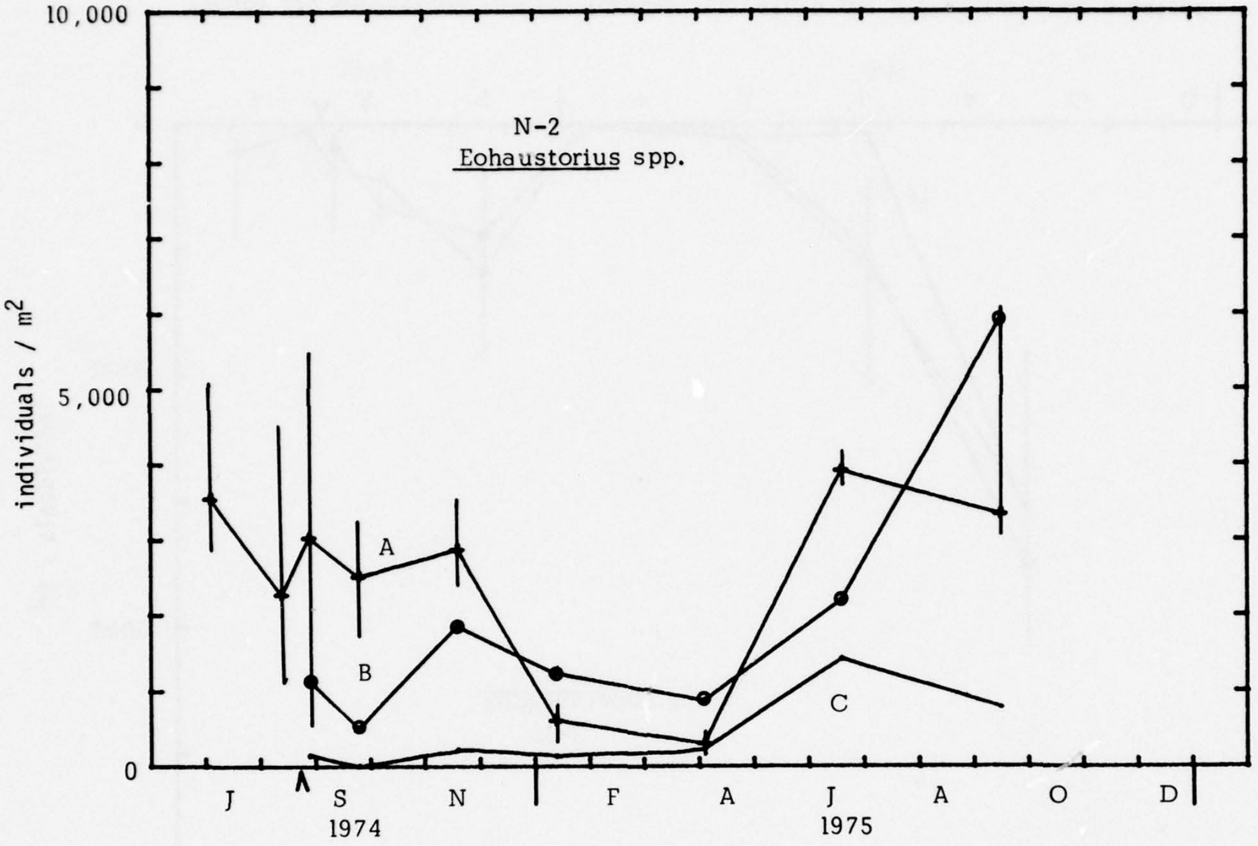

Figure 26. Variations in Eohaustorius spp. along the N-2 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

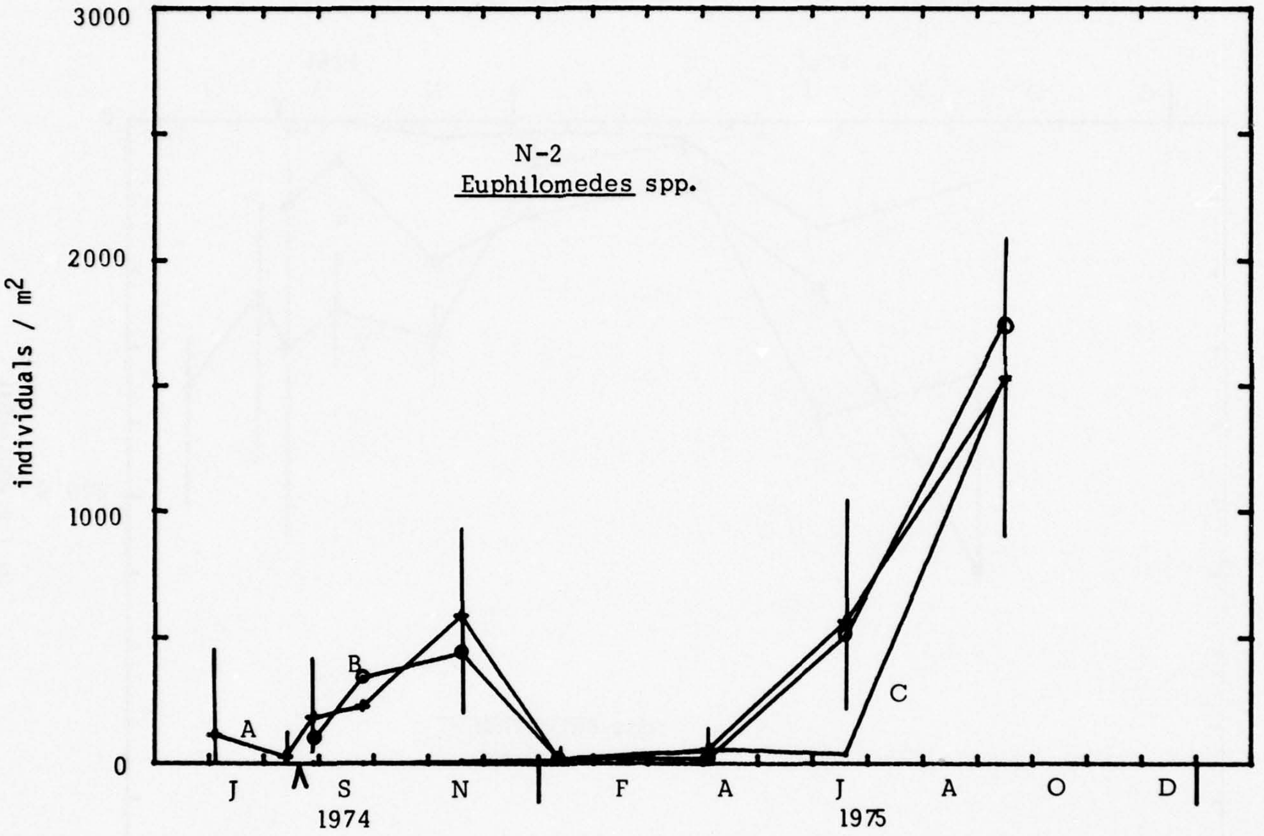

Figure 27. Variations in *Euphilomedes* spp. along the N-2 disturbance gradient (means and ranges on A). Arrow indicates disturbance.

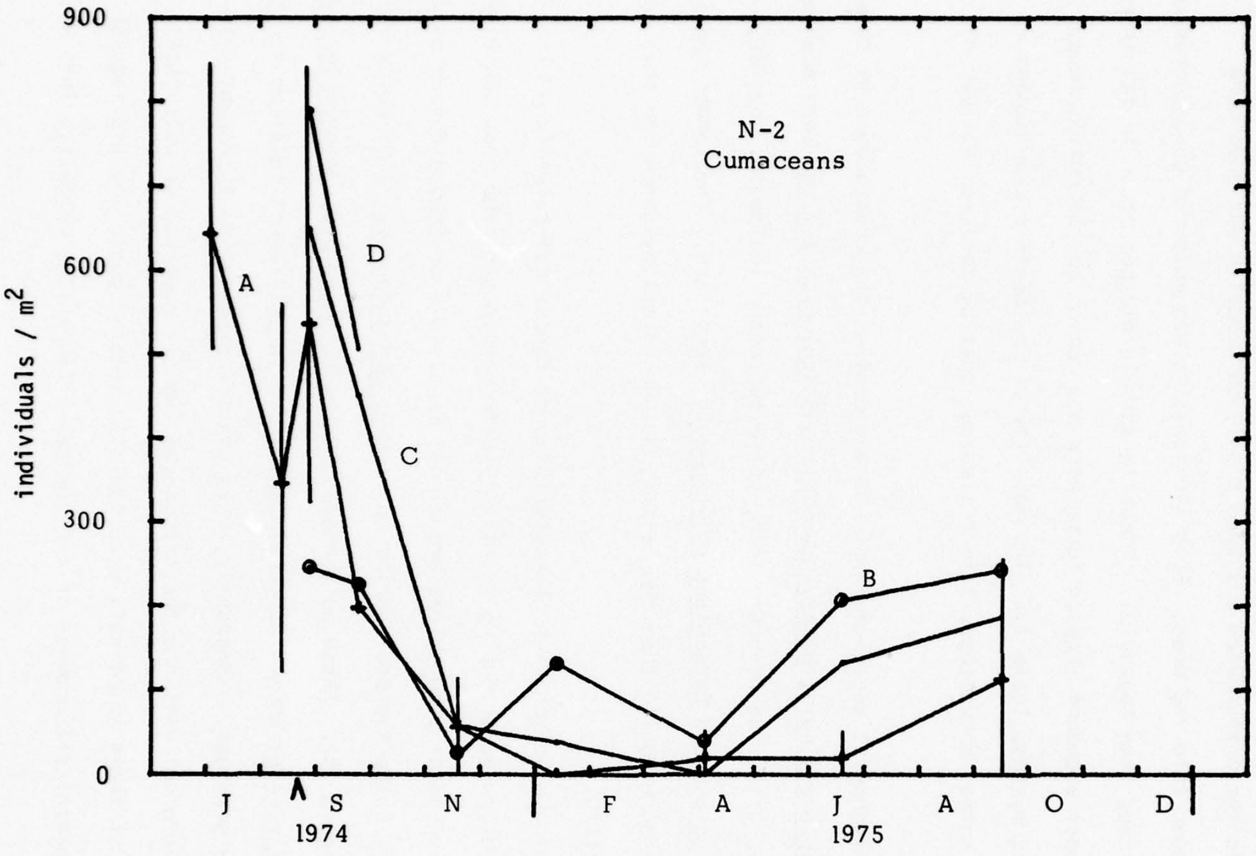

Figure 28. Variations in cumacean density along the N-2 disturbance gradient (means and ranges on A). Arrow indicates disturbance.

lidium spp. and Megaluropus longimerus (Figure 29) were abundant at the C station soon after the disturbance. These species were probably not attracted to the disturbance but were simply more mobile and thus more likely to move into the area. Relative mobility was measured by occurrence in funnel traps (see Appendix). Immobile animals did not occur in the traps, while the most abundant trapped forms were not common on the bottom (e.g., hyperbenthic mysids, Table 1). The mobility of the benthic crustaceans is related to animal morphology, life cycles and spatial zonation (Oliver et al., M.S.).

The polychaetes were not nearly as abundant as the crustaceans at this depth. Dispio uncinata, Nephtys caecoides and Scoloplos armiger were abundant at station C after the October storm, while two other indigenous species, Chaetozone setosa and Paranoides polybranchia, were rare. The former species is probably more mobile than the latter, but no direct evidence for this relationship exists.

Some of the polychaetes characteristic of deeper water settle periodically in shallow water during relatively calm portions of the year (Chapter 2). These seasonal populations are almost completely destroyed during heavy winter swell. The temporal variation in Magelona sacculata illustrates this pattern (Figure 15). These polychaetes (Magelona sacculata, Prionospio pygmaea, P. cirrifera) showed no consistent trend in settlement relative to the disturbance gradient. Apparently, this shallow zone was so thoroughly disturbed by wave activity and the introduced deposit reworked so well that the larvae of these relatively opportunistic species could not distinguish the experimental disturbance or experienced differential mortality that was

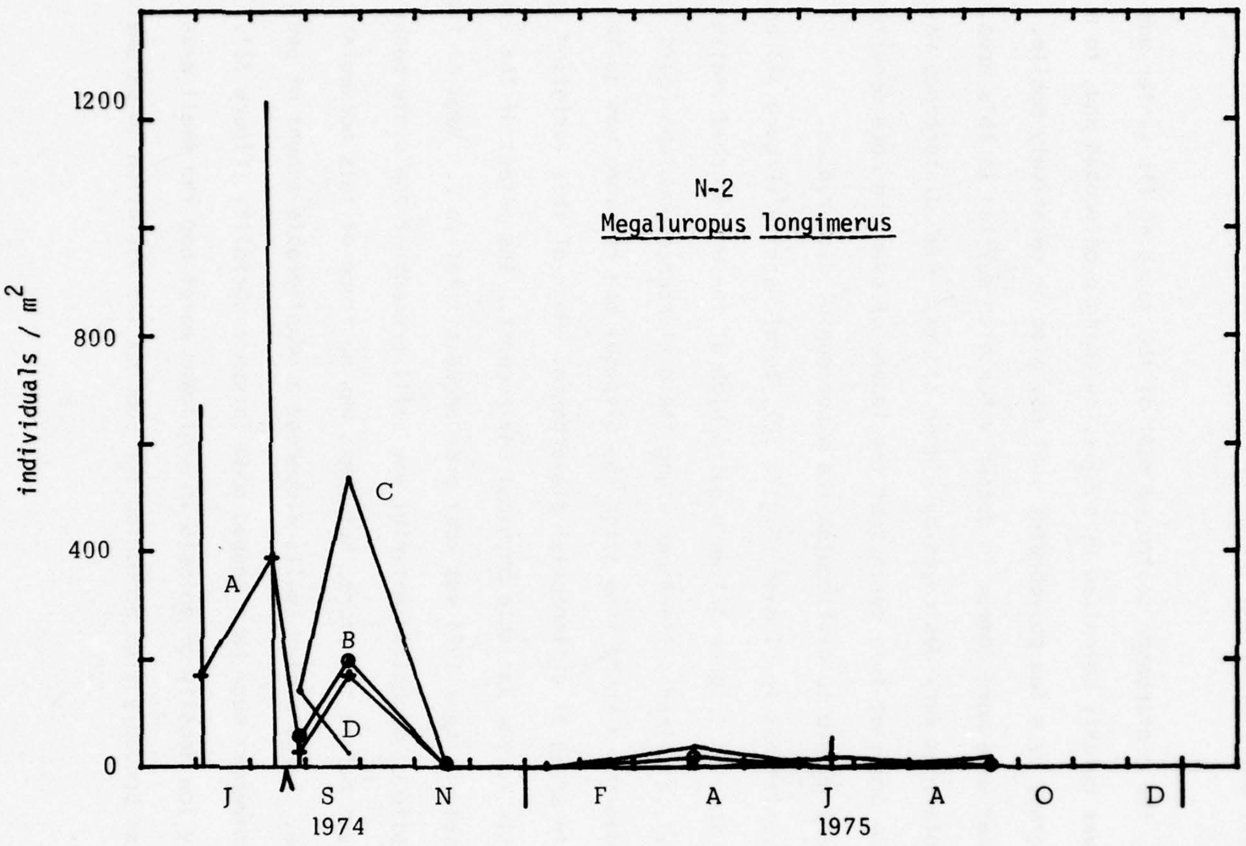

Figure 29. Variations in Megaluropus longimerus along the N-2 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

unrelated to it. Opportunistic polychaetes are characterized by short generation times, small size, low fecundity and high larval availability (Tables 6 and 7).

Thus, the disturbance destroyed most of the fauna at its center and the area was quickly colonized by mobile, swimming crustaceans and, to a much lesser degree, by a few polychaetes that may also be relatively mobile. Polychaetes that were more common in deeper water also settled in this area, but their populations were destroyed by winter storms. Wave disturbance was apparently so great at this depth that the larvae of even the more opportunistic species were unable to distinguish the experimental disturbance.

The variations in biomass (Figure 30), total density (Figure 31) and number of species (Figure 32) were quite high at the undisturbed station (A). As a result, distinct differences along the disturbance gradient could only be discerned for a short time after the disposal and recovery was quite variable in areas of differential disturbance. Much of this variation is attributable to the variable physical environment. The effect of the large storm in late October 1974 was most pronounced at station C. Some of the original pile of deposited material was still present at the disturbance center (D) just before the storm, but there was no trace of this accumulation afterwards. Large winter swells dispersed a considerable amount of sediment and this movement must have caused some infaunal mortality (Figure 31). The relatively low density of animals in shallower water and the small area of the samples probably also accounted for some of the variation in parameter estimates.

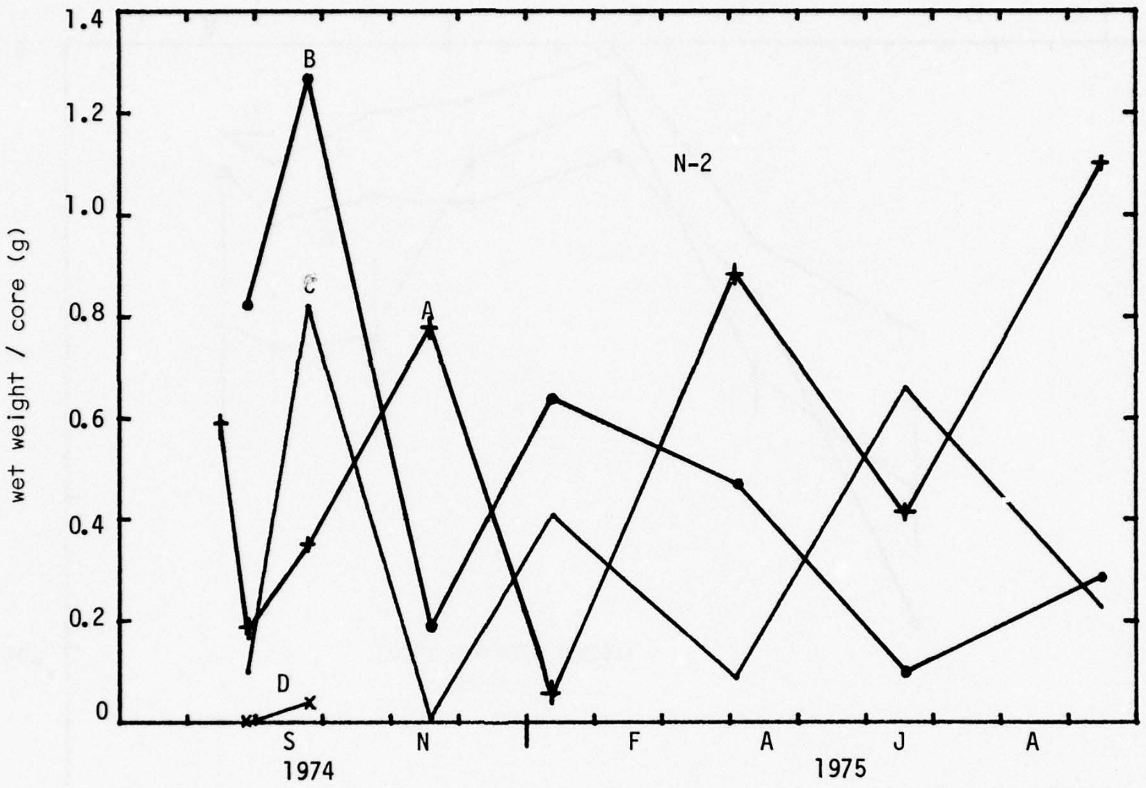

Figure 30. Variations in the biomass of vermes (wet weight) along the N-2 disturbance gradient.

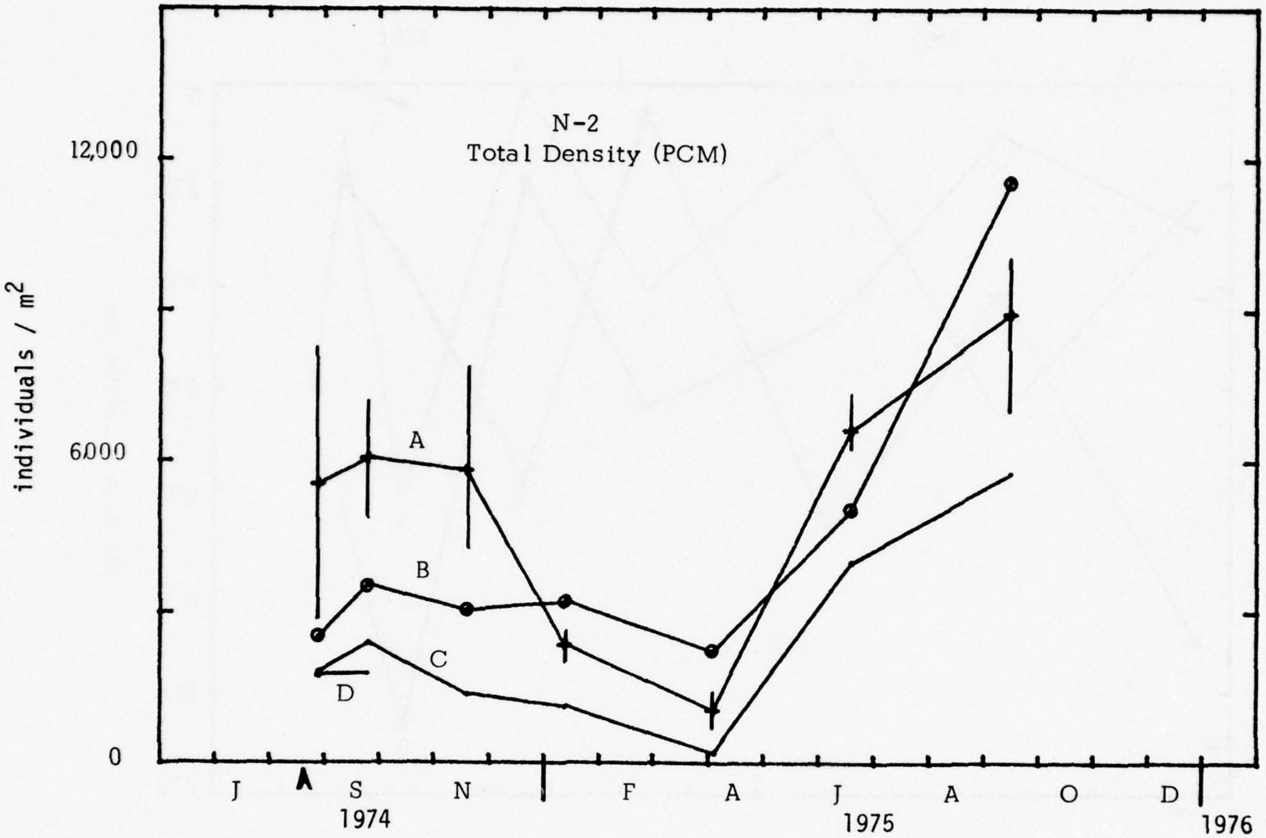

Figure 31. Variations in the total density (polychaete, crustacean, molluscan (PCM)) along the N-2 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

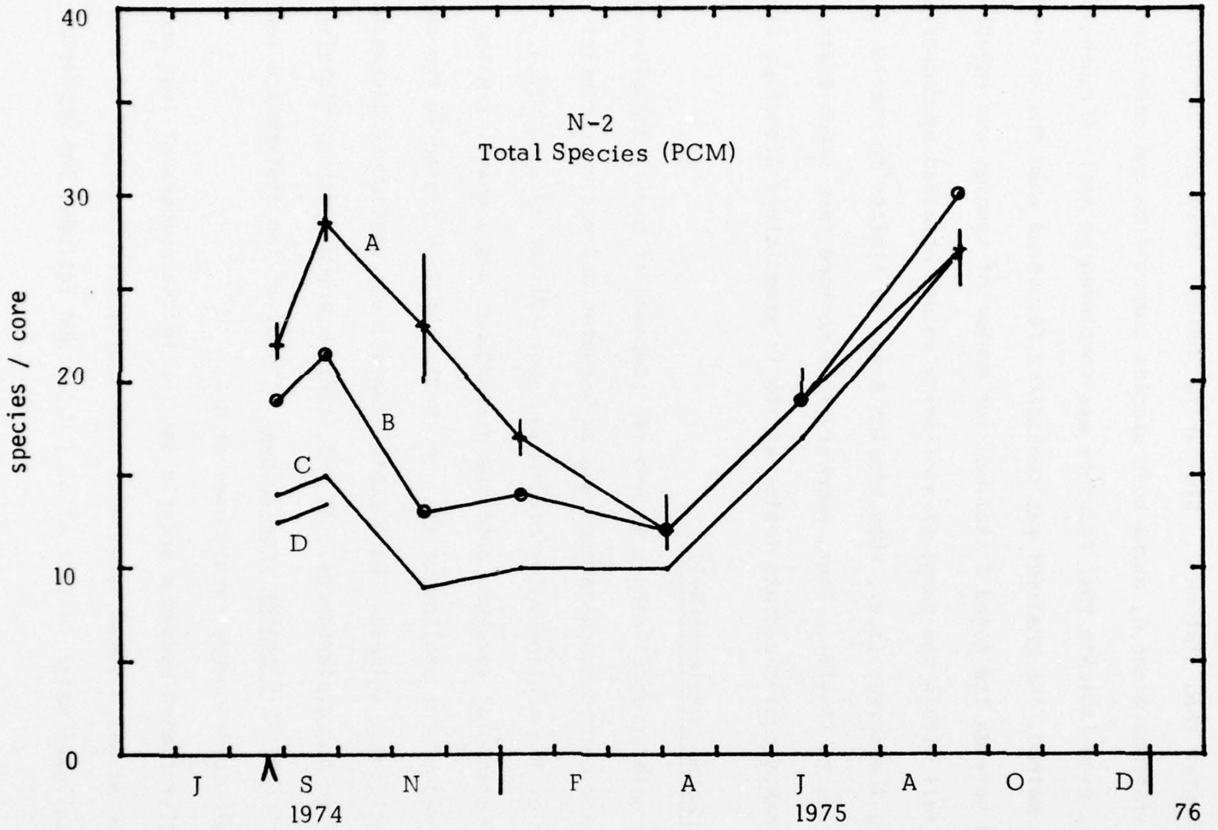

Figure 32. Variations in total species (polychaete, crustacean, molluscan) along the N-2 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

The number of species (Figure 32) and individuals (Figure 31) at the disturbance center was essentially recovered by April 1975 and station B recovered faster than station C. Similarity indices (Bray and Curtis, 1957) comparing stations A and C, using both species composition and relative abundance data, also indicate that recovery was completed by April (Figure 33). Using this method, the gradient was considered recovered when the similarity calculated between the A and C stations for number of species and relative abundance fell within the range of similarity values obtained by comparing A cores among themselves (i.e., when station A was as similar to station C as station A was to itself). Thus, recovery took no more than seven months at the disturbance center and was faster at the intermediately disturbed site.

18-m Disturbance Gradient (N-3)

The predisturbance infauna at N-3 was composed of small, deposit-feeding peracarid and ostracod crustaceans and polychaetes and was characteristic of the center of the shallow water crustacean zone (Oliver et al., M.S.).

The pattern of recovery from the disturbance was somewhat similar to that observed at the shallowest station (N-2), but it differed in the response of large epifaunal animals. Each depth gradient was visited by divers within minutes after the disturbances. At N-3, they observed numerous flatfish and seastars (primarily Pisaster brevispinus) already at the disturbance center. These larger animals were rarely seen at N-2.

The disturbance caused a drastic decline in the numbers of less mobile crustaceans at N-3. These forms were numerically more important at this depth than in shallower water (Oliver et al., M.S.) and included the amphipods Para-

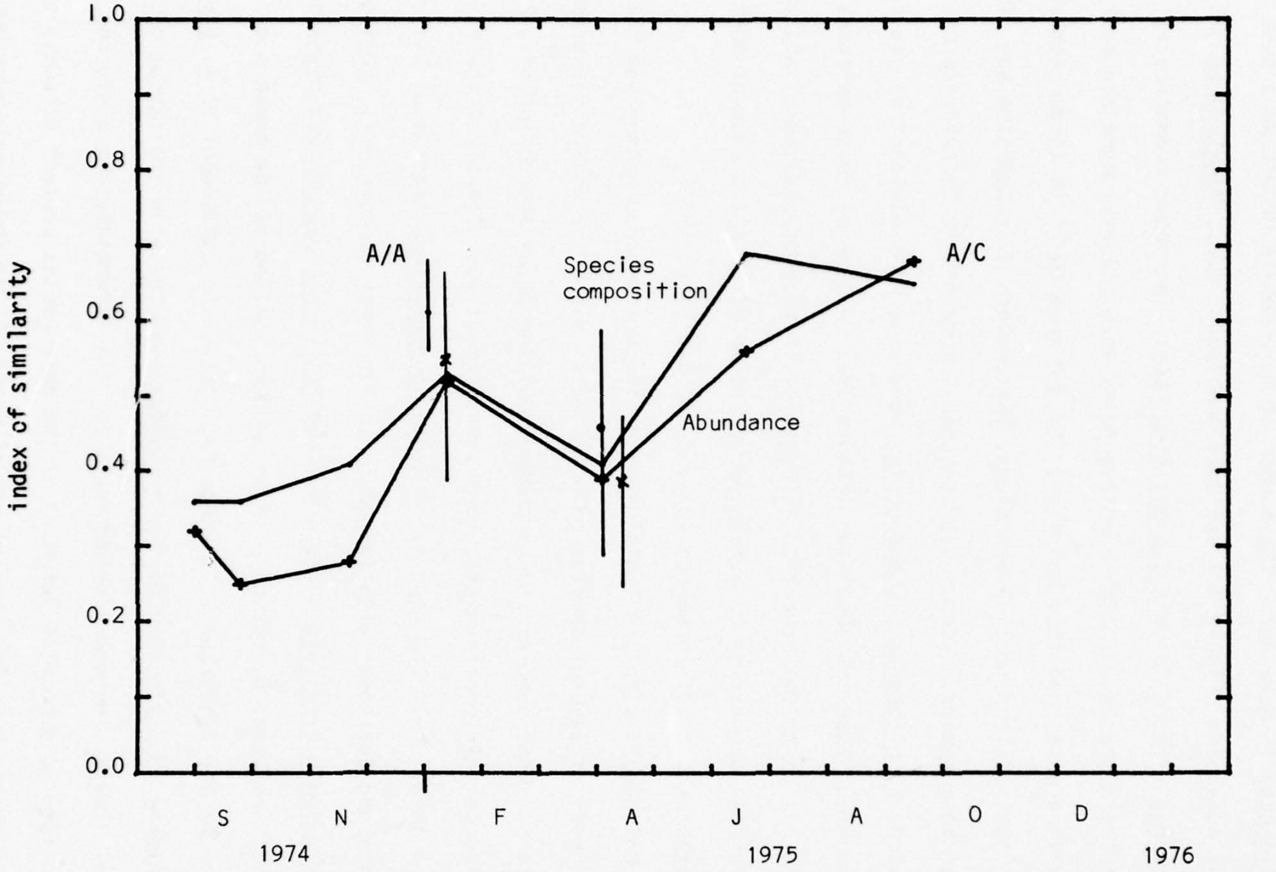

Figure 33. Recovery of the fauna along the N-2 disturbance gradient: Bray-Curtis similarity index calculated for pairs of A and C cores compared to indices calculated among A cores for species composition and abundance. Vertical lines give the mean and range of the similarity values among A cores.

phoxus (Figure 34) and Eohaustorius (Figure 35) and the ostracod Euphilomedes (Figure 36). The number of more mobile crustaceans such as the cumaceans (Figure 37) and some amphipods e.g., Megaluropus longimerus (Figure 38) and Synchelidium spp., increased dramatically after the disturbance. These active forms were slightly more abundant in shallow water and thus colonized the 9-m area (N-2) in larger numbers after that disturbance; nevertheless, the pattern of succession was similar at both depths. Larger and presumably more mobile individuals of the ostracod, Euphilomedes carcharodonta, were also more abundant at the disturbed areas than the juveniles (Figure 39). None of these patterns were the result of animal migration through the introduced sediment. All small crustaceans are killed by a mass accumulation of deposits such as that of the experimental disturbances (Oliver and Slattery, 1976).

Coincident with the immigration of the mobile crustaceans was the settlement of several species of polychaetes along the entire disturbance gradient. Most species showed reduced settlement at the disturbed sites, but for certain opportunistic forms, settlement was highest at the disturbed locations. The density of Armandia brevis was highest at the A station and decreased with increasing disturbance (Figure 40). Settlement of Prionospio cirrifera (Figure 41) and Prionospio pygmaea was highest at stations C and B, but both these species settled in low numbers at the center of the disturbance (station D). Thus, the settlement of A. brevis was nearly opposite that of the Prionospio species with the larvae of the latter showing increased selectivity for the intermediately disturbed sites. These species accounted for most of the polychaetes present directly after the disturbance. The periodic settlement of the Prionospio species

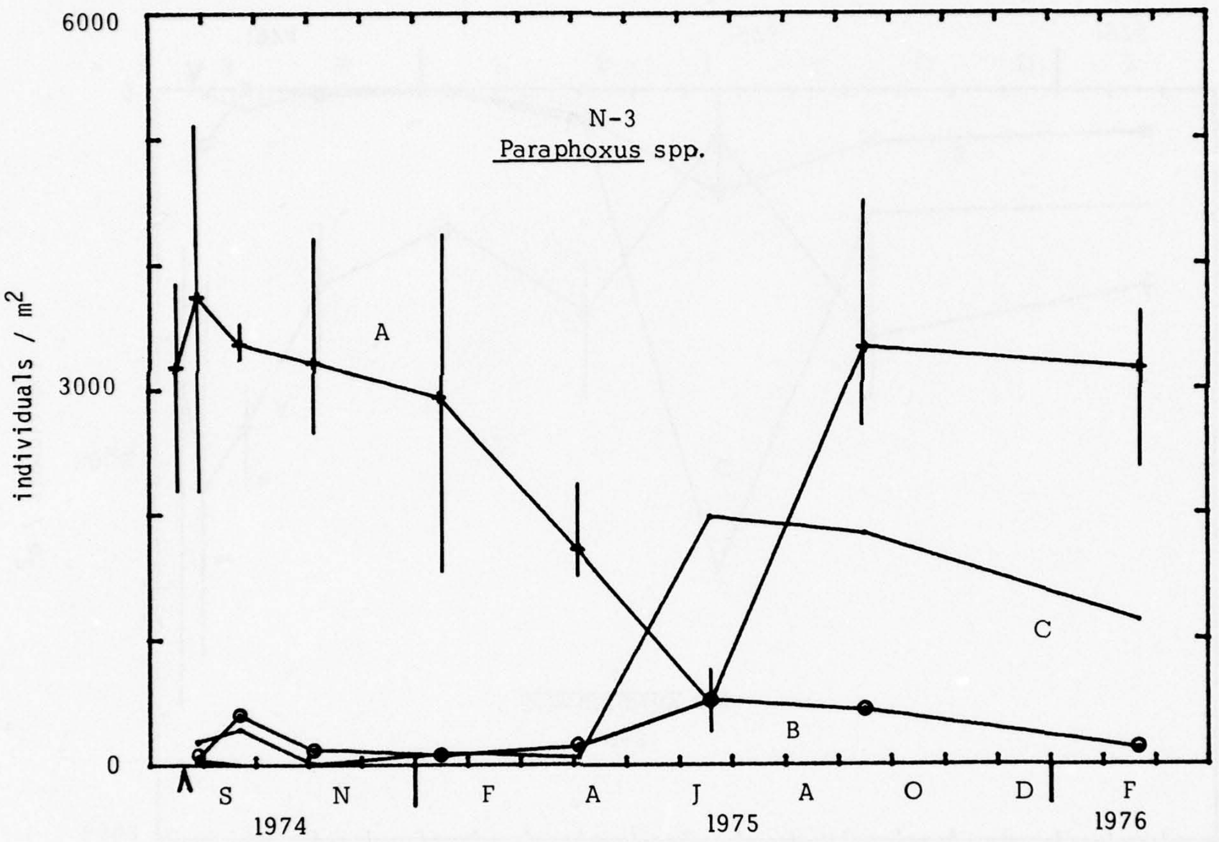

Figure 34. Variations in Paraphoxus spp. along the N-3 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

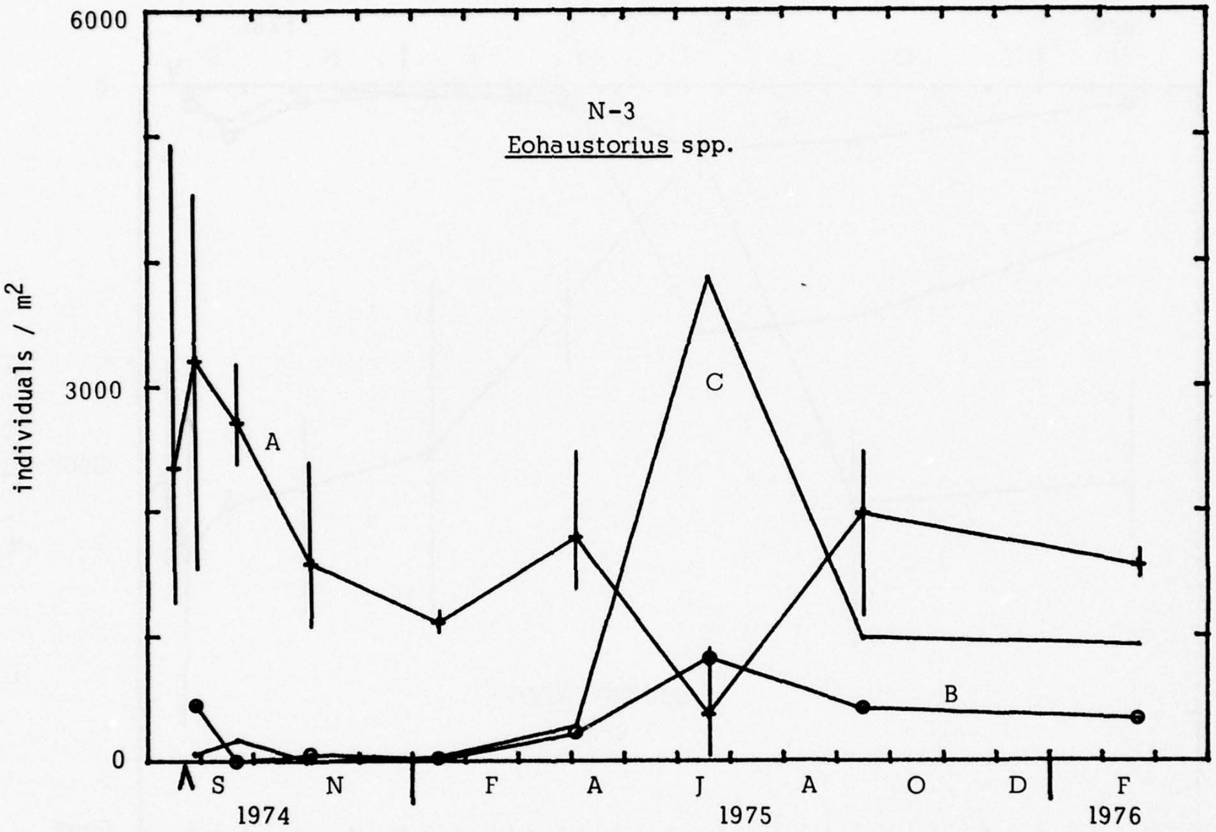

Figure 35. Variations in Eohaustorius spp. along the N-3 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

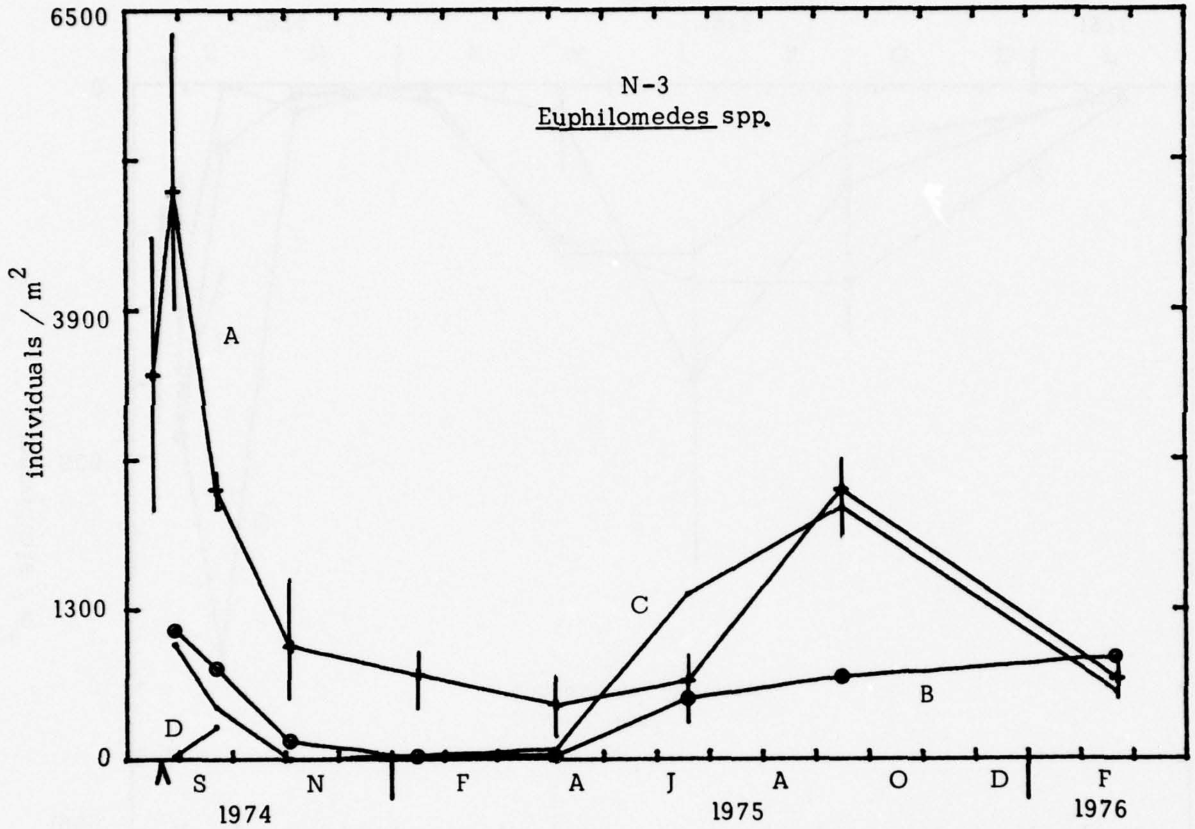

Figure 36. Variations in Euphilomedes spp. along the N-3 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

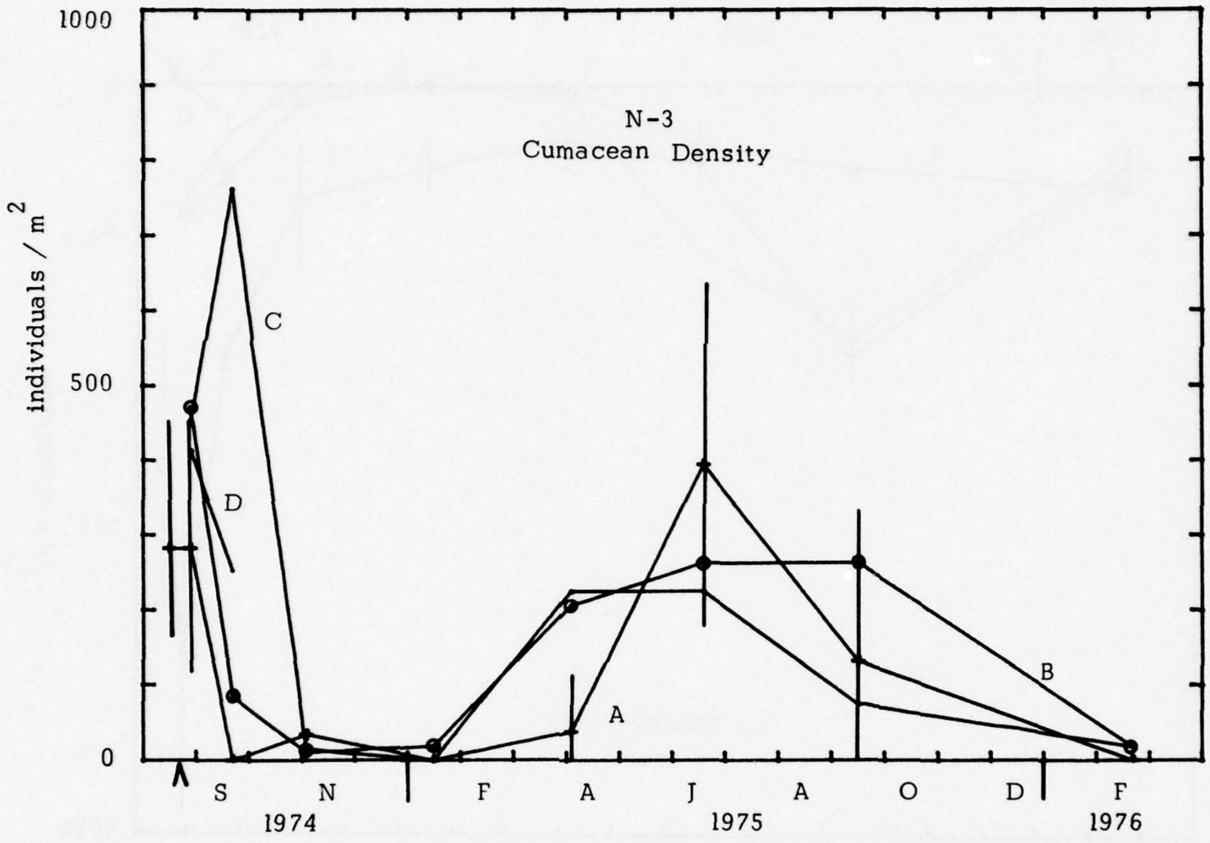

Figure 37. Variations in cumacean density along the N-3 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

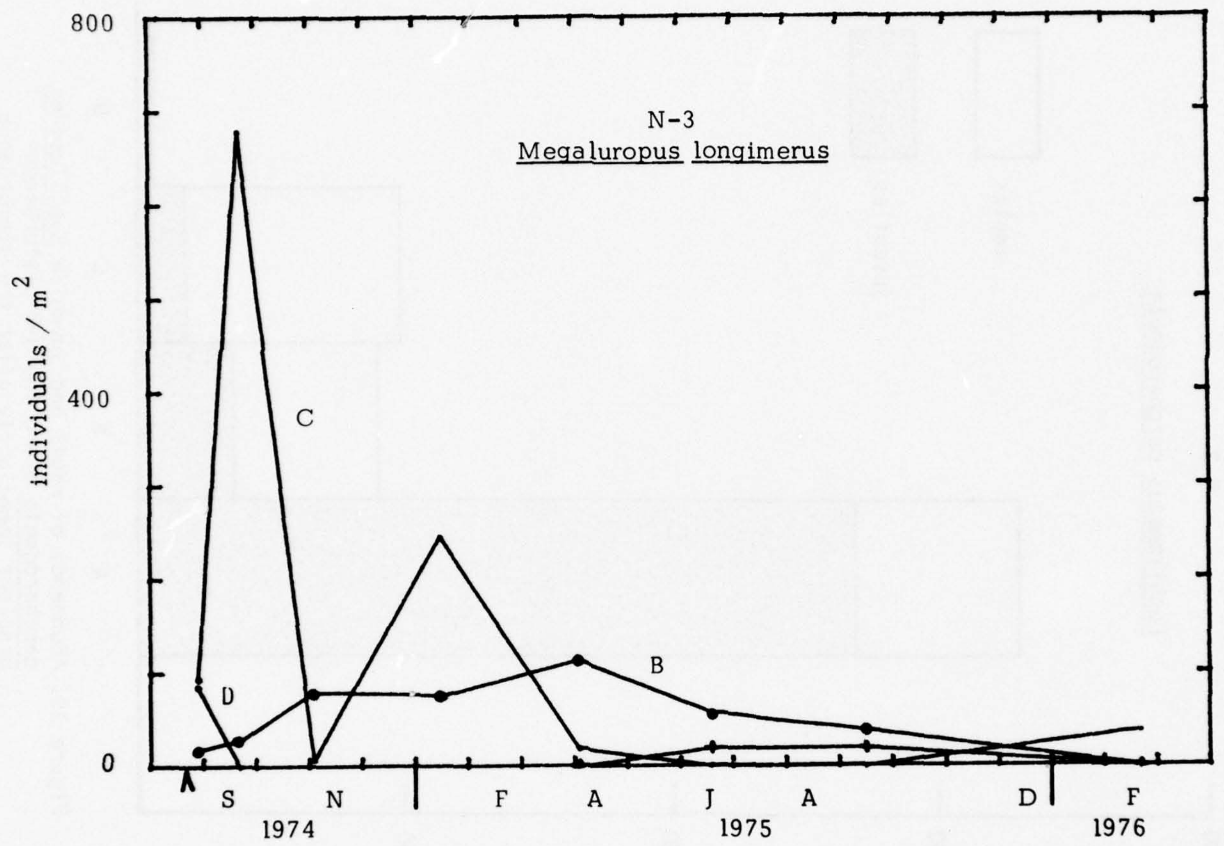

Figure 38. Variations in *Megaluropus longimerus* along the N-3 disturbance gradient (means with no ranges given). Arrow indicates disturbance.

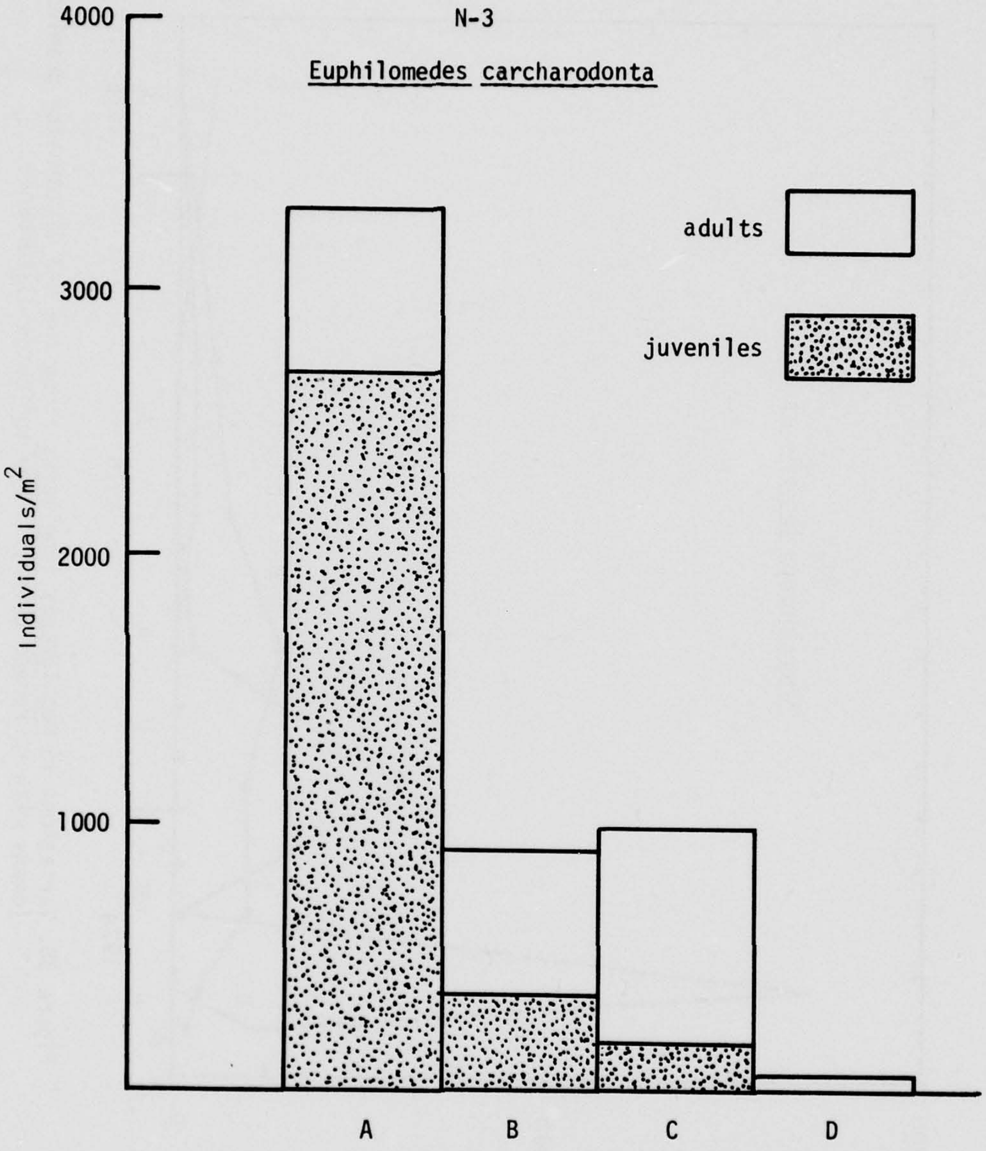

Figure 39. Abundance of adult and juvenile *Euphilomedes carcharodonta* along the N-3 disturbance gradient immediately after the disturbance (29 August 1974).

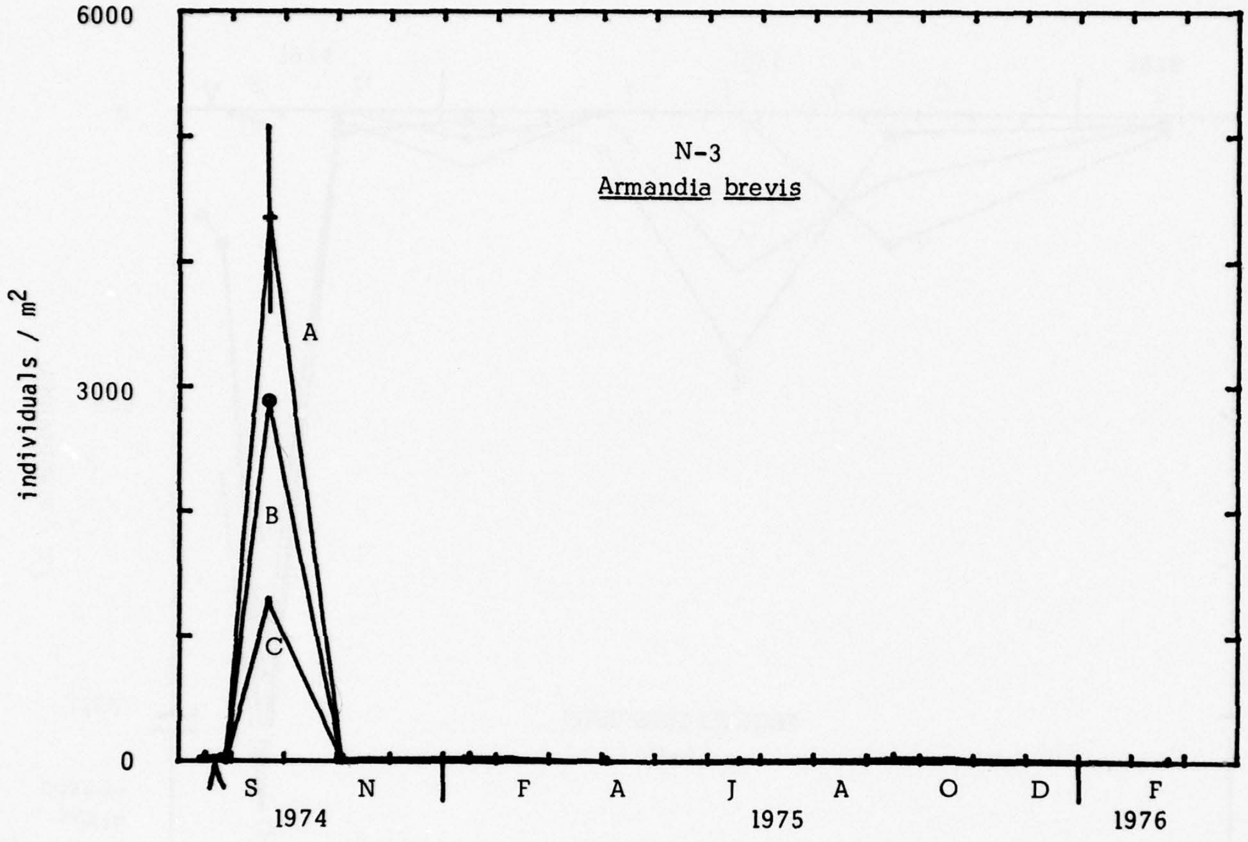

Figure 40. Variations in *Armandia brevis* along the N-3 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

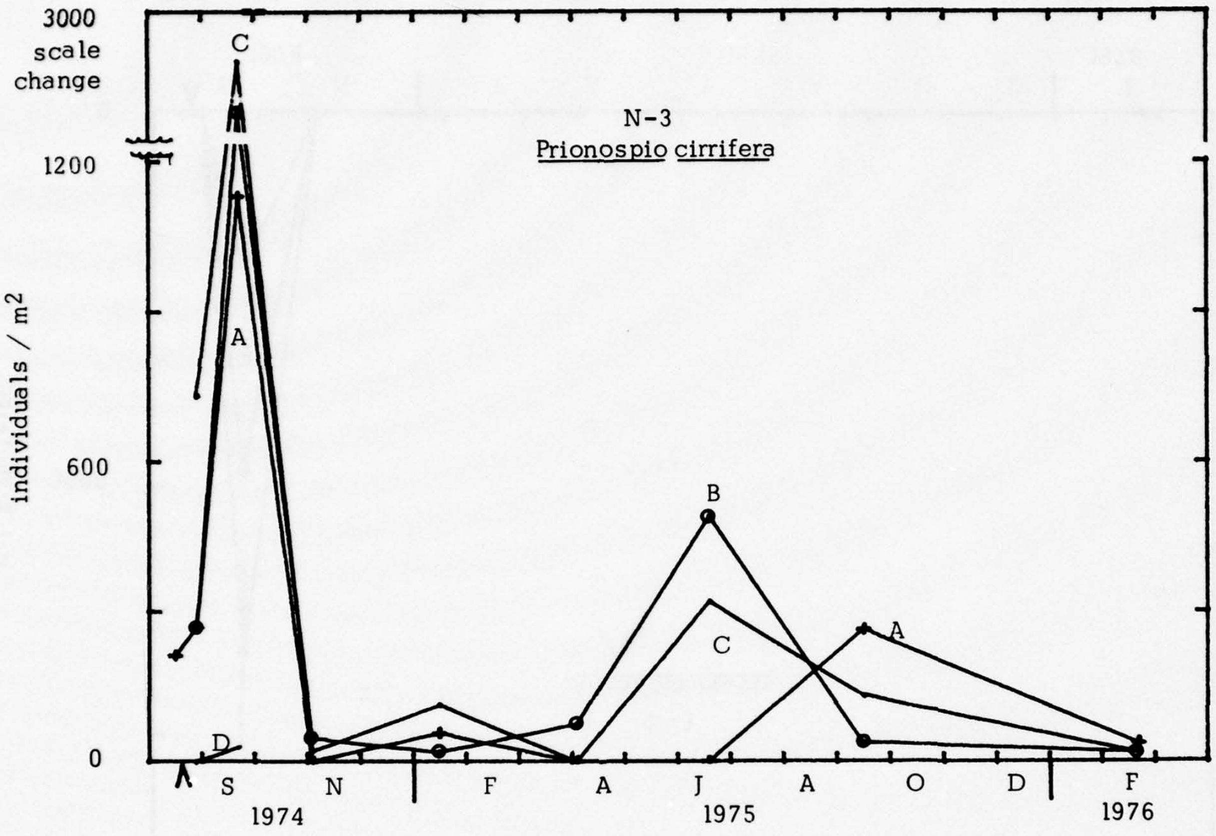

Figure 41. Variations in Prionospio cirrifera along the N-3 disturbance gradient (means with no ranges given). Arrow indicates disturbance.

was consistent with their appearance in the larval jars (see Appendix). Dispio uncinata and Dendraster excentricus live in very shallow water and in coarse, shifting sediments and also periodically settled in relatively high numbers at the disturbed sites. Their presence probably indicated a relatively unstable substrate.

The increase in less mobile crustaceans (Figures 34 and 35) and less opportunistic polychaetes (Figures 42 to 45) characterized the later phase of succession. The high seasonal mortality and low winter recruitment of the polychaetes at the shallowest station was not as pronounced at N-3; however, seasonal recruitment was observed in forms with seasonal breeding cycles like Magelona sacculata and the common amphipods and ostracods (Chapter 2). Most of the molluscs were juvenile bivalves that were present in low numbers until the summer and fall of 1975 (Figure 46).

The variations in the total number of individuals reflected: the large polychaete settlement (Figures 47 and 48) and to a lesser extent the influx of mobile crustaceans during early recovery (Figures 36 and 37); the mortality related to the late October storm; and the gradual recovery of the pre-disturbance infauna after the winter period. The abundance of almost all species and the total number of species were decreased by the heavy storm in late October 1974 (Figures 46 to 50). Higher storm mortality occurred in areas of greater initial disturbance due to more extensive substrate motion. The number of individuals of polychaetes, crustaceans and molluscs at the disturbance center (station C) was similar to that at the undisturbed station (A) by June 1975 (Figures 46, 47, 49). Recovery was quite variable and there was a distinct drop in polychaete numbers at disturbance stations B and C after June 1975. The number of species, how-

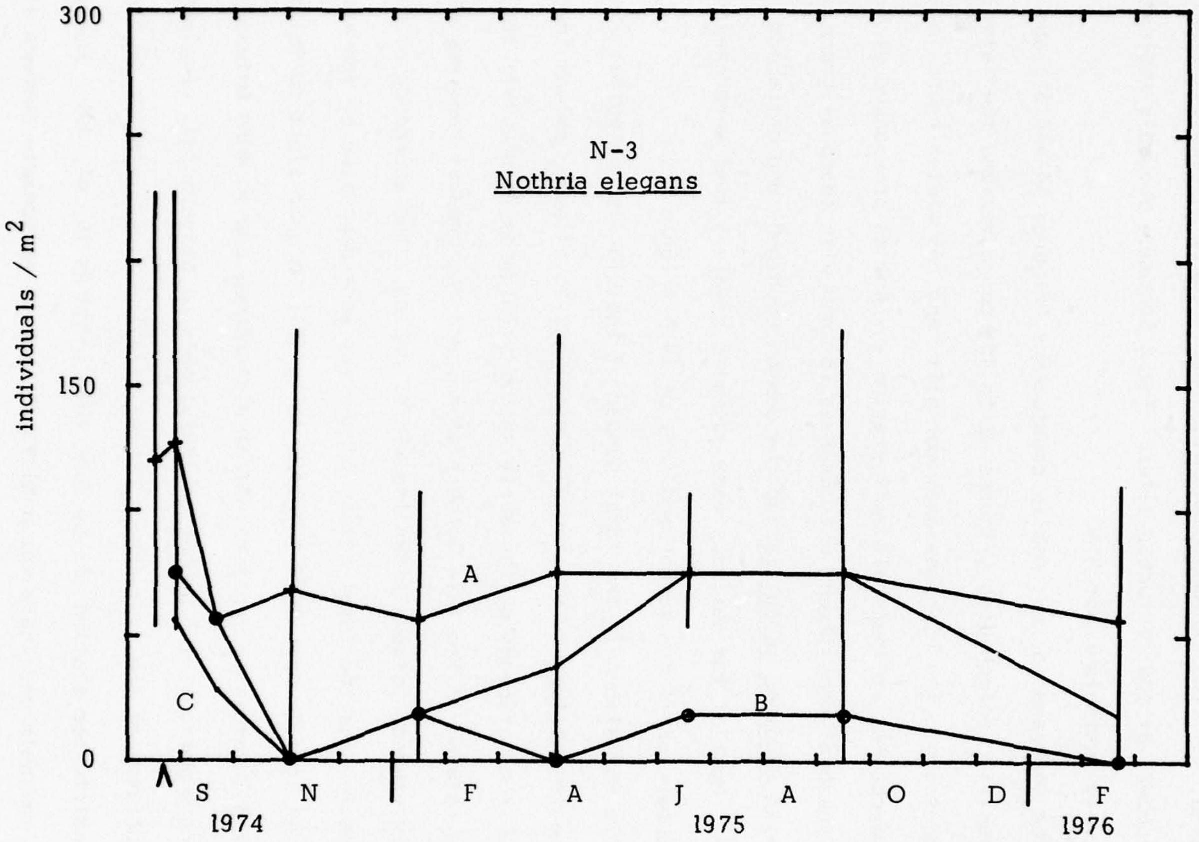

Figure 42. Variations in <u>Nothria elegans</u> along the N-3 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

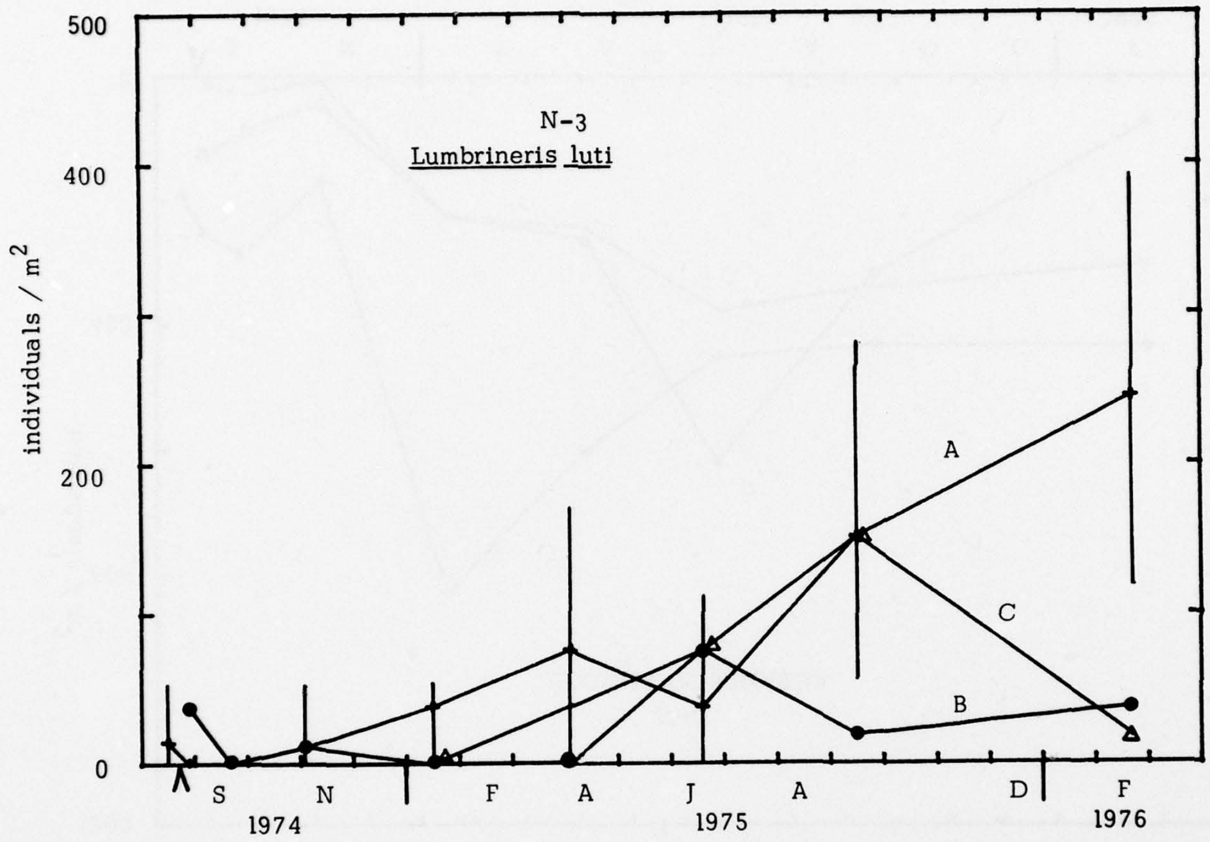

Figure 43. Variations in Lumbrineris luti along the N-3 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

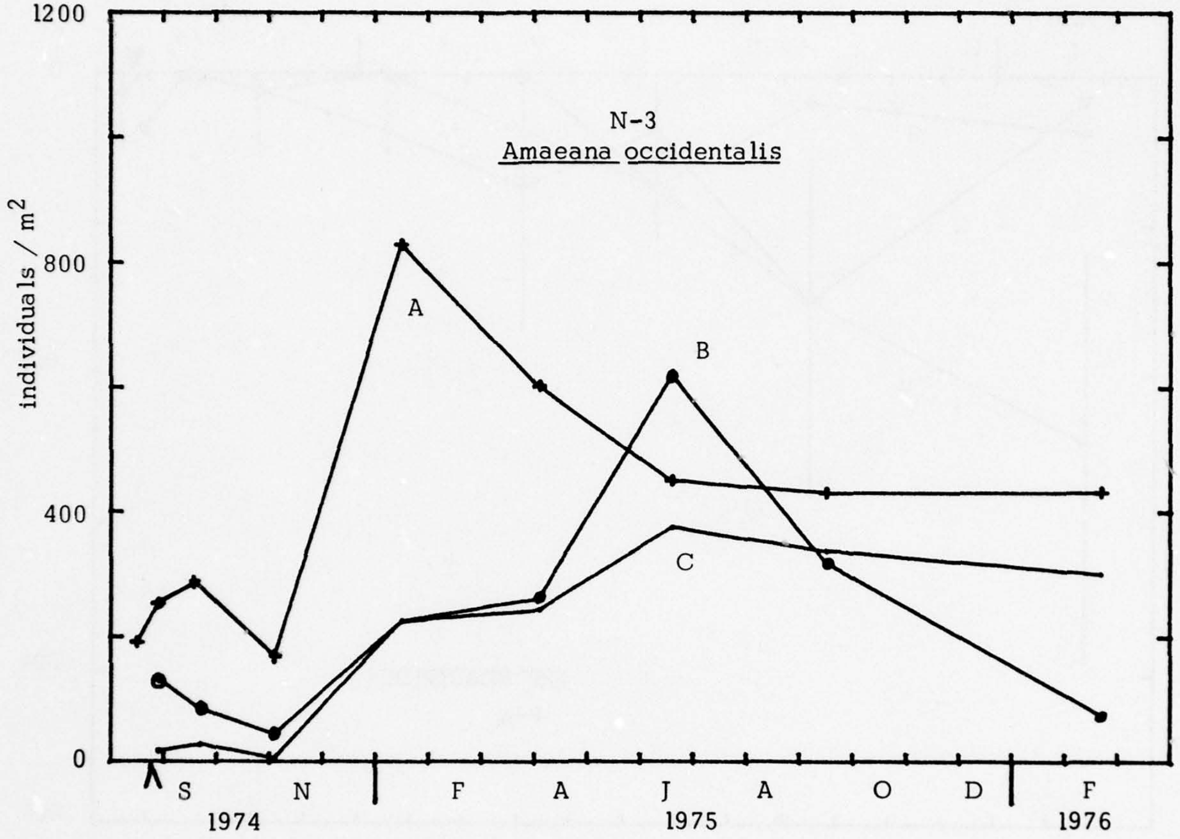

Figure 44. Variations in Amaeana occidentalis along the N-3 disturbance gradient (means with no ranges given). Arrow indicates disturbance.

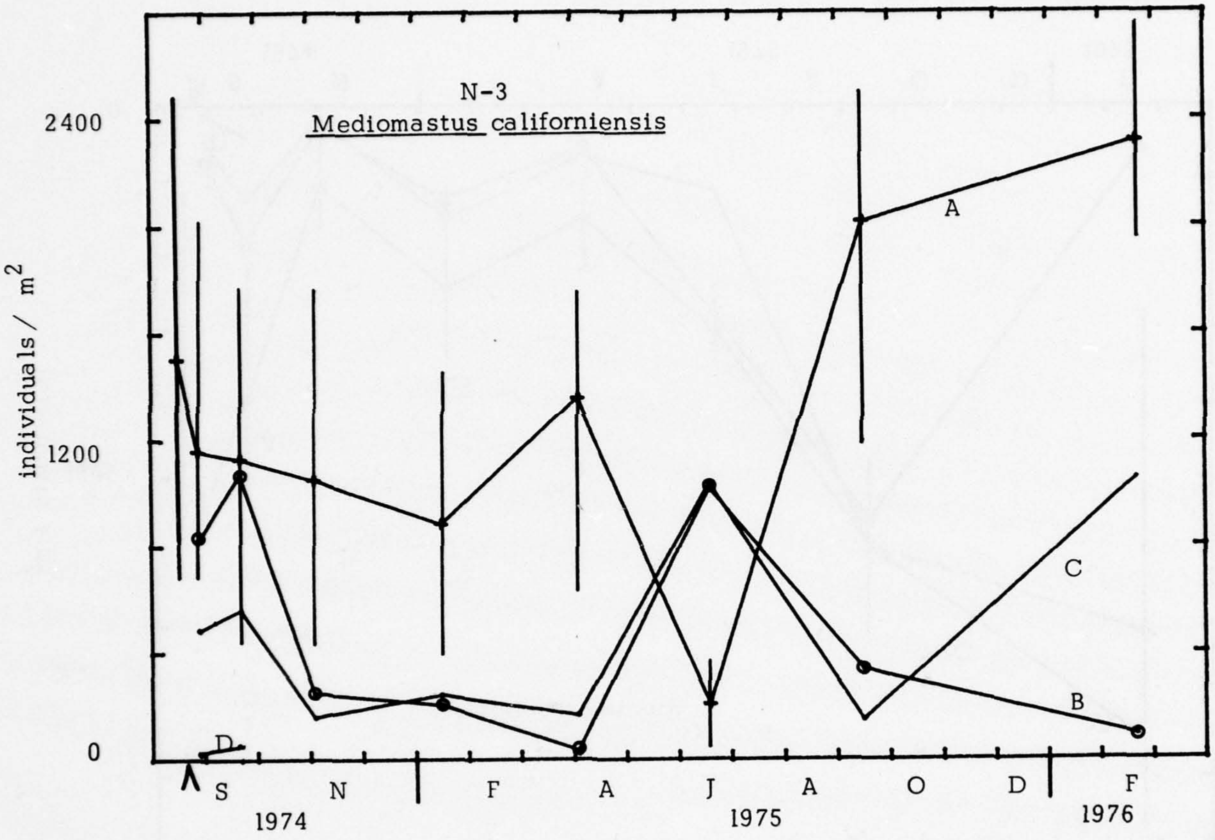

Figure 45. Variations in Mediomastus californiensis along the N-3 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

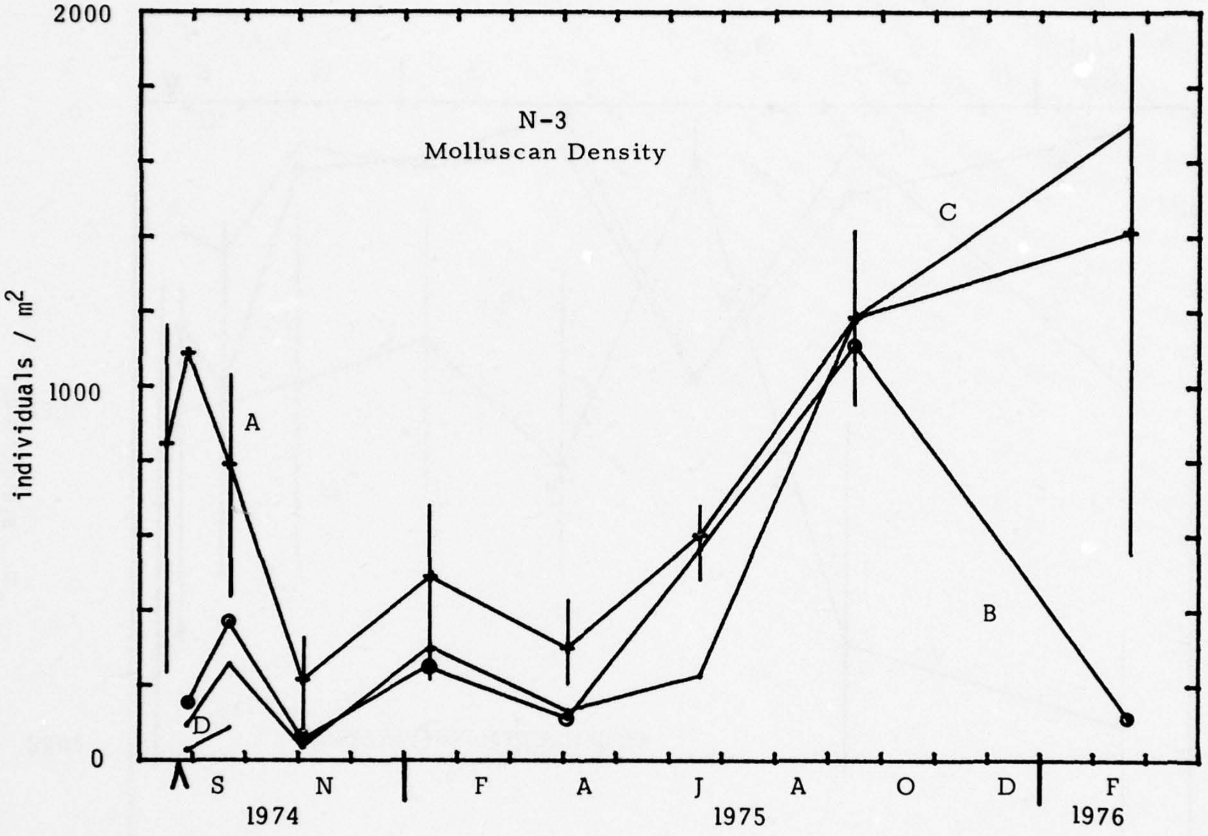

Figure 46. Variations in molluscan density along the N-3 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

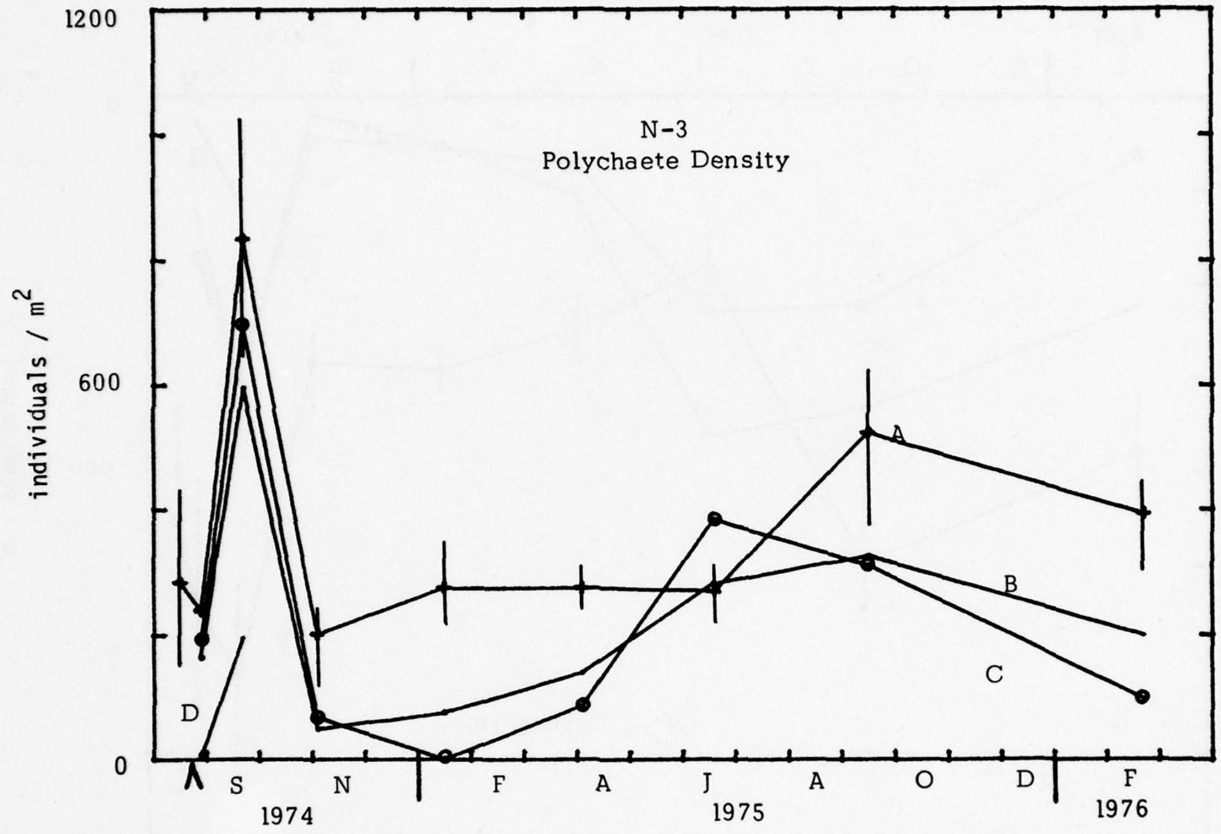

Figure 47. Variations in polychaete density along the N-3 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

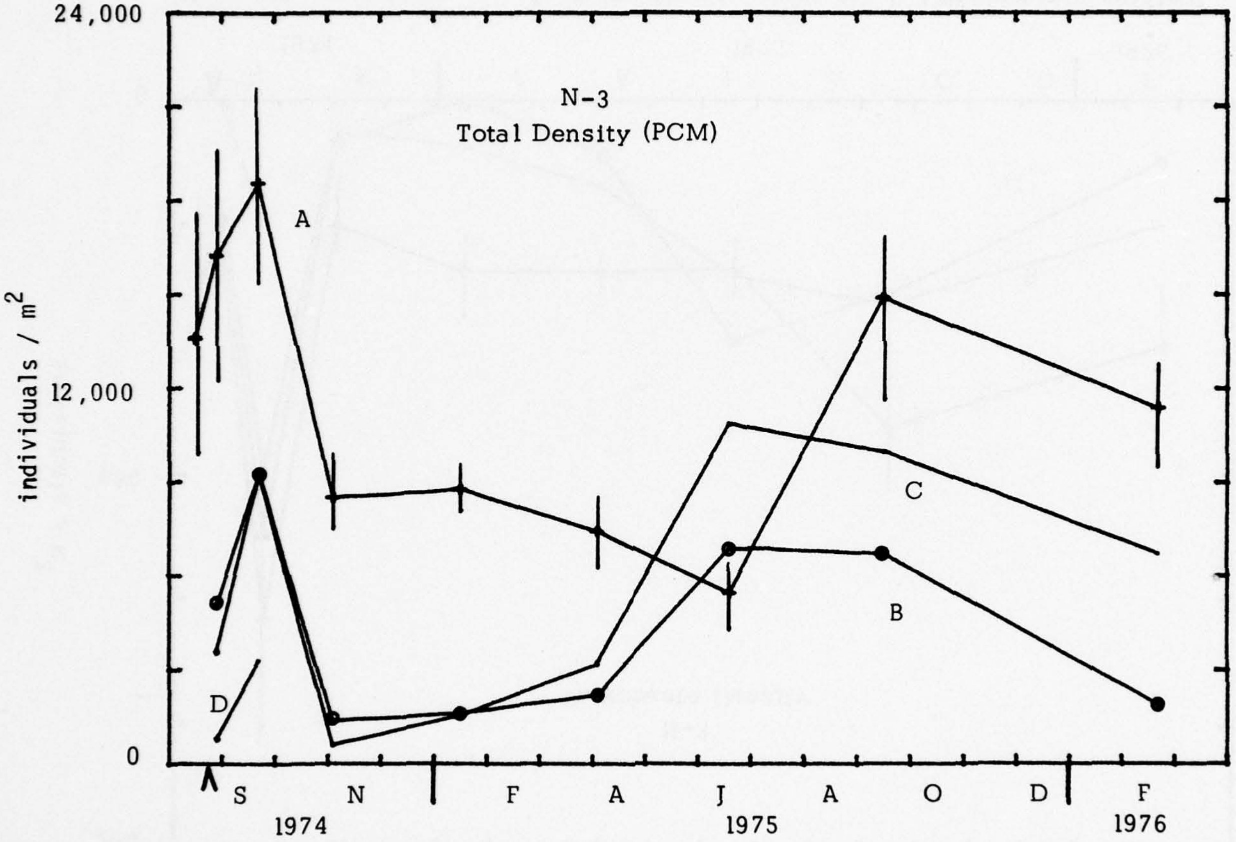

Figure 48. Variations in total density (polychaete, crustacean, molluscan) along the N-3 disturbance gradient (means and ranges on A). Arrow indicates disturbance.

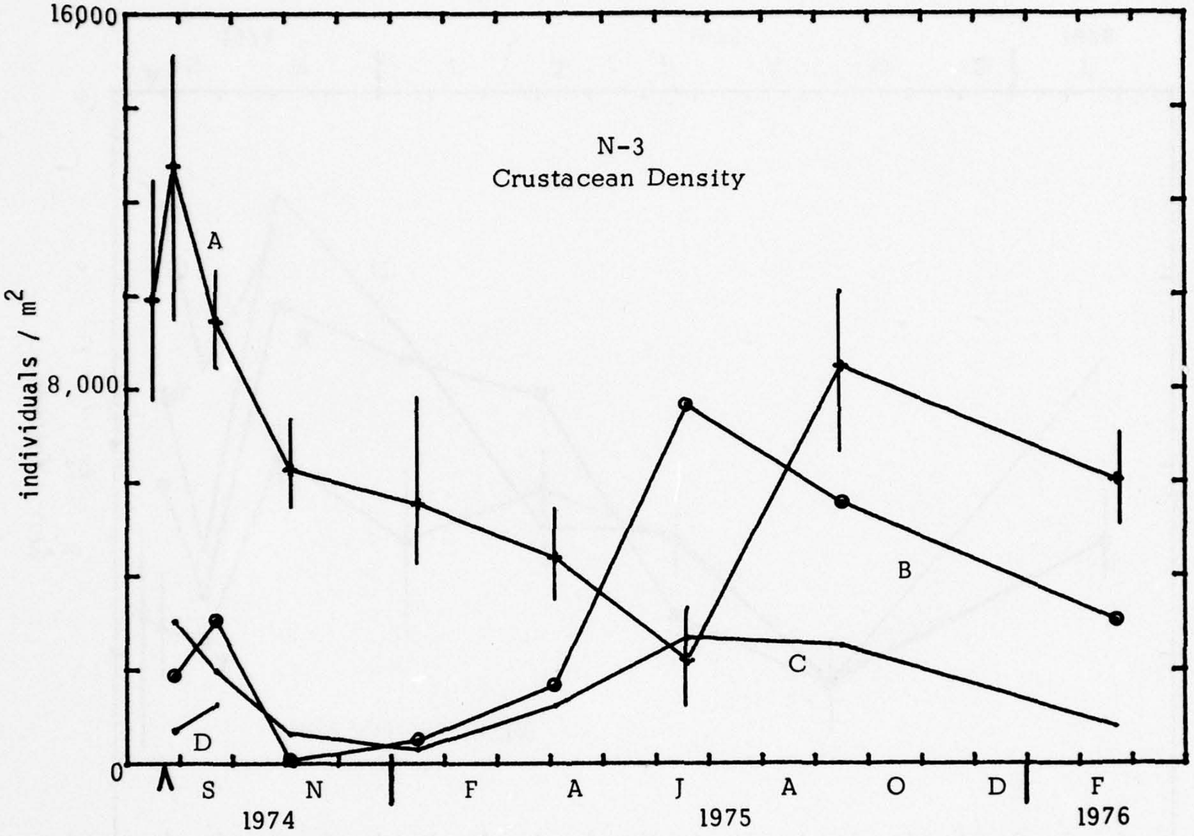

Figure 49. Variations in crustacean density along the N-3 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

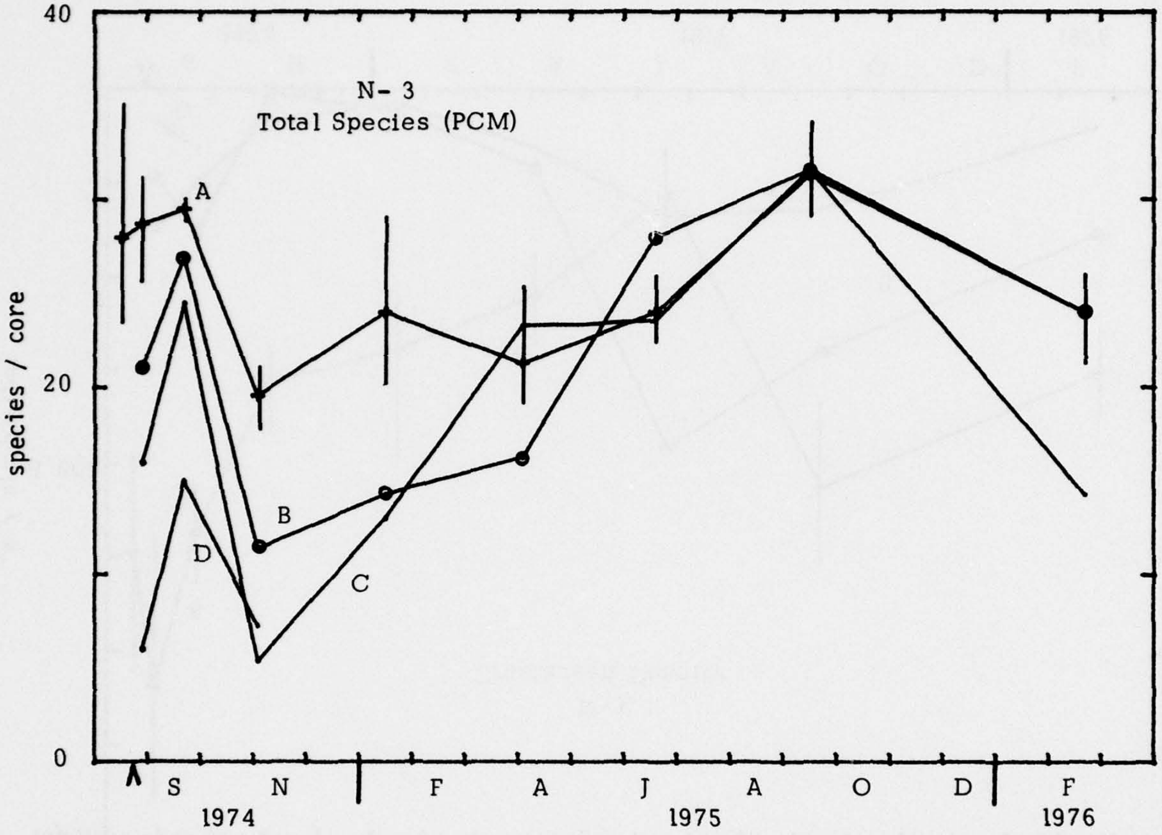

Figure 50. Variations in total species (polychaete, crustacean, molluscan) along the N-3 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

ever, appeared to recover as early as March 1975 (Figure 50). Biomass followed a similar but more variable trend (Figure 51). The similarity in species composition and relative abundances computed between stations A and C was similar to values calculated among pairs of station A replicate samples by September 1975 (Figure 52).

In summary, most of the infauna were destroyed at the center of the disturbance. The early phase of succession was characterized by the settlement of several species of more opportunistic polychaetes and the immigration of mobile crustaceans. The density of early colonists was highest at the C rather than the D stations prior to the October storm. The later phase was characterized by a gradual increase in the pre-disturbance fauna (i.e., less mobile crustaceans and less opportunistic polychaetes). Recovery of the pre-disturbance assemblage occurred within a year. There was a general decline in the density of crustaceans and polychaetes at all stations during the second winter, but the variation in total abundance among stations could not be explained by the initial disturbance (Figure 49).

24-m Disturbance Gradient (N-4)

The pre-disturbance infauna at the deepest station had more polychaetes and somewhat fewer crustaceans than the shallower stations. The reduced wave disturbance and more stable substrate at this depth were accompanied by a reduction in the number of more mobile crustaceans that were characteristic of shallow water (Oliver et al., M.S.). As a result, these forms were not as abundant during the early phase of succession (e.g., Figure 53). Instead, there was a gradual post-disturbance increase in crustaceans that was interrupted by the October 1974 storm. The most

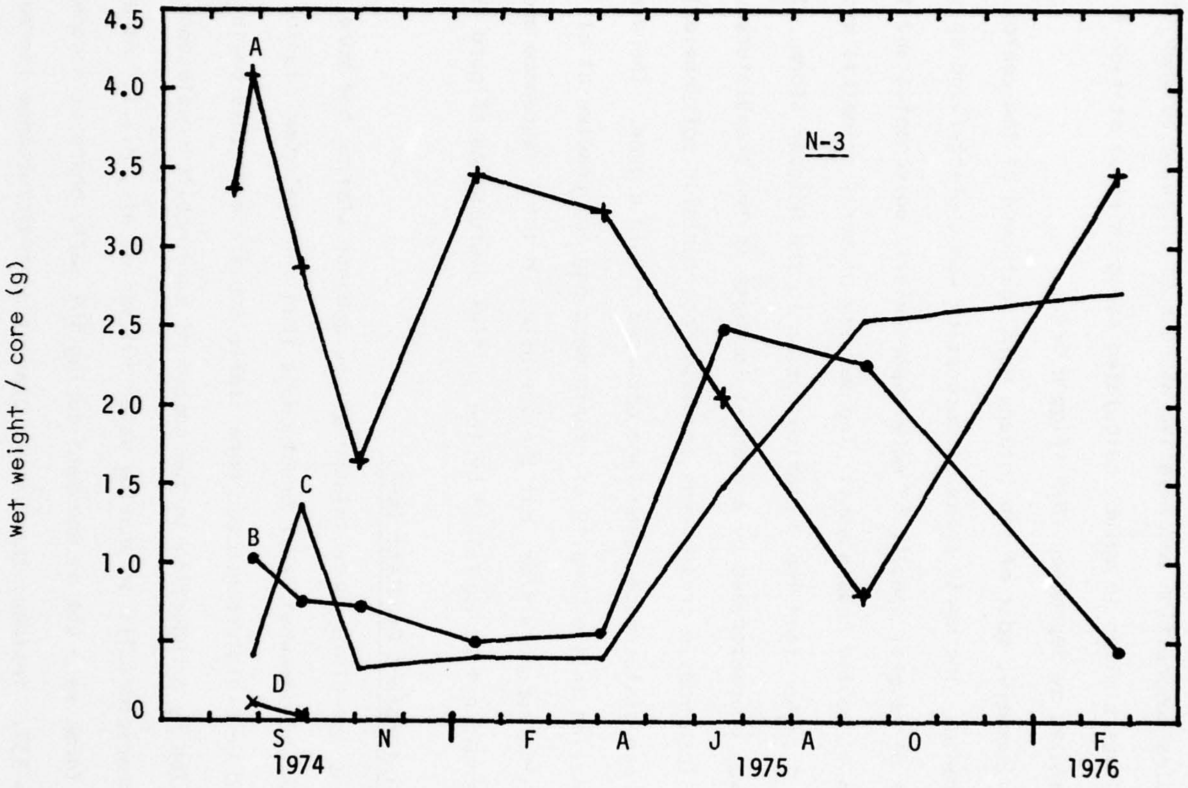

Figure 51. Variations in the biomass of vermes (wet weight) along the N-3 disturbance gradient.

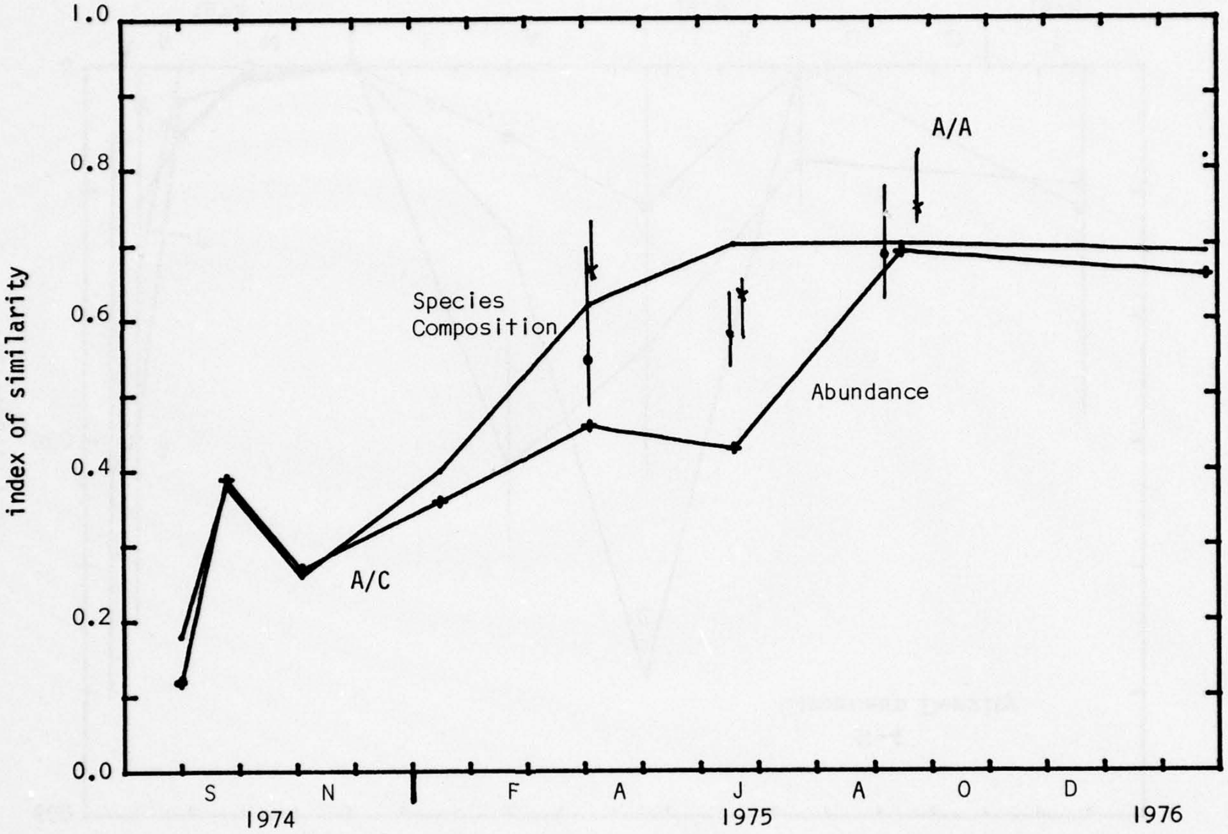

Figure 52. Recovery of the fauna along the N-3 disturbance gradient: Bray-Curtis similarity index calculated for pairs of A and C cores compared to indices calculated among A cores for species composition and abundance. Vertical lines give the mean and range of the similarity values among A cores.

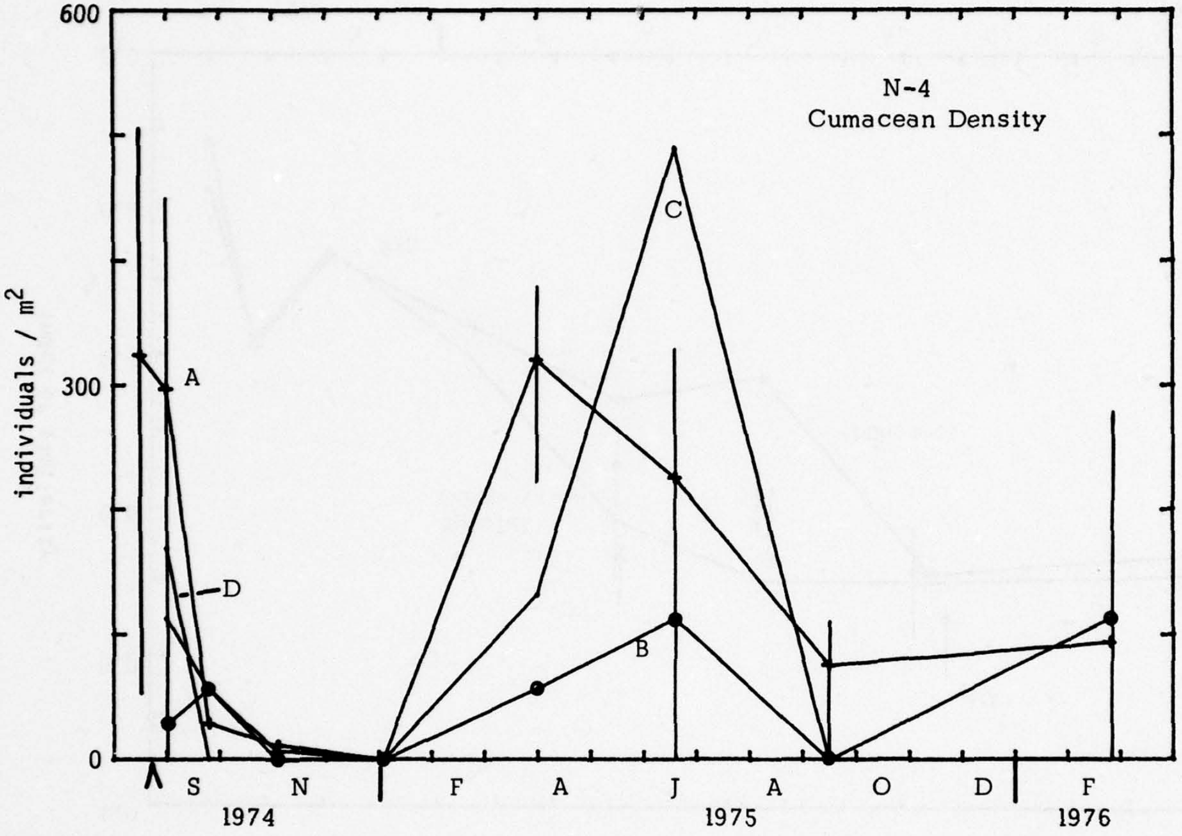

Figure 53. Variation in cumacean density along the N-4 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

abundant crustaceans were the paraphoxid amphipods and ostracods. Their populations had not recovered by February 1976 (Figures 54 and 55).

The early phase of recovery was dominated by the settlement of several relatively opportunistic polychaetes. Armandia brevis, Prionospio pygmaea and P. cirrifera settled in largest numbers at the disturbance center (D) but experienced high mortality rates (Figures 56 to 58). Their benthic abundances reflected their availability in the plankton (Table 6). There was also a large settlement of Gyptis brevipalpa at the disturbance center in the winter and the shallow water species, Dispio uncinata, was found only in the disturbed areas. The late phase of recovery involved a gradual increase in the pre-disturbance polychaete fauna. The seasonal recruitment of Magelona sacculata was very similar along the gradient (Figure 59). The numbers of Amaeana occidentalis (Figure 60) and Nothria elegans appeared to recover during the study period but Mediomastus californiensis (Figure 61) and several others did not.

The bivalve recovery pattern was similar to the 18-m station, but numerical recovery had not occurred by February 1976 (Figure 62).

The variations in total faunal density in the disturbed areas reflected; the settlement and high mortality of several more opportunistic polychaetes (Figure 63), the low migration of crustaceans at this depth (Figure 64) and a gradual increase among all the major taxa, though none reached the density of the undisturbed site by February 1976 (Figure 65). The B station (intermediate disturbance) was more completely recovered than the C station by February 1976. The number of species and biomass had not recovered by the end of the study (Figures 66 and 67); how-

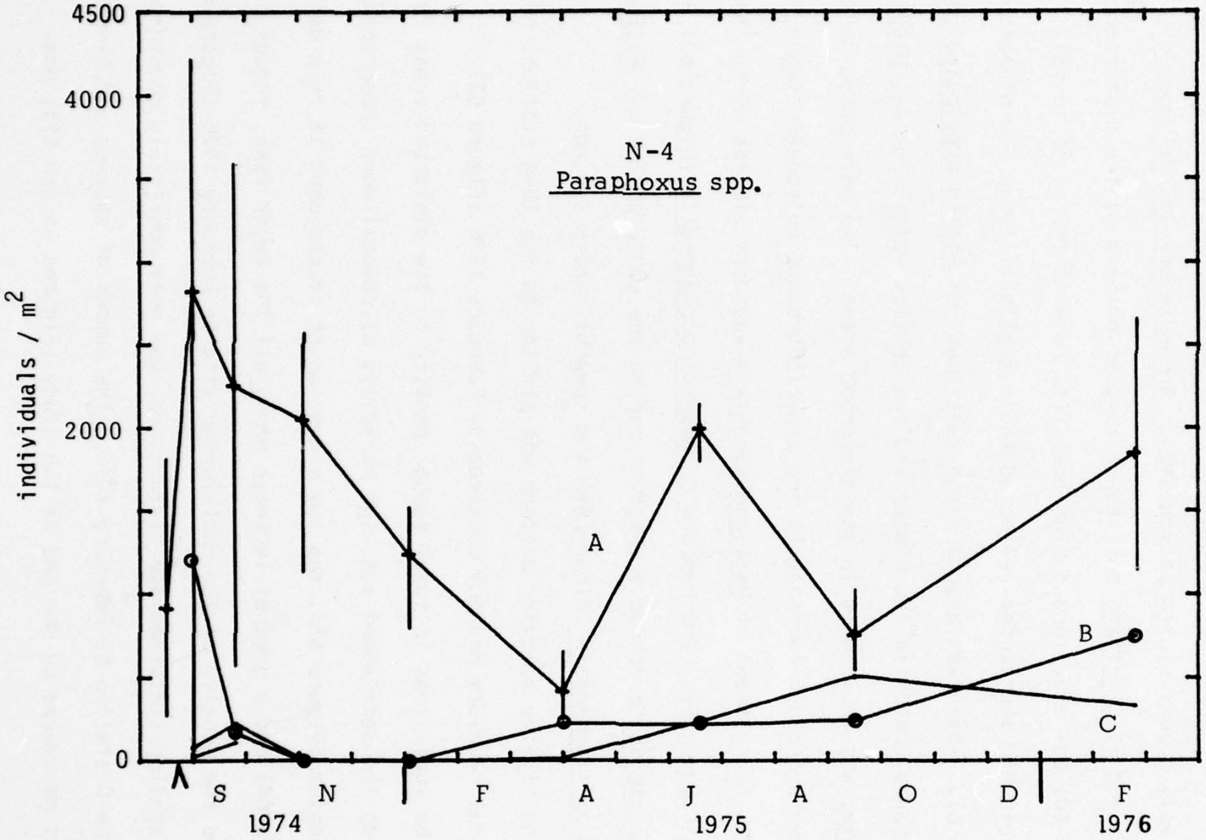

Figure 54. Variations in Paraphoxus spp. along the N-4 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

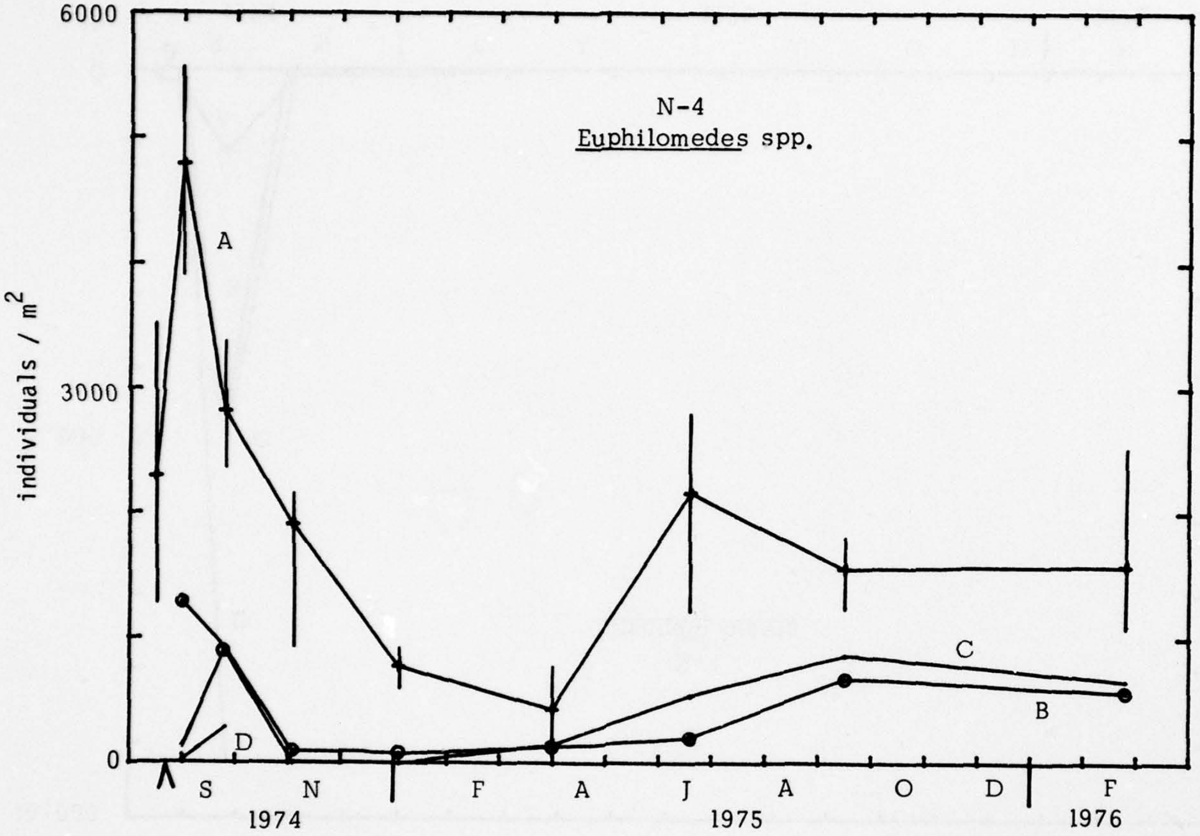

Figure 55. Variations in <u>Euphilomedes</u> spp. along the N-4 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

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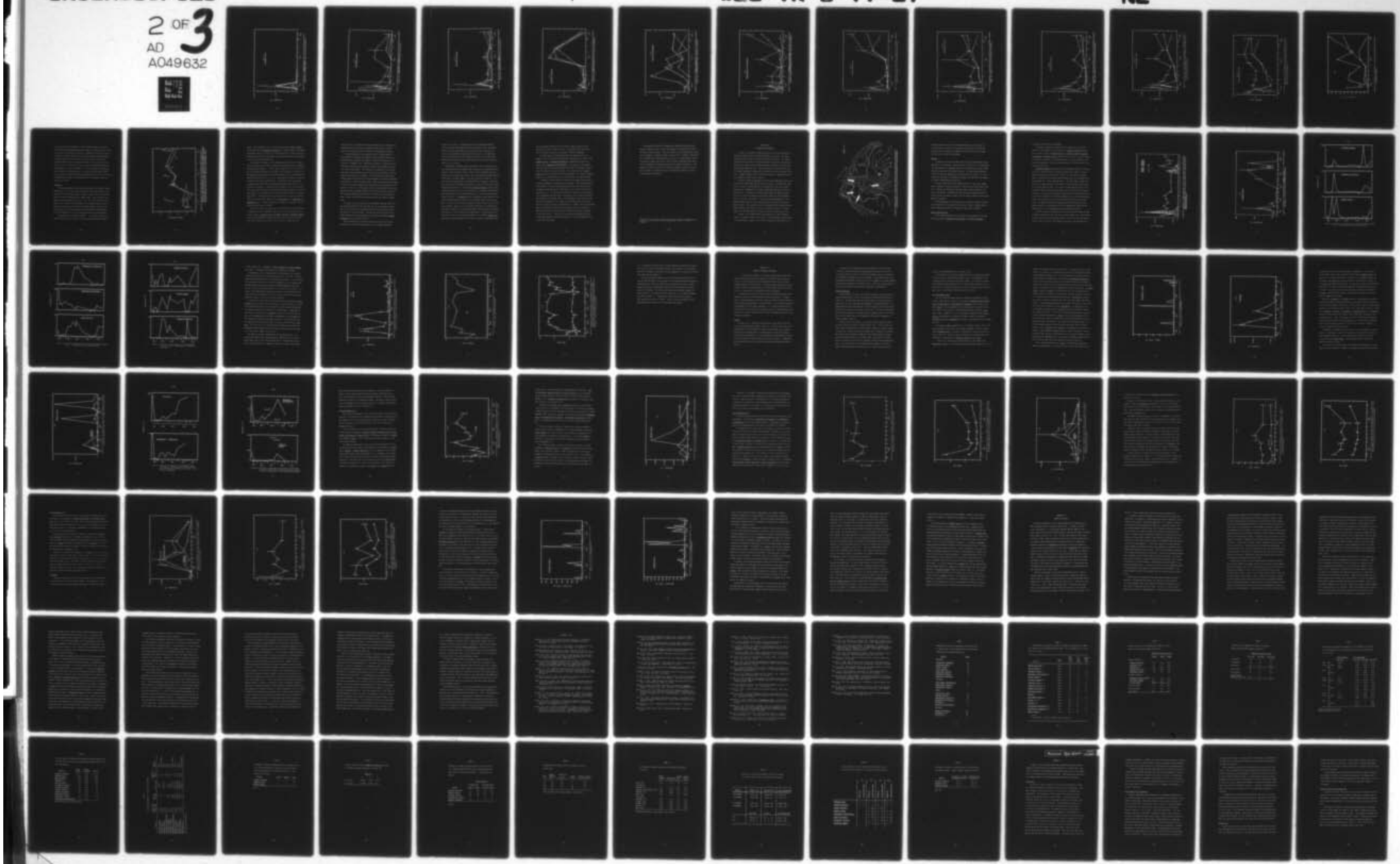

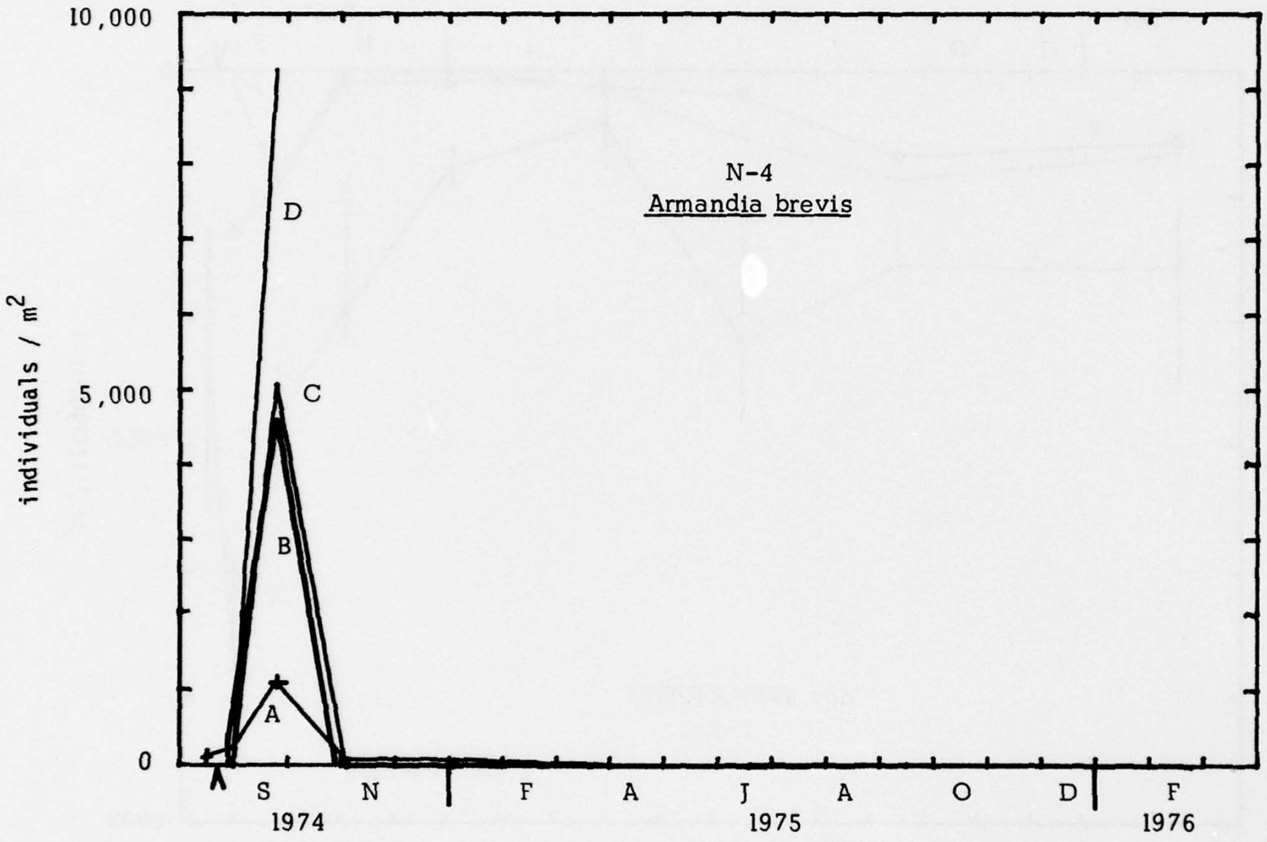

Figure 56. Variations in Armandia brevis along the N-4 disturbance gradient (means with no ranges given). Arrow indicates disturbance.

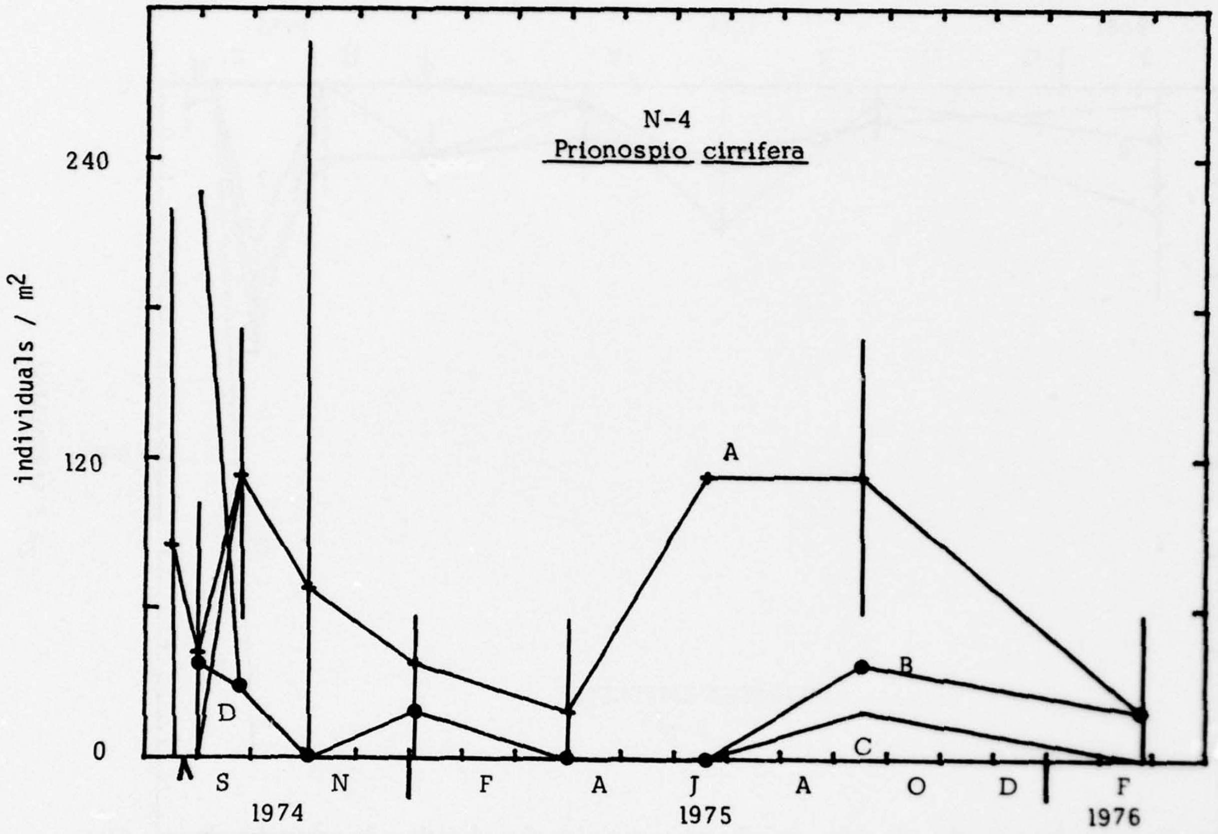

Figure 57. Variations in Prionospio cirrifera along the N-4 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

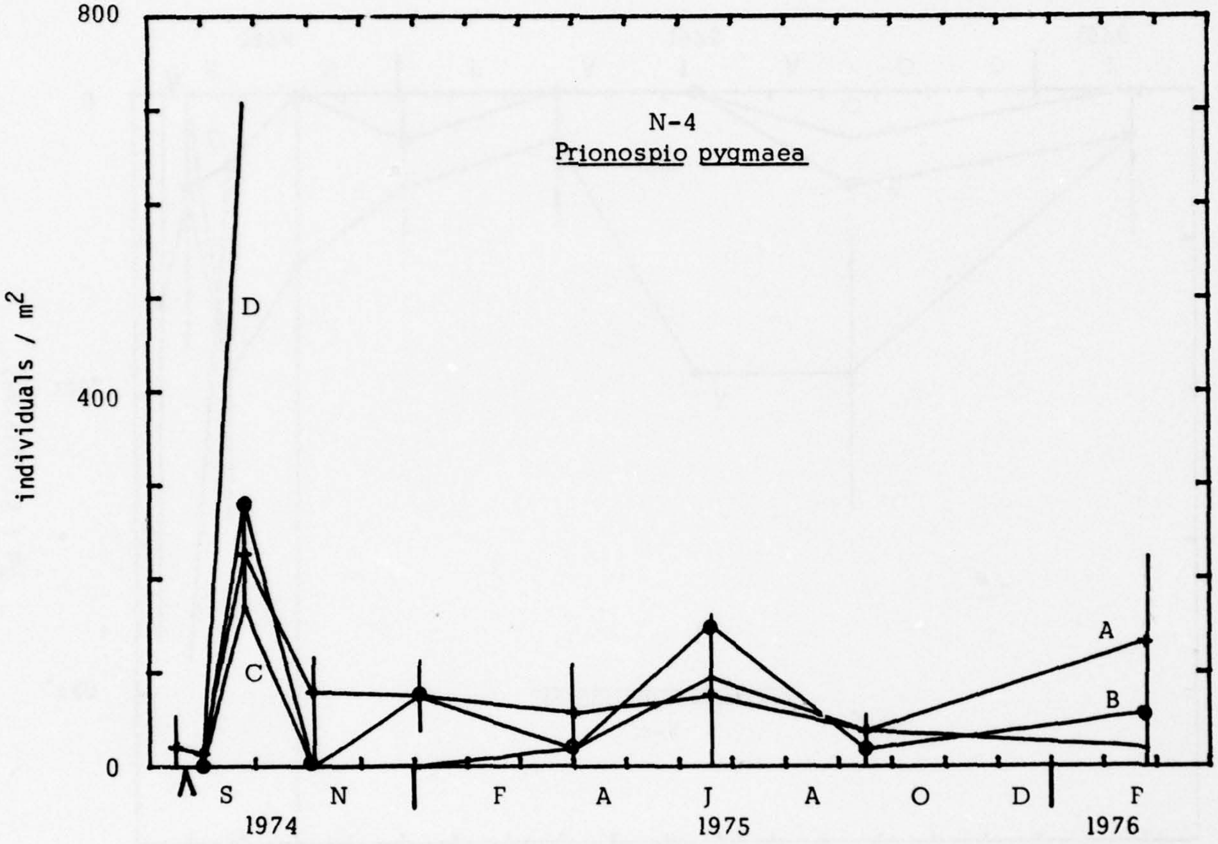

Figure 58. Variations in *Prionospio pygmaea* along the N-4 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

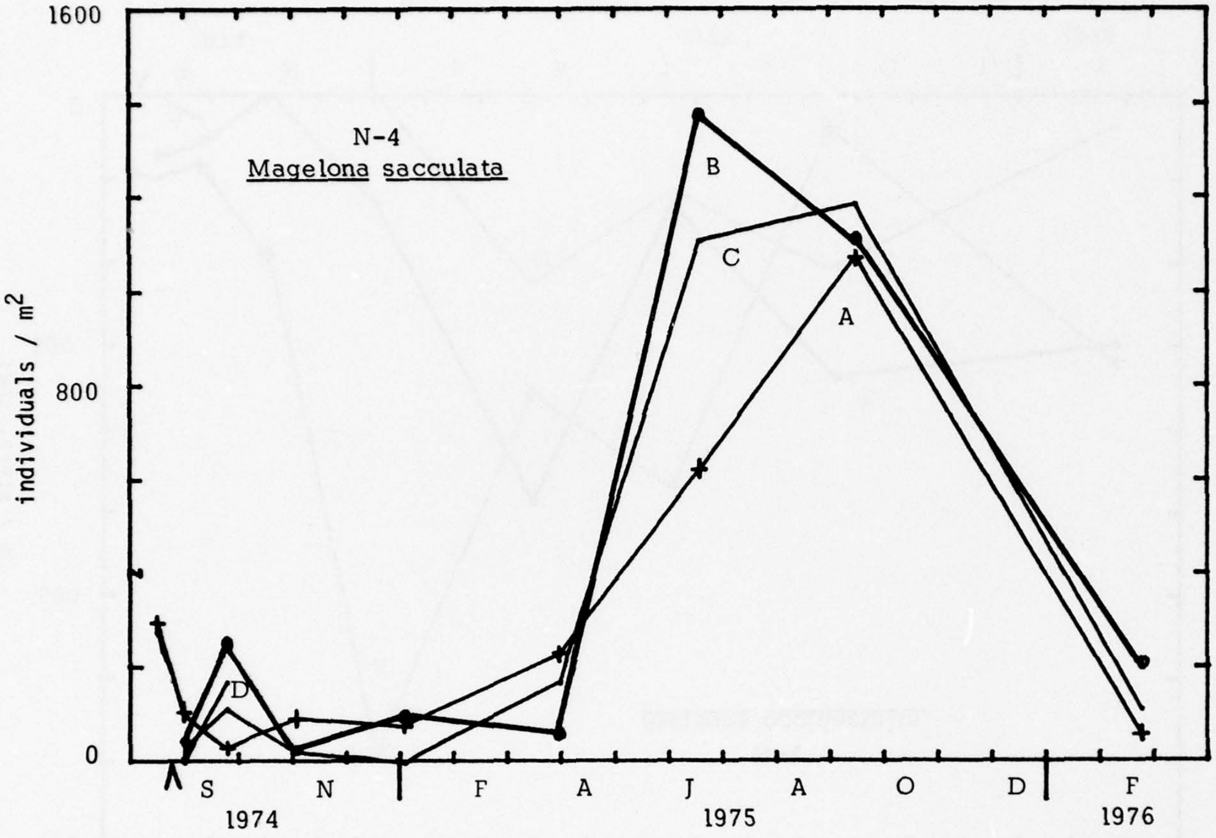

Figure 59. Variations in <u>Magelona sacculata</u> along the N-4 disturbance gradient (means with ranges not given). Arrow indicates disturbance.

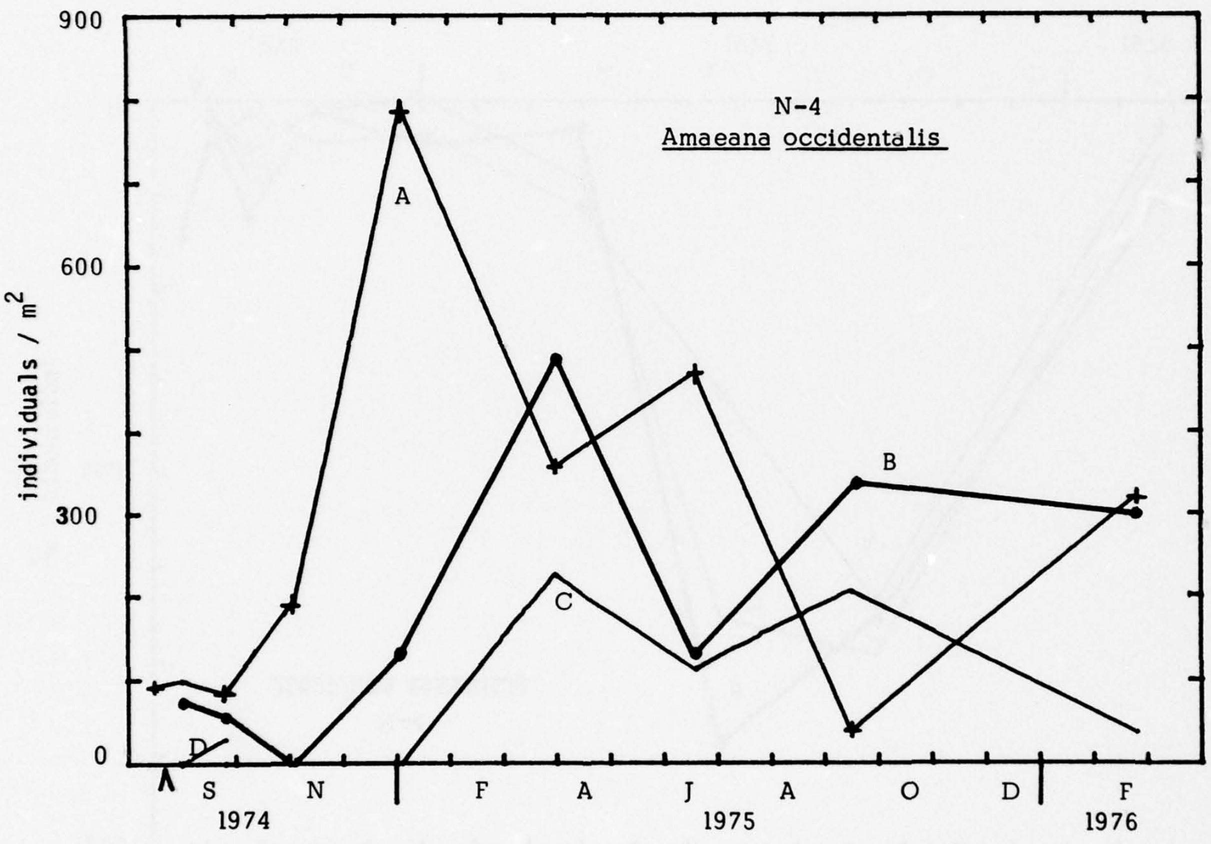

Figure 60. Variations in Amaeana occidentalis along the N-4 disturbance gradient (means with no ranges given). Arrow indicates disturbance.

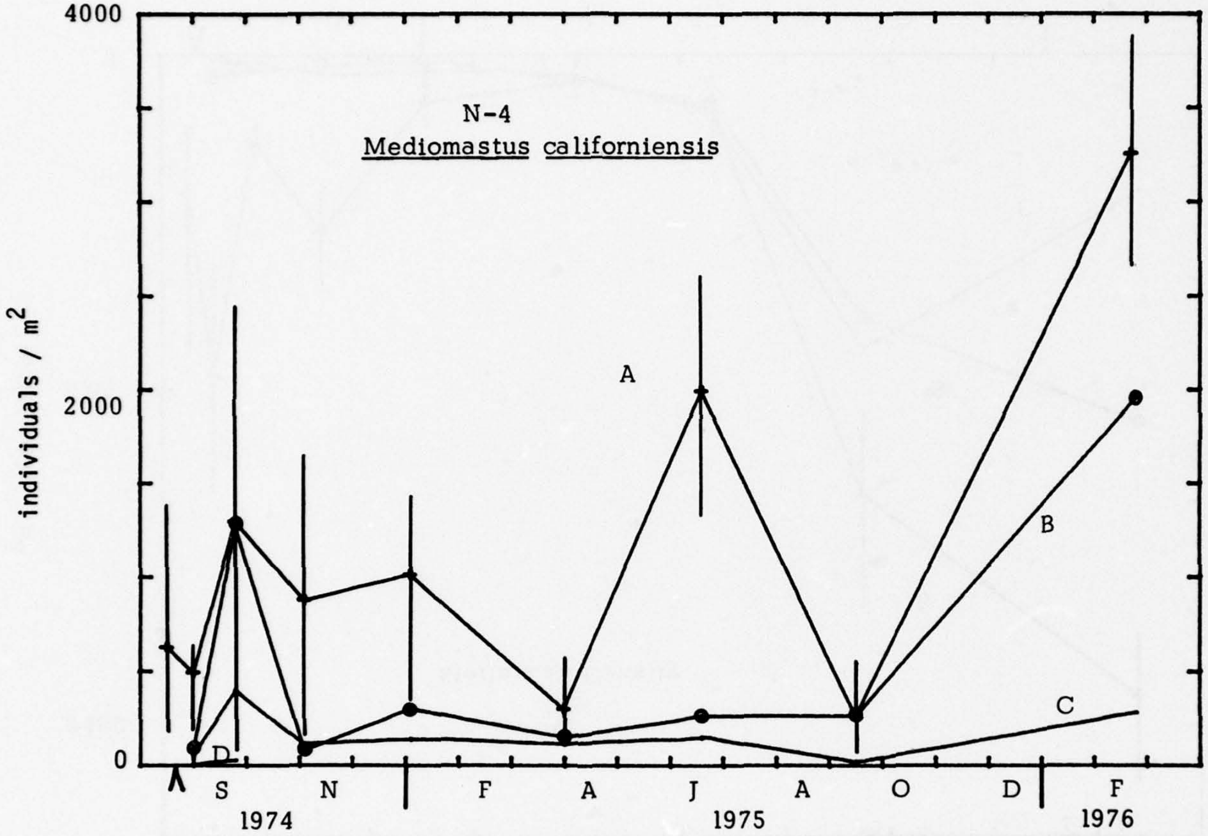

Figure 61. Variations in Mediomastus californiensis along the N-4 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

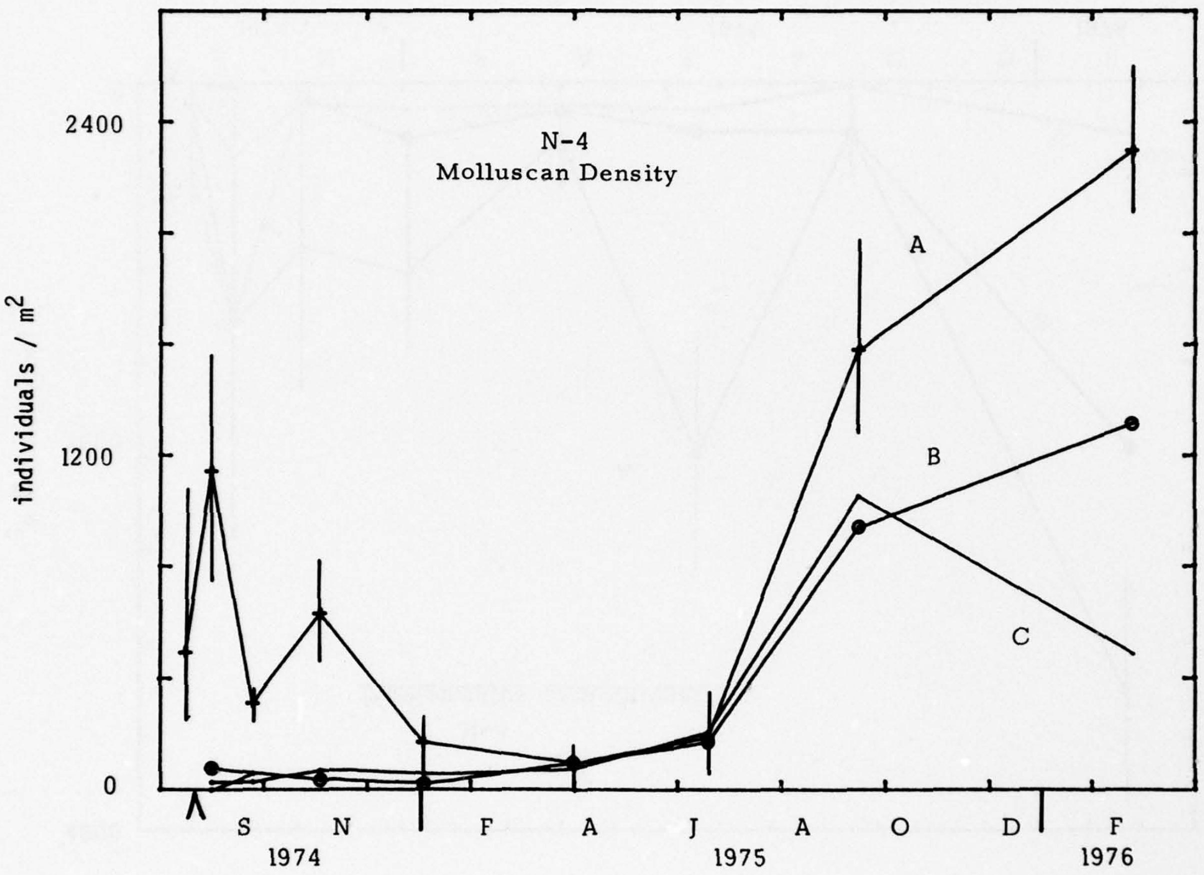

Figure 62. Variations in molluscan density along the N-4 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

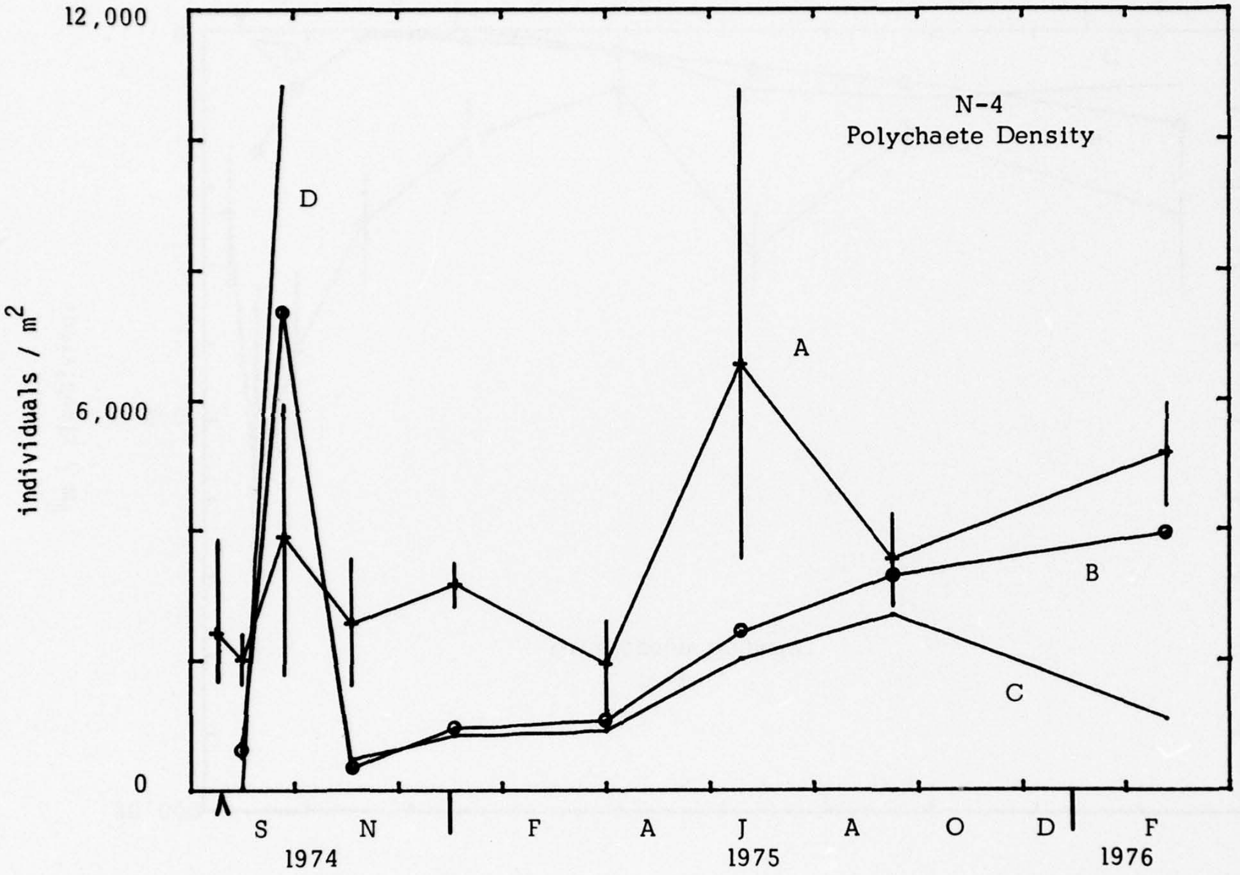

Figure 63. Variations in polychaete density along the N-4 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

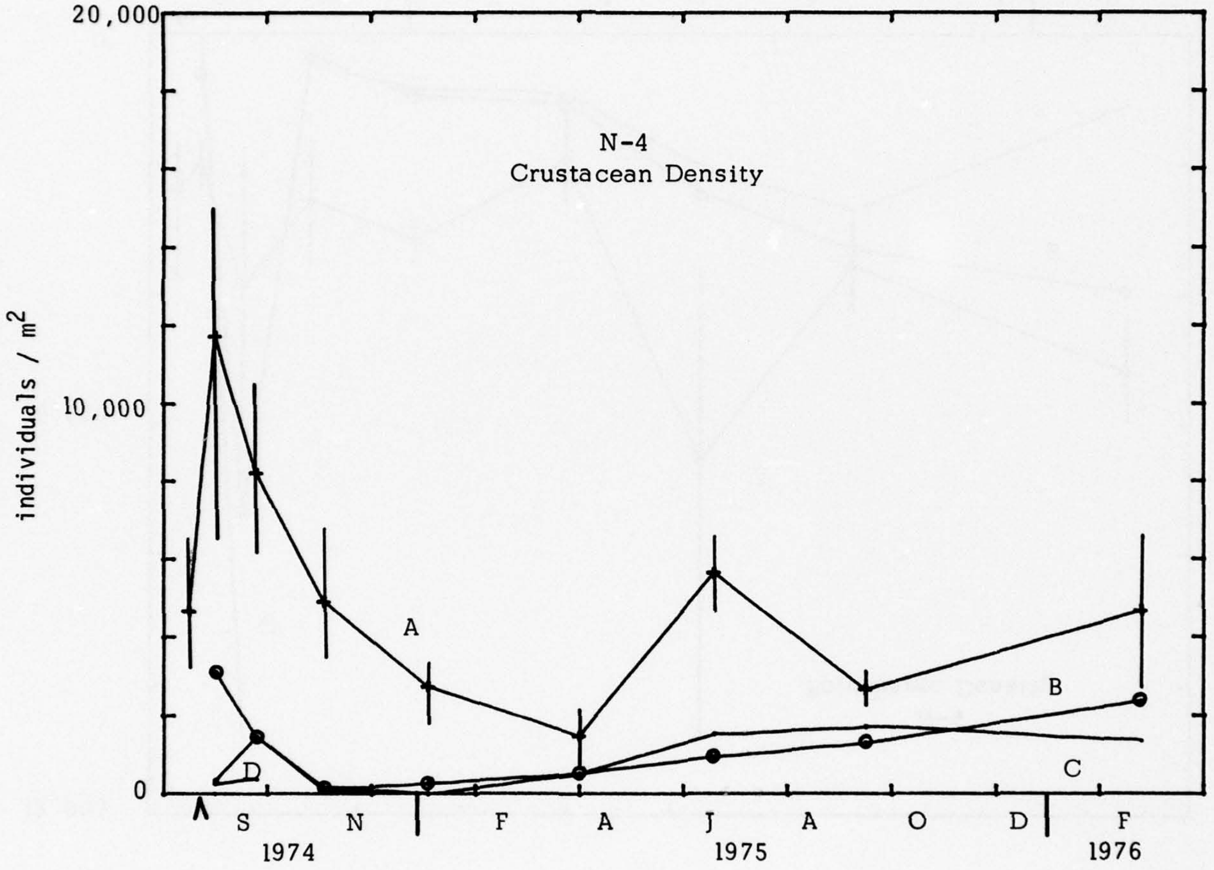

Figure 64. Variations in crustacean density along the N-4 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

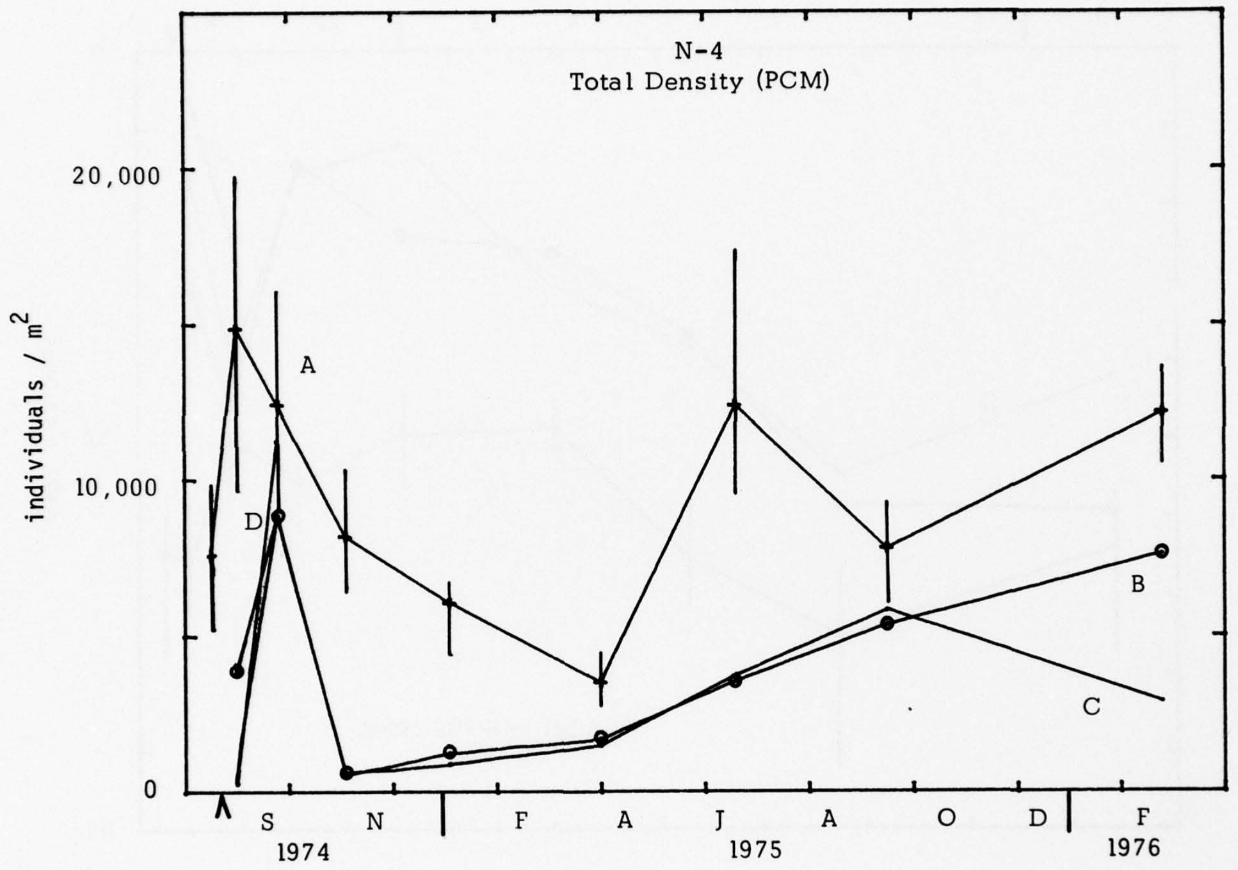

Figure 65. Variations in total density (polychaete, crustacean, molluscan) along the N-4 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

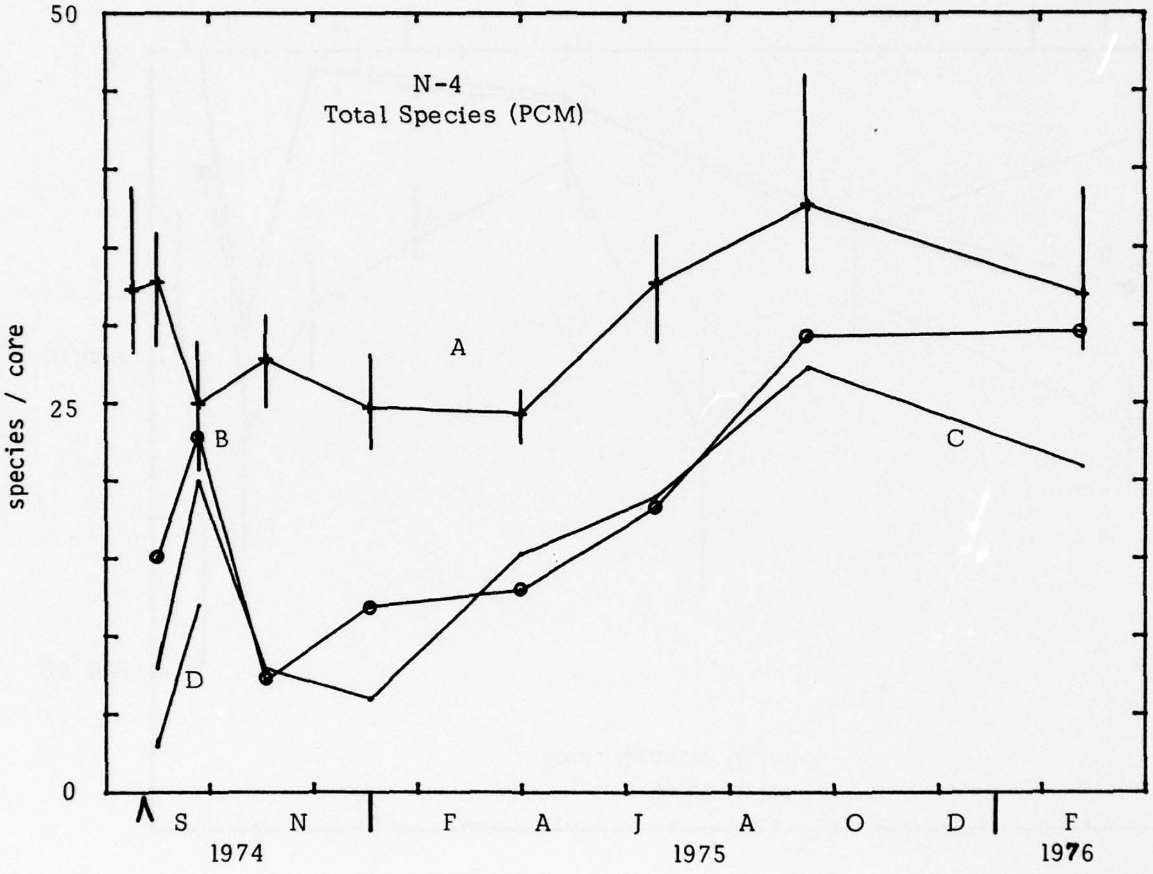

Figure 66. Variations in total species (polychaete, crustacean, molluscan) along the N-4 disturbance gradient (means with ranges on A). Arrow indicates disturbance.

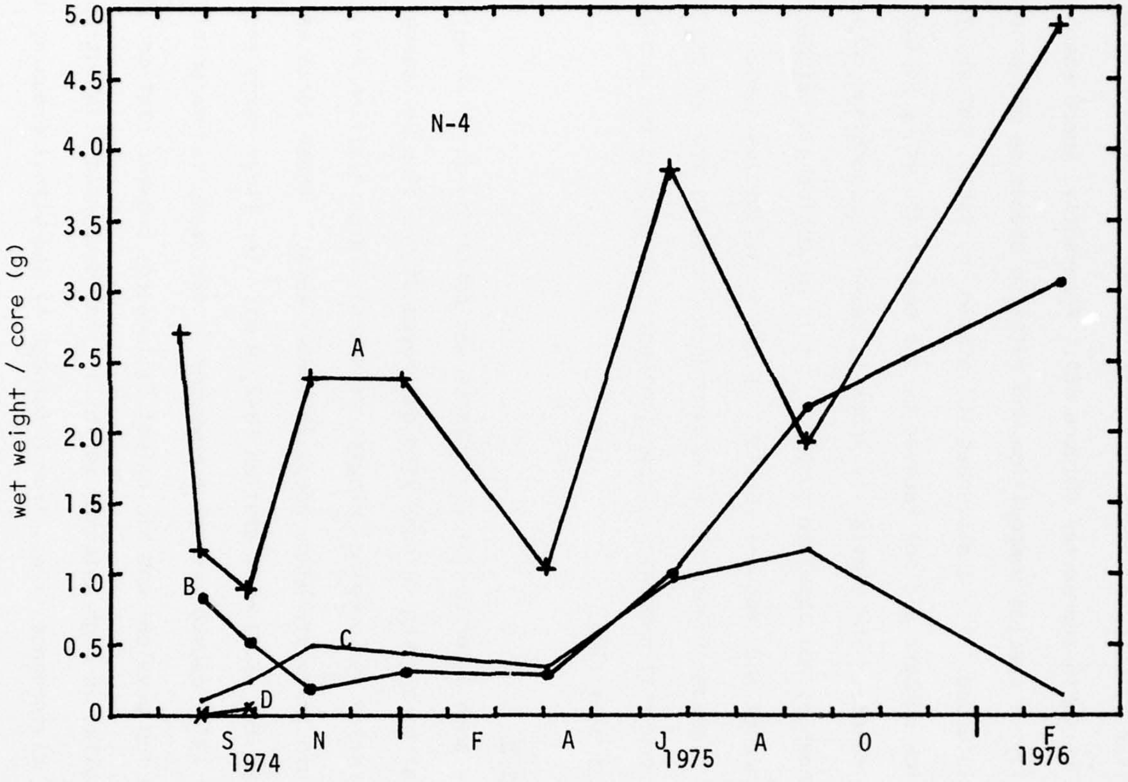

Figure 67. Variations in the biomass of vermes (wet weight) along the N-4 disturbance gradient.

ever, the similarity between the A and C stations reached a value near the similarity computed among replicate samples at station A in April 1975 and was variable thereafter (Figure 68). Apparently, there was a general similarity in species composition and relative abundance patterns between the undisturbed (A) and disturbed (C) station by April, but absolute population numbers did not recover by the end of the study period (Figures 62 to 65). The similarity index is based on percentage composition and abundance, not absolute numbers. It is also strongly affected by the more abundant and frequent species. Since total species number (Figure 66) and biomass (Figure 67) were also unrecovered by the end of the study, it is concluded that community succession was still in progress and not completed at that time.

Discussion

The same experimental disturbance was performed at three water depths. Essentially, all the infauna were destroyed at the disposal center. Immidiately after the dumping (minutes to hours), large flatfish and starfish moved into the disturbance areas in deeper water. These forms were less common at the shallowest station (N-2, 9 m). The first large storm (late October 1974) caused extensive movement of the deposited material, obliterated the physical and biological differences between stations C and D and resulted in high infaunal mortality that decreased with decreasing initial disturbance (i.e., from D through A) and with increasing depth.

The disturbance centers were characterized by coarse, shifting sediments that took longer to rework into the natural bottom at the greater

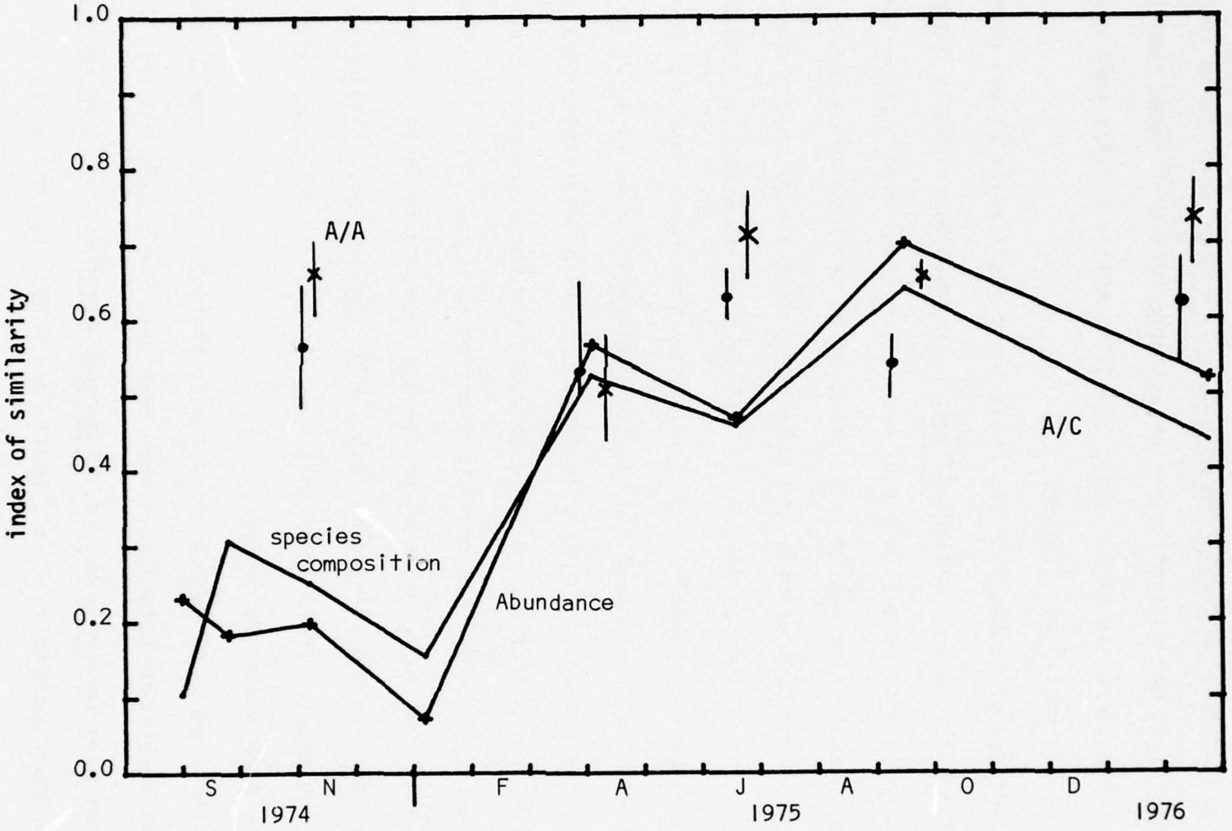

Figure 68. Recovery of the fauna along the N-4 disturbance gradient: Bray-Curtis similarity index calculated for pairs of A and C cores compared to indices calculated among A cores for species composition and abundance. Vertical lines give the mean and range of the similarity values among A cores.

depths. The settlement of the shallow water polychaete, Dispio uncinata, and the sand dollar, Dendraster excentricus, in highest numbers in the deeper disturbance areas was indicative of the unstable nature of these substrata. Both species occurred in high numbers along the entire depositional gradient (A to D) at the shallowest station.

The pattern of recovery of the crustaceans was similar at all depths. The first colonizers were active, swimming crustaceans, primarily cumaceans and oedicerotid amphipods. In deeper water, there was also a trend for larger and presumably more mobile individuals of an ostracod to colonize first. The cumaceans and oedicerotids were more characteristic of, and abundant in, shallower water (Oliver et al., M.S.). Their mobility probably allows them to adjust to periodic substrate motion. These forms were less abundant in deeper water and colonized the deepest disturbance area (N-4, 24 m) in relatively low numbers. Colonization was probably a result of higher activity rather than attraction to the introduced sediments; however, populations were larger at the disturbed areas, indicating some preference or advantage upon arrival. The later phase of crustacean recovery involved the gradual return of the less mobile species (e.g., Euphilomedes spp., Paraphoxus spp., Eohaustorius spp.). These forms were most abundant at the deeper stations, where they took longer to recover.

The early phase of succession was also characterized by the settlement of several species of polychaetes that have relatively opportunistic life history patterns (Armandia brevis, Prionospio cirrifera, Prionospio pygmea). They have short generation times, small body size, high mortality rates, high larval availability and settle first in many disturbed habitats

(Tables 6 and 7). Apparently, natural disturbance was so intense at the shallowest station that these polychaetes settled along the entire depositional gradient and did not "detect" the experimental disposal.

The same opportunistic polychaetes settled in higher numbers in deeper water and they were more numerous at the disturbed stations. At the 18-m depth, settlement was highest at station C and rather low at station D in September 1974. Apparently, the motion of substrate at the disturbance center was severe enough to prevent the settlement and survival of most polychaetes. This contention is supported by the results from larval choice experiments using tall and short containers of coarse sediment (see Appendix for methods). The tall containers reduced wave-induced substrate motion while the coarse sediment in the short containers was constantly disturbed by water motion. More larvae settled and survived in the tall containers compared with the shifting, coarse sediment of the short ones (Table 8). At the deepest station, the same opportunistic polychaetes settled in greatest number at the disturbance center (station D). The introduced sediment was the same at all depths, but wave-generated water currents and the resulting substrate motion was reduced in deeper water.

By January 1975, the coarse introduced sediment had been mixed into the surrounding bottom at the 18-m depth but not at the deepest station. Thus, the only area that contained relatively coarse shifting sediment was station C at the 24-m depth. This was the only station at the two deeper depths where the non-opportunistic sedentary polychaete, Amaeana occidentalis, did not settle (Table 9).

Many polychaetes were prevented from establishing or maintaining populations in very shallow water because of the unstable substrata

(Oliver et al., M.S.). The seasonal nature of polychaete settlement at the 9-m station (N-2) may be partially explained by their settlement pattern after the experimental disturbances and the results from the larval choice experiments (Appendix, Tables 8 and 10). Settlement and survival occurred when a coarse sediment was stable (e.g., during calm weather) but did not occur when coarse sediment was stirred by bottom currents (e.g., in winter).

The seasonal settlement patterns observed at the shallowest station were less pronounced at the deeper areas, probably due to decreased bottom currents. When tall/short container larval choice experiments were performed with fine, rather than coarse, sand, some polychaete species settled and survived in greater numbers in the short containers (Table 10). The results were not unequivocal but demonstrated that differential settlement and survival could be affected by variations in grain size and water motion. (Compare Tables 8 and 10.) One species, <u>Capitella capitata</u>, always showed a marked preference for the tall containers (i.e., reduced substrate motion and finer material due to increased deposition) in the larval experiments (Tables 8 and 10). <u>C. capitata</u> settled in relatively large numbers at the canyon head disturbance site and at all the harbor stations and was abundant in larval jars at the time the northern sandflat areas (N-2, N-3, N-4) were disturbed. However, it did not settle along any of the experimental disturbance gradients. The choice experiments indicated greater settlement and survival in finer sediment and/or calmer water. These conditions certainly did not occur on the northern sandflat. In contrast, <u>Armandia brevis</u> showed a slight preference for the tall containers in some experiments but a considerable proportion of the animals always settled into the shorter ones as well (Tables 8 and 10). As expected, this species was one of the early colonists in the northern sandflat experiments.

The later phase of polychaete recovery was characterized by the gradual return of the pre-disturbance fauna indigenous to the area. Some (*Nothria elegans* and *Amaeana occidentalis*) recovered much faster than others (e.g., *Mediomastus californiensis*). The larval jar data suggest that the former species were more often available for settlement (Table 6) since the latter was rarely collected. On the other hand, *M. californiensis* may have an abbreviated form of development and a reduced dispersal stage (e.g., brood protection), which might explain its slower recovery.

In summary, the early phase of recovery was characterized by mobile, swimming crustaceans and opportunistic polychaetes. Mobility was measured by occurrence in funnel traps positioned just above the bottom (Table 5), and degree of opportunism was established by life history characteristics (Tables 6 and 7). The later phase involved colonization by less opportunistic polychaetes and less mobile crustaceans, both of which were normally most abundant at the deeper areas. The polychaetes can be ranked by their response to disturbance (i.e., degree of opportunism, which also groups them by similar life history characteristics). However, their actual settlement in a disturbed location was also dependent upon larval substrate selectivity and early survival, which are important but often neglected life history factors. The pattern of succession was somewhat different at each depth because of associated changes in the bottom communities and the physical environment.

Environmental variability increased with decreasing depth along the northern transect and, as a result, the community structure was also more variable in shallower water. The most important and variable physical stress was the movement of substrate caused by wave activity. Community complexity* also increased with increasing depth as a result of reduced physical stress. As predicted, communities found in highly variable environments were more resilient (capable of rebounding quickly from a severe disturbance). Thus, community resilience was inversely related to community complexity and directly related to increasing physical environmental variability and more variable community structure.

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*Relatively high biomass, habitat heterogeneity, density and number of species.

CHAPTER FOUR

CANYON HEAD DISTURBANCE

The head of the Monterey Submarine Canyon has a quite different sedimentary environment than the adjacent sandflats (Figure 69). The steep, sloping bottom is subject to periodic shoaling and slumping. The shallow terrace that borders most of the canyon, deeper canyon walls and especially the axes and channel areas, accumulate sediment and debris during the late spring, summer and early fall. These are periods of relatively calm seas. The largest topographic changes are coincident with the first storms in late fall. Sediment movement down the walls and channels is frequent and extensive throughout winter and early spring.

The canyon slopes are composed of poorly consolidated sands that do not form distinct ripple marks and are easily disturbed. This substrate instability is similar to that observed in shallower water along the adjacent sandflats and, consequently, the animal assemblage inhabiting this area is also similar. In contrast, there are several submarine ridges that have flat crests which are composed of more consolidated and stable sediments that form distinct ripple marks. The ridge animal assemblages are intermediate between those of the less stable canyon substrata and the deeper sandflat areas. The numerically dominant polychaetes that characterize the deeper sandflat have relatively small and variable populations on these ridges, and small crustaceans and large bivalves are conspicucusly rare.

In August 1971, dredged material was deposited on a small submarine ridge in the southern branch of the canyon. The same location was disturbed in the same manner in August 1974 to test the hypothesis that benthic suc-

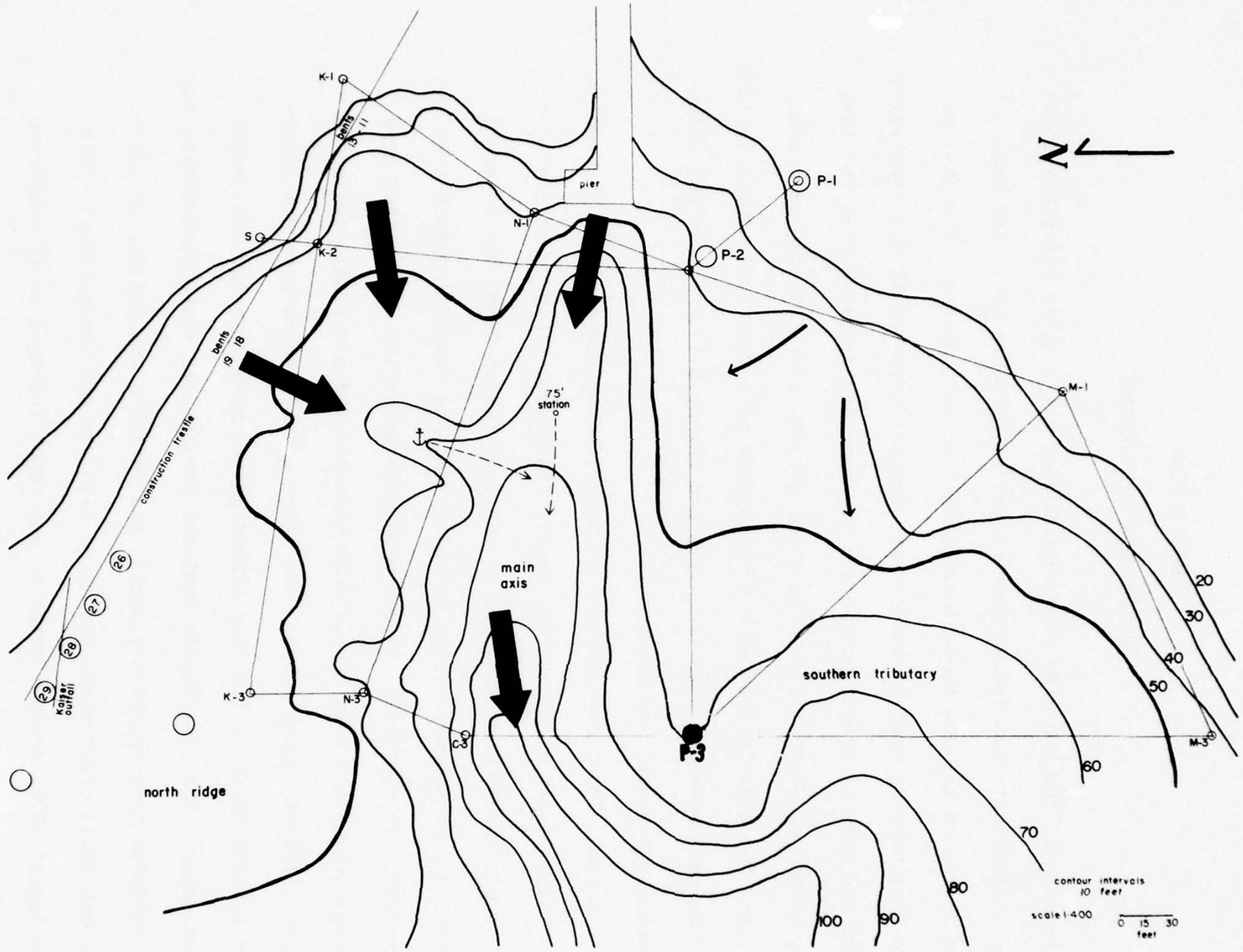

Figure 69. Southern branch of the Monterey Submarine Canyon head based on observations and measurements by divers. Arrows indicate creeping and slumping movement.

cessional patterns are similar when the perturbation and the season of its occurrence are similar. The experiment also allowed a test of the hypothesis that recovery rate (community resilience) can be correlated with the level of natural disturbance.

Methods

In August 1971 and 1974, several barge loads of dredged material were deposited on the submarine ridge station (P-3, Figure 69). The experimental site was marked with a permanent buoy and the same relatively small bottom area was monitored for more than four years. The translocated sediment, a fine, silty mud, was dredged from the back harbor (H-1, Table 11). Thus, the quality and quantity of deposited sediment, the season and the location of the two disturbances were identical.

The canyon head has received dredged material for many years (Wong, 1970); therefore, it was not possible to locate an undisturbed control station. However, the observed successional patterns were compared to the natural variations in community structure along the adjacent sandflat so that the latter provided an index of natural change unrelated to the experimental disturbances.

The ridge area was visited periodically to measure changes in the physical properties of the sediment and the benthic fauna. Sediment and biological samples were taken and processed as described in Chapter 2.

Results and Discussion

The 1971 pre-disturbance fauna was numerically dominated by the capitellid polychaetes, Heteromastus filobranchus and Capitella capitata.

Crustaceans and molluscs were uncommon.

The general sequence of succession was the same after both disturbances and was dominated by the polychaetes. Capitella capitata settled first and was followed by Armandia brevis, Prionospio pygmaea, Spiophanes missionensis and Nephtys cornuta (Figures 70, 71 and 72). This early group of colonists had similar life history patterns, including relatively small size, short generation time, high larval availability (Tables 6 and 7) and high mortality rates.

Capitella capitata exemplified the basic abundance pattern of the early colonist in which there was a high density peak shortly after the disturbance and subsequent high mortality (Figure 70). The later, or second, phase of succession was characterized by another group of polychaetes that had different life history characteristics. They were usually larger species with a longer generation time (Table 7), less available larvae (Table 6) and lower mortality rates. As a result of these characteristics, they maintained smaller populations that were less variable over time (Figures 73 and 74). Early and late polychaete colonists could also be ranked along a continuum in regard to life history parameters (e.g., Grassle and Grassle, 1974) or subdivided into more than two groups of colonists (e.g., McCall, 1975). The observed successional sequences have been divided into two phases primarily for convenience but also to emphasize the more fugitive (Hutchinson, 1951) or transient nature of the earliest colonists.

Periodic molluscan settlement (primarily bivalves) was always followed by almost complete mortality, and none survived to adult size. The bivalves differed from the early polychaete colonists in that they settled throughout the study period with little apparent relation to the experimental dis-

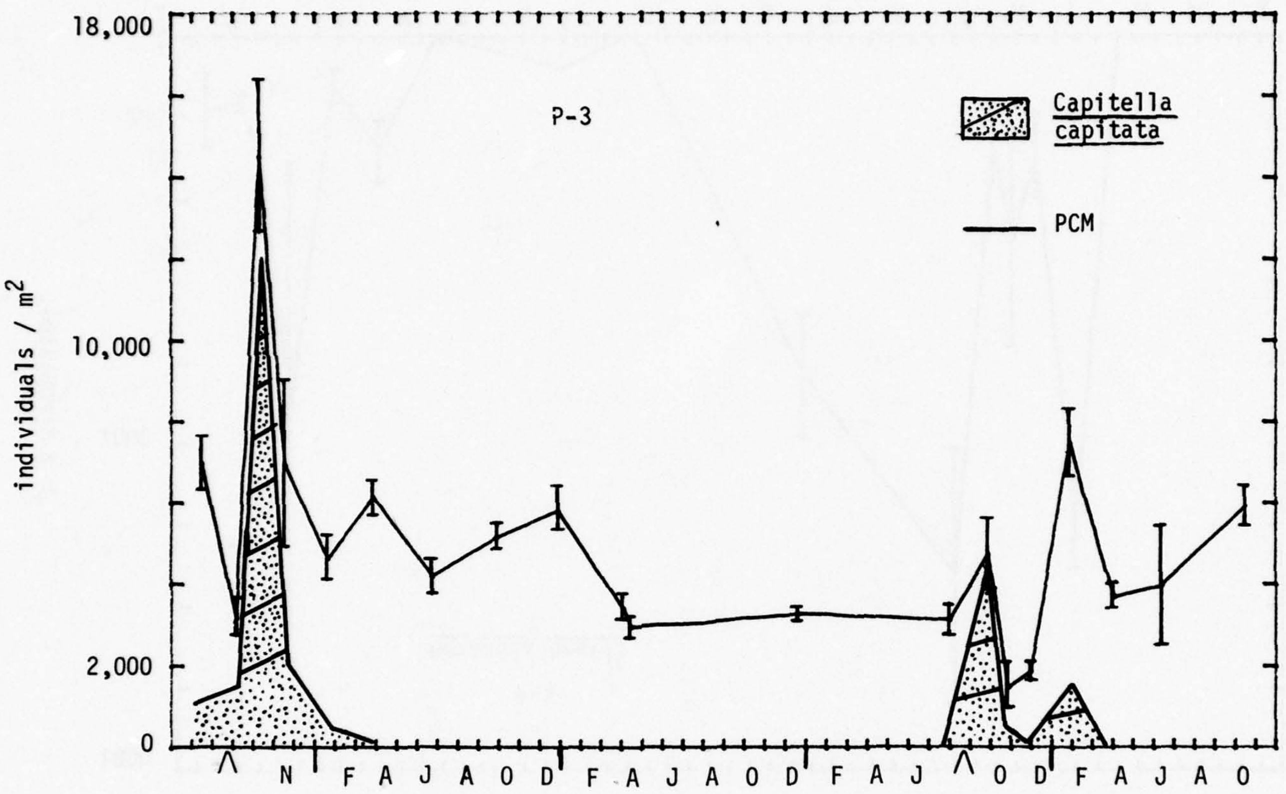

Figure 70. Variations in mean abundance at P-3 of total fauna (PCM) compared with *Capitella capitata* (mean and standard deviation of the mean). Arrows indicate disturbances.

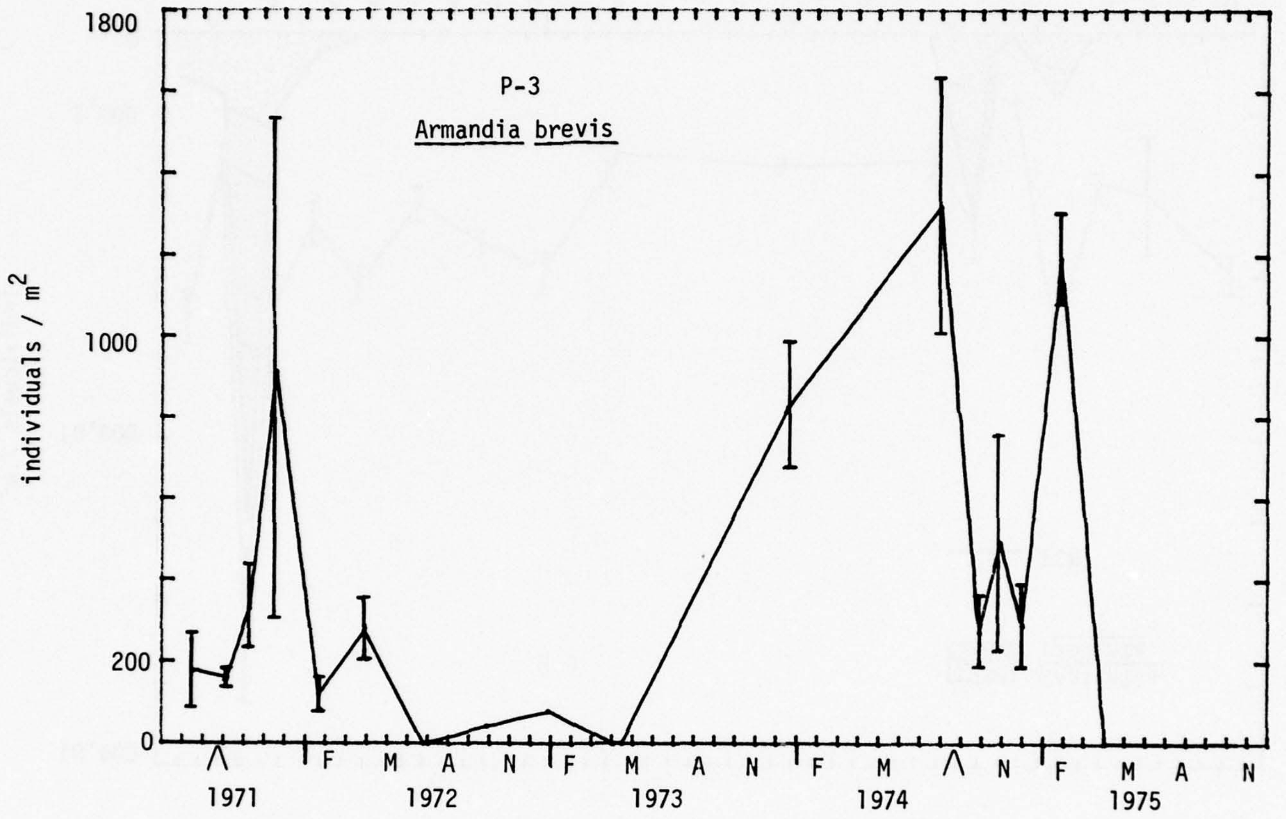

Figure 71. Variations in mean abundance of *Armandia brevis* at P-3 (mean and standard deviation of the mean). Arrows indicate disturbances.

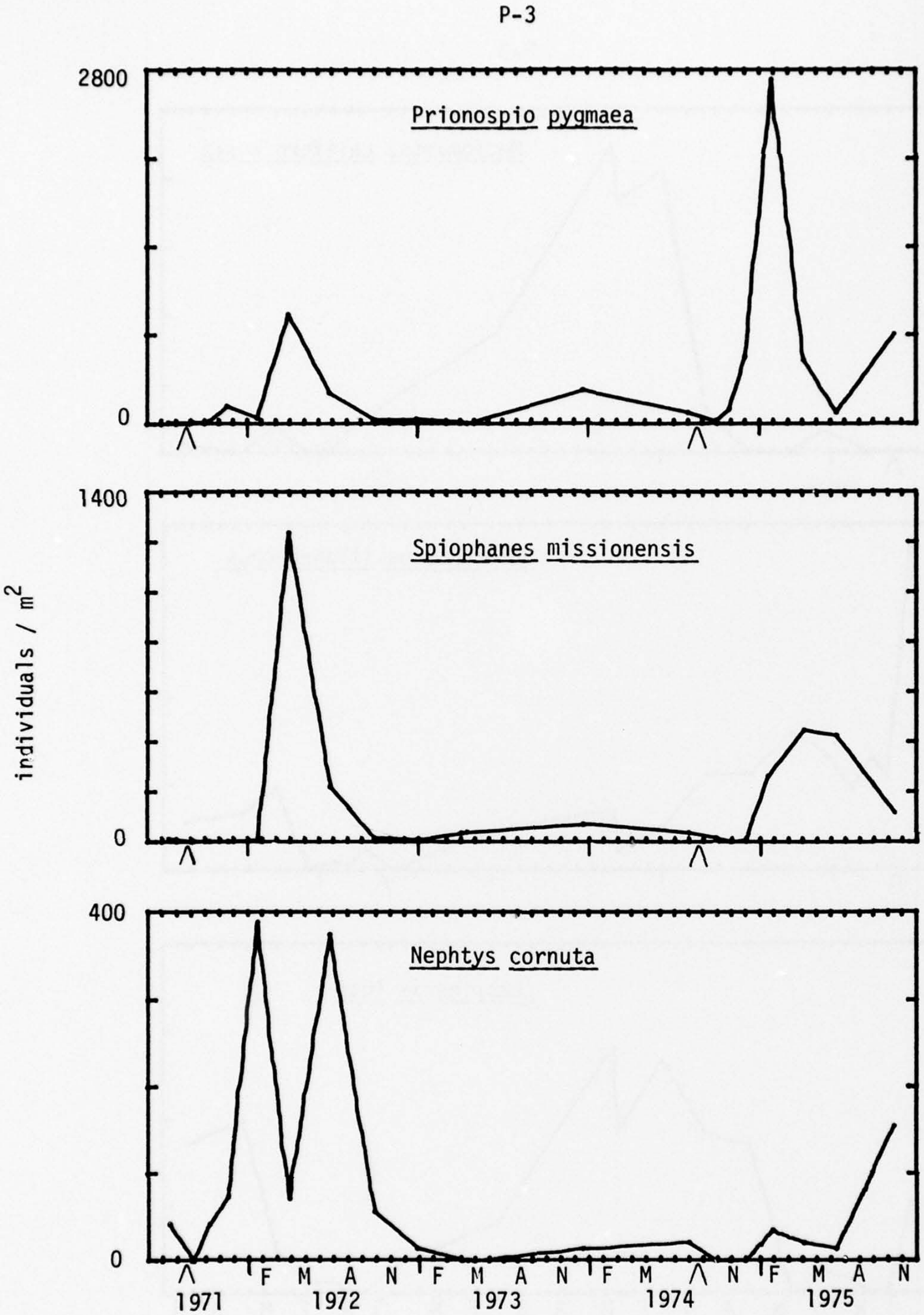

Figure 72. Variation in mean abundance of some polychaete colonists at P-3. Disturbances are indicated by arrows.

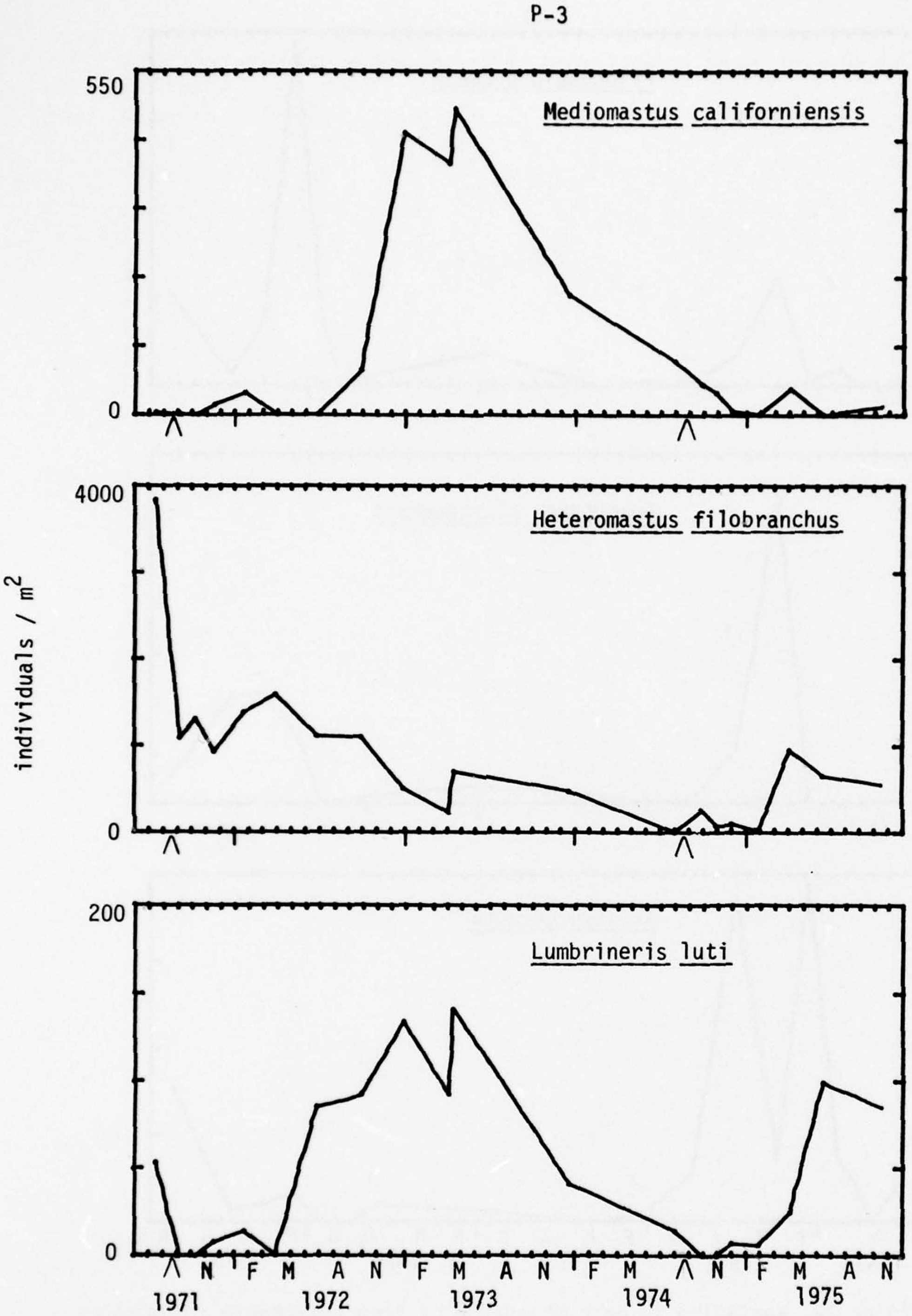

Figure 73. Variation in mean abundance of some polychaete colonists at P-3. Disturbances are indicated by arrows.

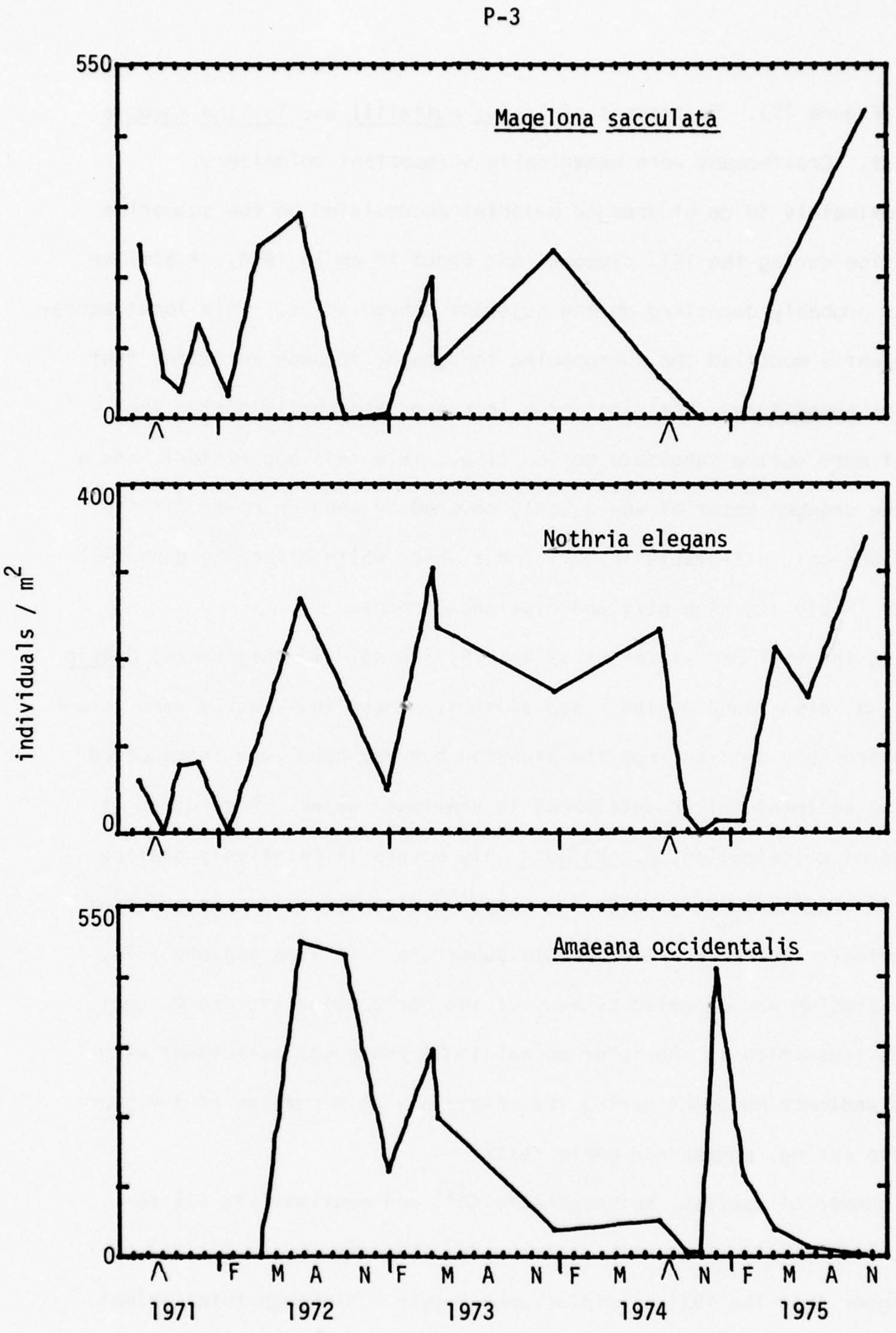

Figure 74. Variation in mean abundance of some polychaete colonists at P-3. Disturbances are indicated by arrows.

turbance (Figure 75). Settlement of Tresus nuttallii and Tellina modesta. was highest. Crustaceans were numerically unimportant colonizers.

Approximately 30 cm of dredged material accumulated on the submarine ridge station during the 1971 disposal and about 15 cm in 1974. A similar amount was probably deposited on the adjacent canyon walls. This local accretion apparently modified the surrounding topography to such an extent that sediment movement across the ridge area increased abnormally during the periods of more active substrate motion (i.e., late fall and winter). As a result, the dredged material was quickly covered by sand or moved off the ridge and was only detectable in 1971 for a short while after the disposal experiment (Table 12; high silt and clay and carbon).

During the fall and winter of 1974-1975, the spionid polychaete, Dispio uncinata, was also found on the ridge station. These individuals were juveniles and probably settled from the plankton but may have been transported by creeping sediments after settlement in shallower water. Regardless of their mode of colonization, D. uncinata only occurs in relatively shallow water or in unconsolidated, shifting, coarse sediment, and its presence at P-3 undoubtedly indicates a less stable substrata. In late January 1975, the ridge station was occupied by many of the early colonists and D. uncinata. The transition to the later successional phase was coincident with decreased sediment movement during the relatively calm portion of the year (i.e., late spring, summer and early fall).

The number of species, heterogeneity (H') and equitability (J) recovered quite rapidly after both disturbances (Figures 76 and 77) and remained higher than the 1971 predisturbance levels. Although total animal density was more variable, it seemed to recover at a similar rate (Figure

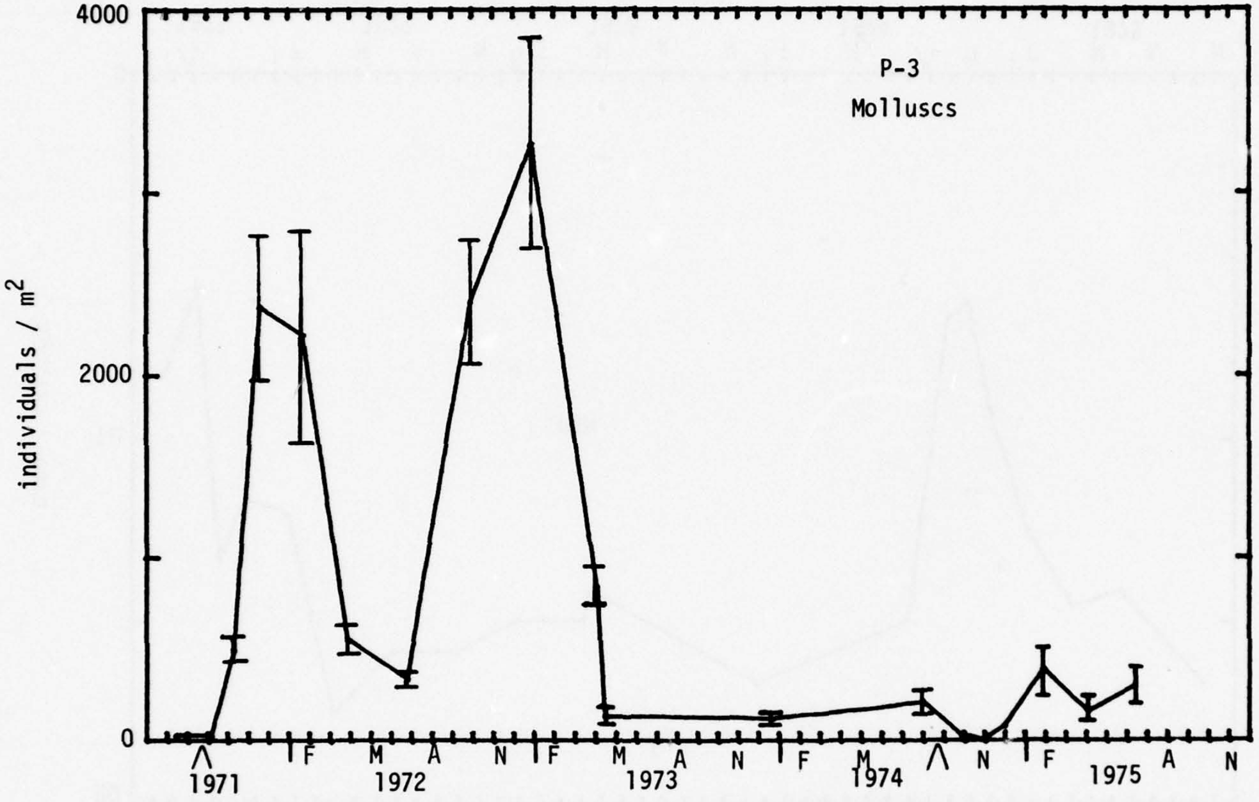

Figure 75. Variations in mean abundance of molluscs at P-3 (mean and standard deviation of the mean). Arrows indicate disturbance.

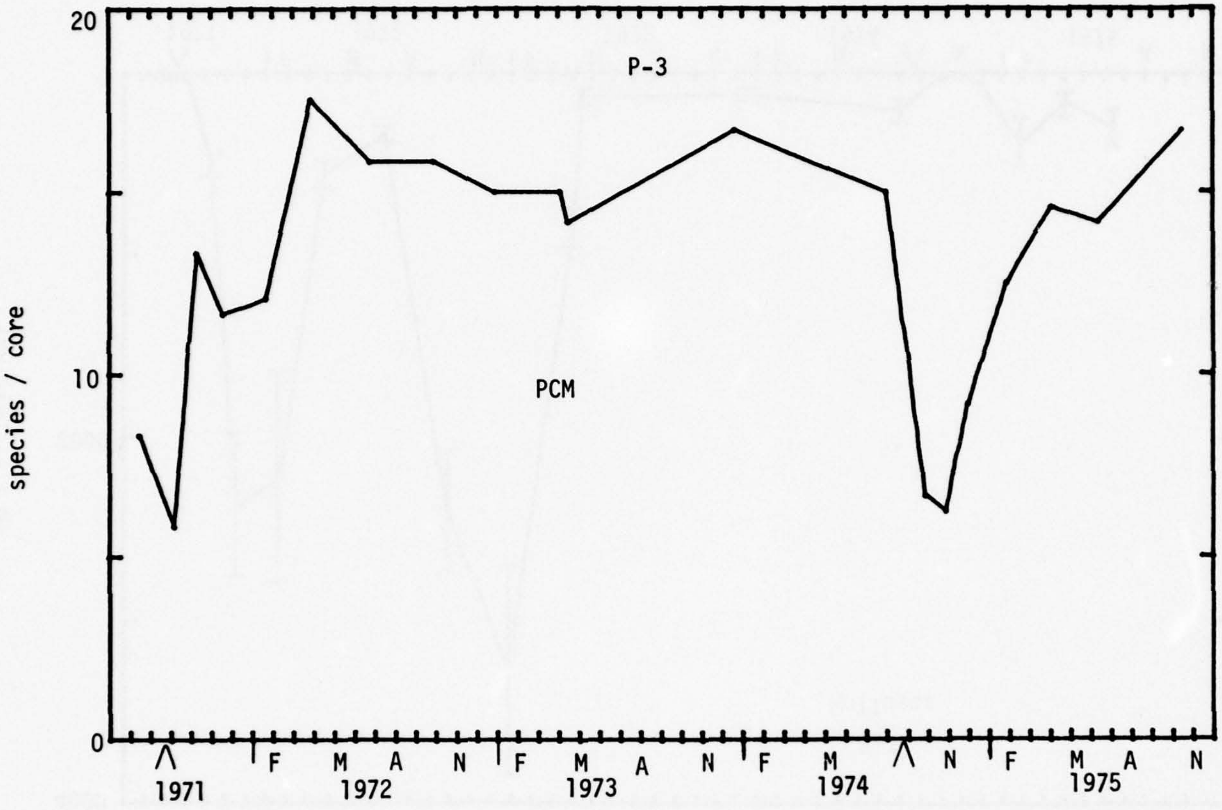

Figure 76. Variations in total species (polychaete, crustacean, molluscan) at P-3. Arrow indicates disturbance.

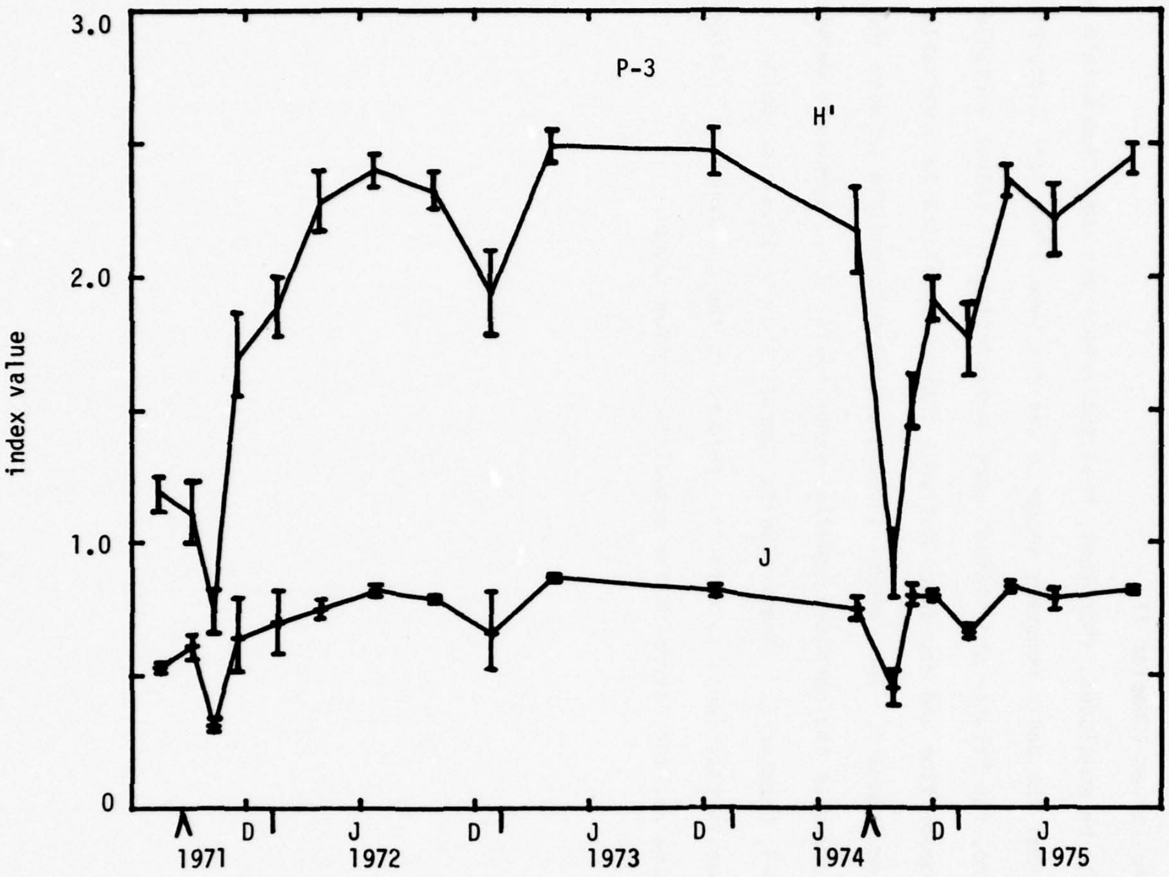

Figure 77. Variation in species diversity or heterogeneity (H') based on the Shannon-Weaver index and species equitability or evenness (J) based on the Pielou method at P-3 (means and standard deviations of means). Arrows indicate disturbances.

70). As expected, the rank order of species abundance was even more variable. Fluctuations in relative abundance patterns often increased with increasing physical environmental disturbance and were exaggerated by forms that colonized via pelagic larvae (Chapter 2).

It can be concluded, therefore, that succession was completed within a year and that the basic recovery sequence was the same after both disturbances. Furthermore, the "stable end states" were characterized by rather variable species composition and abundance patterns that were related to a variable physical environment. The rate of succession was intermediate between the rates observed in the northern sandflat experiments, i.e., somewhere between N-2 and N-3, Chapter 3. These results support the previous conclusion that community resilience is directly related to the environmental disturbance regime and the nature of the associated bottom fauna.

CHAPTER FIVE

HARBOR DISTURBANCE EXPERIMENTS

The Moss Landing Harbor is a coastal estuary that receives fresh water from the Old Salinas River Channel and Moro Cojo Slough (Figure 2). There is a distinct gradient of environmental variability from the main entrance channel to the back harbor. Industrial water pumping, boating and fishery activities and variable input of organic wastes and other nutrients result in a complicated but gradational aquatic environment.

In August 1971, an area of harbor bottom was essentially defaunated by dredging in order to study the pattern of benthic succession. In August 1974, a location adjacent to the first study site and two stations along the harbor channel were excavated in a similar manner. The 1974 field experiment was designed to test two major hypotheses: (1) benthic successional patterns are similar when the season, location and type of disturbance are similar; and (2) benthic recovery rates are higher in communities found in more variable environments.

Methods

In August 1971, a clamshell dredge removed a sandy shoal at the bend in the Moss Landing Harbor Channel (Figure 2). The area of shoal was cut to channel depth for a considerable distance into the channel wall, removing essentially all the macrofauna. The experimental site was established in an area where approximately 1 m of bottom material had been removed and away from the influence of slumping channel walls (HS-8; Figure 2). Immediately after dredging, the station location was surveyed and permanently marked by divers.

In August 1974, a nearby area (H-3) was dredged in a similar manner. In addition, two other sites were dredged along a channel axis (H-2, H-1). It was not possible to control the 1974 disturbances as well as the earlier one; therefore, defaunation was not as complete. These stations were also established and permanently marked by divers and sediment and infaunal samples were taken and processed as described earlier. Larval settling jars were installed at each station and collected as described in the Appendix.

Harbor Environment

The back harbor (H-1) has a more variable physical environment than the entrance channel which is highly influenced by offshore marine conditions (Table 13). More than ten times the volume of water of the south harbor is pumped daily by local industries and subsequently discharged offshore. The pumping stations are located nearest to H-3 and produce a net flow of marine water into this region of the harbor (Smith, 1973). The main entrance channel and the bend area are also swept by much stronger currents (up to 80 cm/sec) than the back harbor, and, consequently, the bottom is composed of coarser sediment (Table 11).

There are often fish remains, oil and other debris traceable to man's activity in and on the water in the back harbor (H-1). Tidal currents are milder, water exchange with the outer harbor is relatively low and turbidity is always high. The Old Salinas River Channel and a tributary, the Tembladero Slough, receive domestic sewage and local drainage from fertile agricultural tillage and drain into the back harbor. Many areas in the back harbor are relatively shallow due to reduced currents and high sedimentation rates. As a result, boats often resuspend bottom sediments or actually gouge the bottom, especially during low tides. These disturbances do not occur at H-3 and probably occur only rarely at H-2.

The net effect of industrial pumping near the outer harbor and reduced diffusion rates in the back harbor (Smith, 1973) is to accentuate the environment gradient along the south harbor channel. At one end of the gradient (harbor entrance channel, H-3) is a less variable, more marine situation and at the other (back harbor, H-1) a more variable, estuarine environment, which is also highly stressed by man's activities.

1971 Disturbance (HS-8)

The 1971 pre-disturbance infauna was numerically dominated by oligochaetes, three species of capitellid polychaetes (*Notomastus tenuis*, *Mediomastus californiensis* and *Heteromastus filobranchus*) and bivalves of the genus *Macoma*. The oligochaetes were most abundant but accounted for less than 1/20th of the biomass of the second most abundant animal, *N. tenuis*. Large siphons (diameter 2-3 cm) of the suspension feeding bivalve, *Tresus nuttallii*, were present in low density and small patches of macroalgae (*Gracilaria*, *Ulva* and *Enteromorpha*) also grew on the bottom during the summer and fall.

The dredging removed essentially all of the benthic fauna. Most of the animals present directly after the dredging (September 1971) were recently settled *Armandia brevis*. The order of occurrence of the early colonists is shown in Table 14. The early phase of succession was characterized by the settlement of the polychaetes, *Capitella capitata* and *A. brevis*.

In March 1972, there was a large recruitment of the phoronid worm, *Phoronopsis viridis*. All of these individuals were small juveniles (< 1 cm in length) that reached adult size by June 1972. The population incurred 27% mortality from March to June, 60% mortality from June to September and 60% from September to December 1972. The high mortality rates after June were probably related to predation by the nudibranch, *Hermissenda crassicornis*. In late June, the predators occurred at the phoronid patch in the highest density ever observed by the investigators and the individuals were extremely large for the species (3-5 cm), suggesting an abundant food supply. *H. crassicornis* consumed *P. viridis* in the laboratory, and the field observations strongly support the contention that they are important predators in nature. It is interesting to note that dense populations of *P.viridis* are normally only found in the very high intertidal zone in the north harbor and Elkhorn Slough. Adult abundance patterns may be strongly influenced by lower intertidal and subtidal predators like *H. crassicornis*. *P. viridis* has a distinct seasonal breeding cycle and spawning occurred in the spring (Rattenbury, 1953; Figure 78). In April 1973, the next breeding season, there was a second large recruitment of *P. viridis* into the existing patch at HS-8. At the same time, there was essentially no phoronid recruitment into an undisturbed control area located in the center of the entrance channel. The first recruitment episode (1972) was three times larger than the second (1973). Thus, *P. viridis* larvae appeared to be attracted to the adults but settled in fewer numbers presumably because of space limitations. During the second year, mortality was higher and only a few adults remained by the following winter (December 1973). During the third breeding season (spring 1974), there was even lower recruitment and survival (Figure 79).

Thus, a dense population of *P. viridis*, a tube-building suspension feeder, was established in the spring of 1972, incurred high mortality, re-

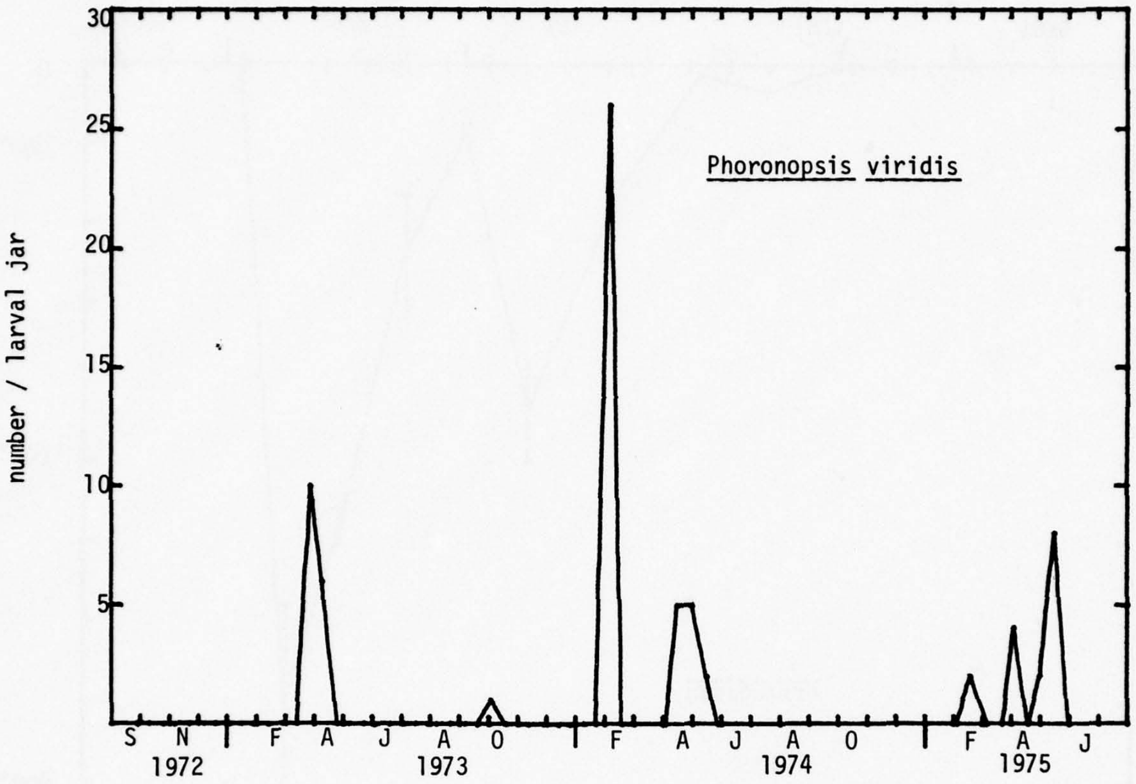

Figure 78. Number of post-larval <u>Phoronopsis</u> <u>viridis</u> collected in larval settling jars per 14-day exposure.

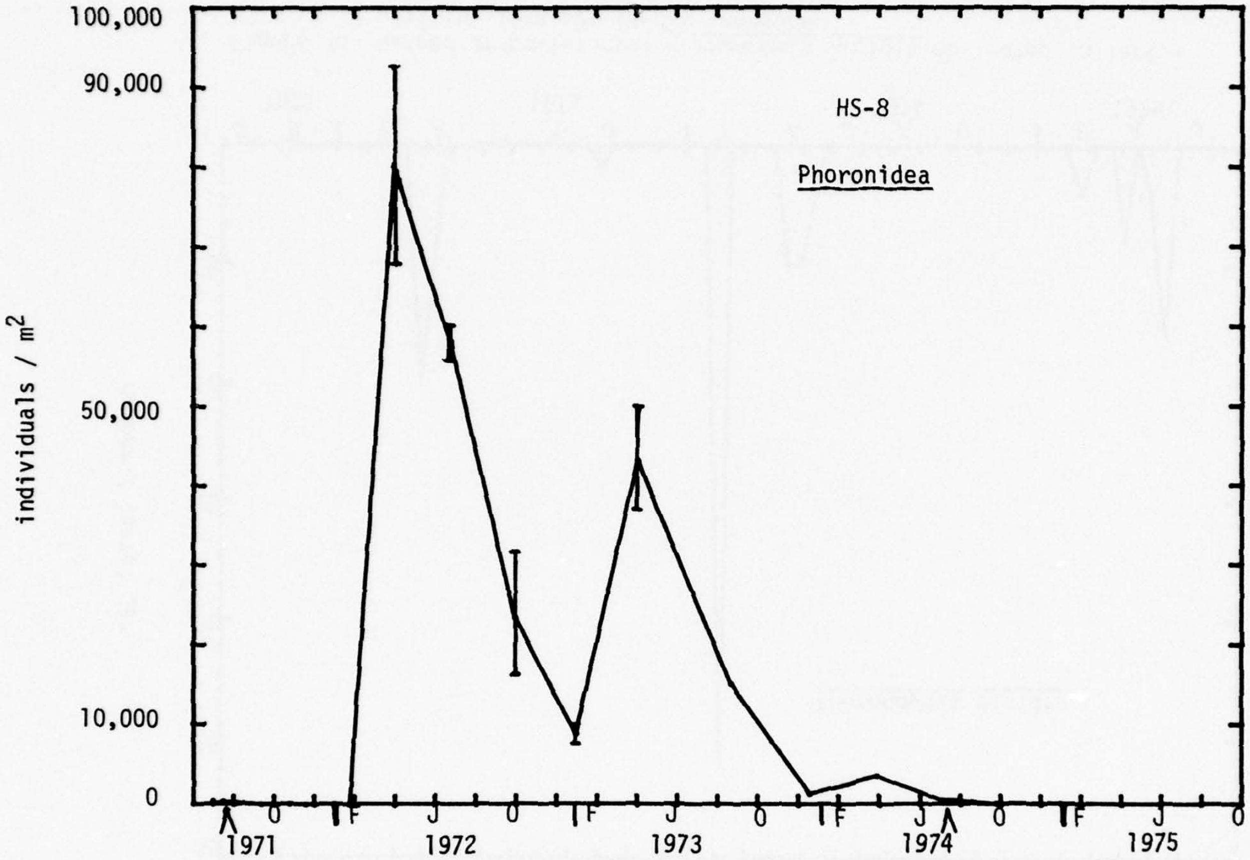

Figure 79. Variation in abundance of Phoronidea at HS-8 (mean and standard deviation of the mean). Arrows indicate disturbance.

cruited during the next spring and gradually disappeared. The first phoronid settlement occurred when the motile deposit feeder, *Armandia brevis*, was present in a relatively high density (Figure 80). The subsequent decline in the number of *A. brevis* may have been related to the reduction of space, as *P. viridis* constructed tubes and grew. (By June 1972, there were 60,000 large adults per m^2.) Woodin (1974) demonstrated that the experimental exclusion of another tube builder resulted in a significant increase in the number of *A. brevis*. Woodin's results support the hypothesis that tube builders are superior competitors for space.

Neither *C. capitata* nor *A. brevis* settled in the experimental area once the phoronid patch was established; however, both species settled periodically after the patch breakdown (Figure 80). During the entire period, neither species settled at the undisturbed channel control site. Other early colonists, including *P. pygmaea*, *N. cornuta*, *G. brevipalpa*, *P. bicanaliculata* and *P. cirrifera*, settled into the phoronid bed and most had a second peak in abundance after the patch decline. Thus, the recovery of the 1971 pre-disturbance fauna was retarded by the presence of the *P. viridis* patch. After the patch breakdown, each of the pre-dredging dominants or later colonists showed a marked increase in abundance (Figures 81 and 82).

Settlement of a number of bivalve species occurred throughout the study period. In most cases, a peak in the abundance of juveniles was followed by almost complete mortality. The only exception was a member of the pre-disturbance fauna, *Macoma nasuta*. The crustaceans were not numerically important colonists at HS-8.

Variations in the total number of individuals were dominated by *P. viridis* during early succession. Changes in polychaete, crustacean and molluscan

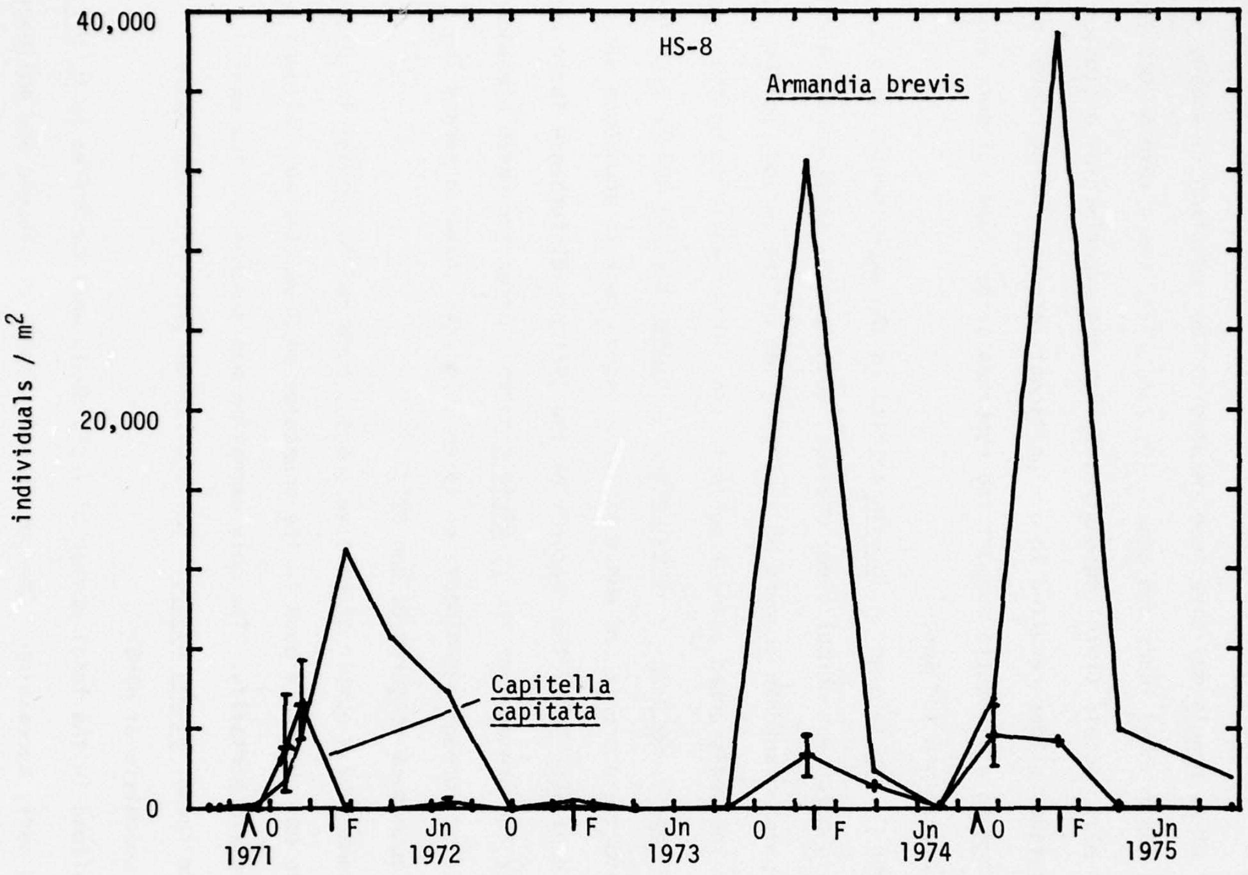

Figure 80. Variation in mean abundance of two polychaete species at HS-8 (mean and standard deviation of the mean). Arrows indicate disturbances.

HS-8

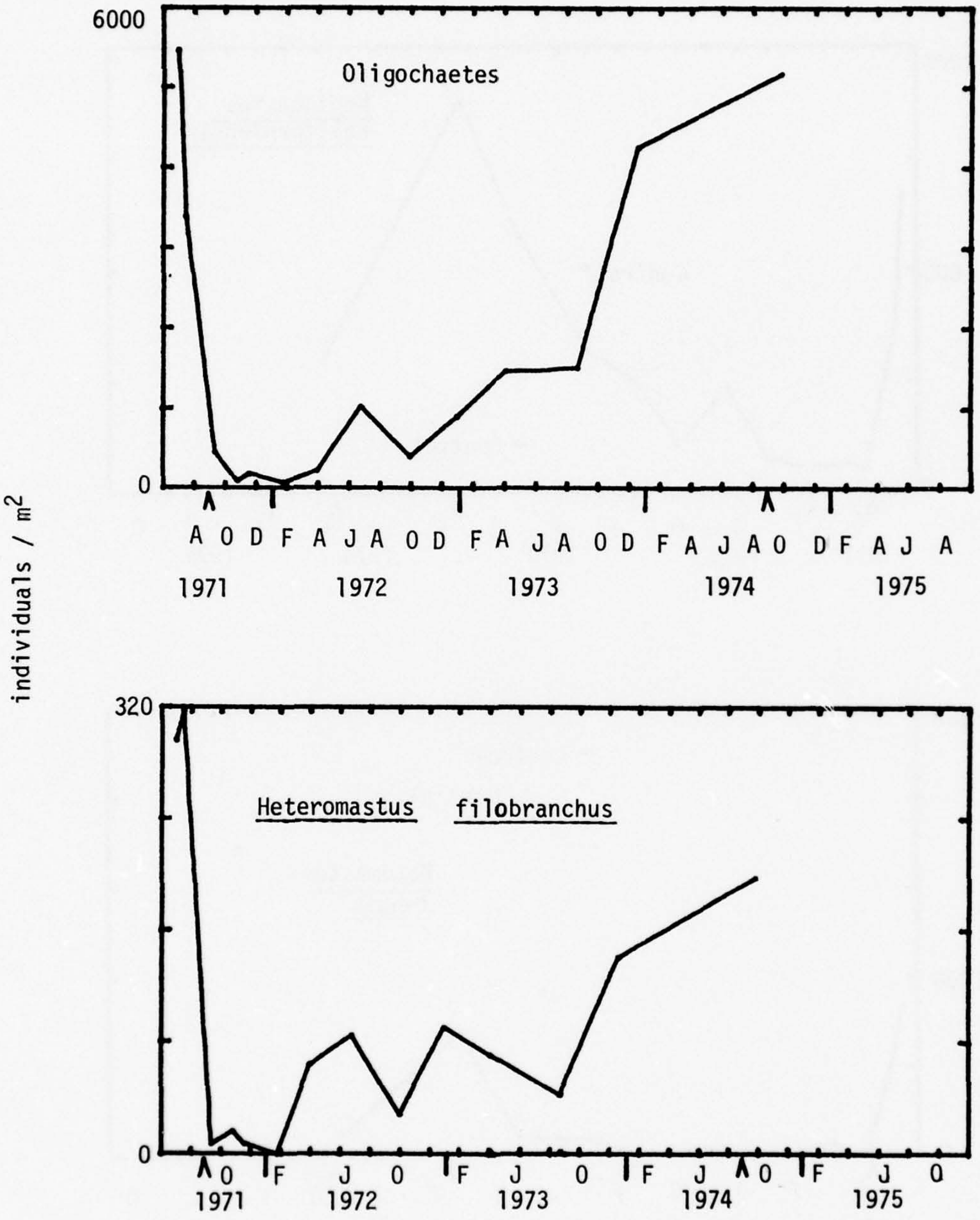

Figure 81. Variations in abundance of a polychaete and an oligochaete at HS-8 and nearby control station (mean and standard deviation of the mean). Arrows indicate disturbance.

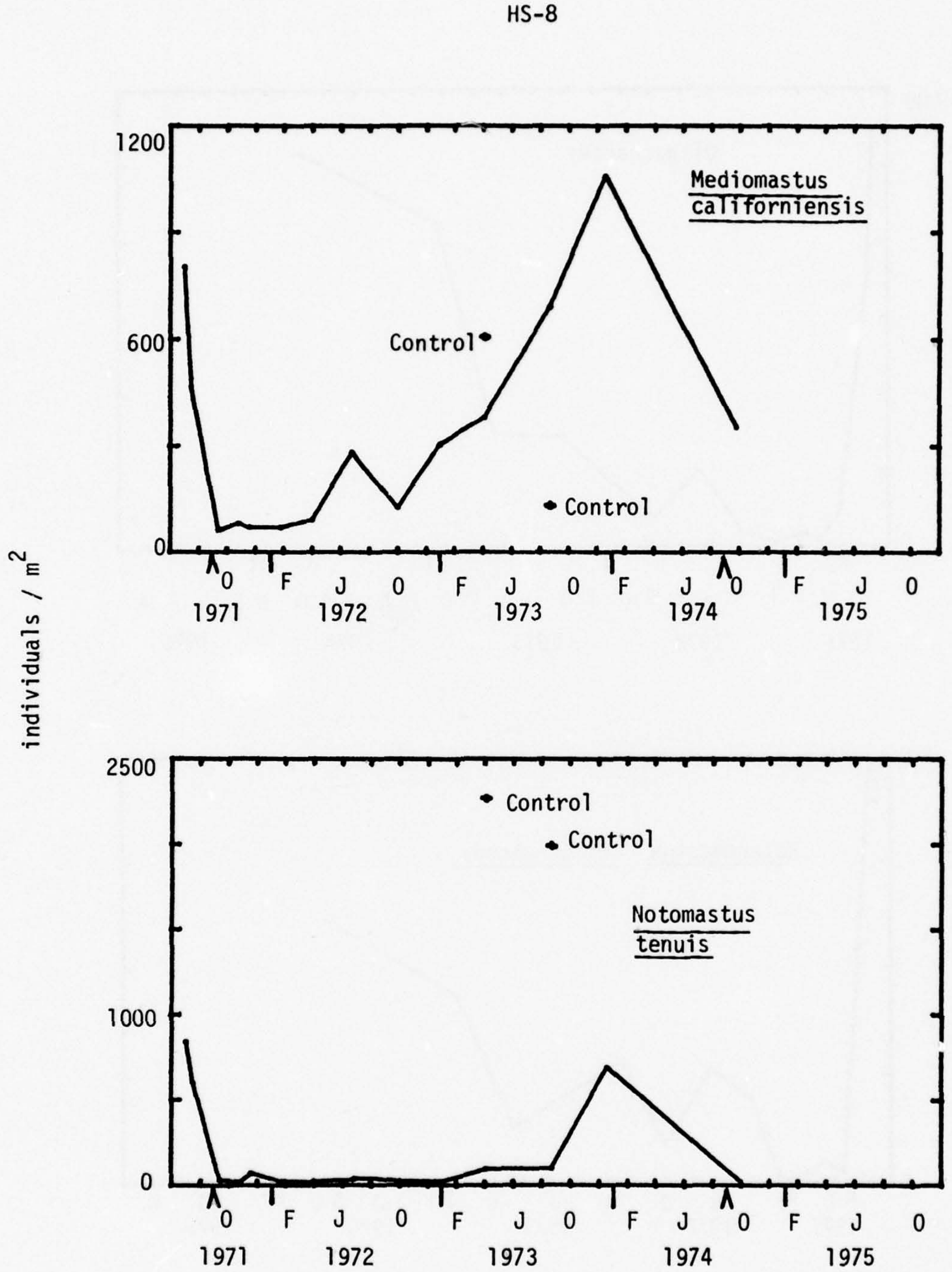

Figure 82. Variation in abundance of two species of polychaetes at HS-8 and nearby control station (mean and standard deviation of the mean). Arrows indicate disturbances.

density (PCM) were dominated by the polychaetes. The largest number of species occurred when the phoronid patch was maximally developed (June 1972) and remained relatively high thereafter (Figure 83). Most of these species were present in low abundance, however. Decreases in species diversity or heterogeneity (H') and species evenness (J) primarily reflected the numerical dominance of one or a few species.

1974 Disturbance (H-3)

This station was composed of fine sand with a higher silt/clay fraction than HS-8. The dredging did not change the gross physical characteristics of the sediment at any of the harbor stations, except for a slight increase in the sand fraction of the two outer stations (HS-8, H-3) directly after dredging (Table 11).

Prior to dredging, the H-3 infauna was similar to that at HS-8 and included capitellid polychaetes (Capitella capitata, Notomastus tenuis, Mediomastus californiensis), Armandia brevis, oligochaetes, nematodes and Macoma spp. (mostly M. nasuta). All of these forms are deposit feeders or relatively mobile croppers.

The dredging removed most of the fauna from the experimental area and was followed by the settlement of the opportunistic polychaetes, A. brevis and C. capitata. Capitella capitata was the only abundant pre-disturbance species also present after the dredging (i.e., in September 1974); however, all of these individuals were quite small relative to the pre-disturbance population. The largest peak in total density was due to A. brevis (80% of total PCM) in December 1974. Most of the variation in total density was caused by the polychaetes, especially A. brevis and C. capitata, and the

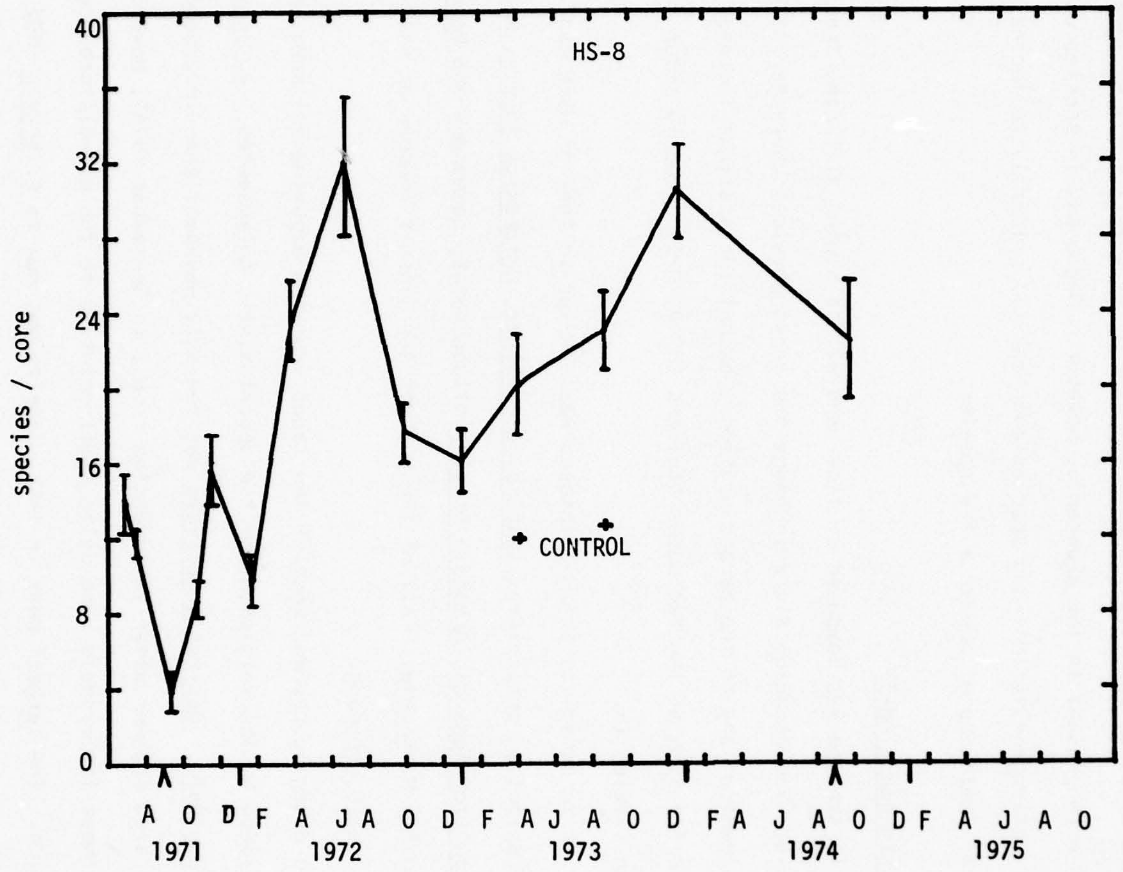

Figure 83. Variation in abundance of species at HS-8 and nearby control station (mean and standard deviation of the mean). Arrows indicate disturbances.

larger peaks in their abundances were non-complementary (Figure 84). Gyptis brevipalpa, Nephtys cornuta and Eumida tubiformis were less abundant early polychaete colonists (Table 14) that had a distinct density peak in December 1974. Platynereis bicanaliculata was abundant in December but was most abundant in late February 1975.

The number of A. brevis and C. capitata decreased to pre-disturbance levels by May 1975 and September 1975, respectively. There was not, however, a complete recovery of the oligochaetes (27,000/m^2, pre-disturbance; 1,700/m^2, September 1975) or the other abundant pre-disturbance polychaetes, Notomastus tenuis and Mediomastus californiensis. Heteromastus filobranchus was abundant in undisturbed harbor areas but did not reach an equal abundance at H-3.

There was a gradual increase in bivalves until a large settlement of several species occurred in September 1975. The most abundant of these was Tellina modesta, which often settles in large numbers and subsequently incurs extremely high mortality (see Chapter Two). In contrast, Macoma spp. increased at a very steady rate but had not reached the pre-disturbance level by September 1975.

Thus, the early phase of recovery involved the settlement of several polychaetes. Armandia brevis and C. capitata periodically settled in large numbers until May 1975; a number of other polychaete species settled and subsequently experienced relatively high mortality rates. A large number of T. modesta settled in September 1975, but based on previous patterns, these probably survived only a short while. The pre-disturbance polychaete, oligochaete and bivalve populations were not re-established one year after disturbance.

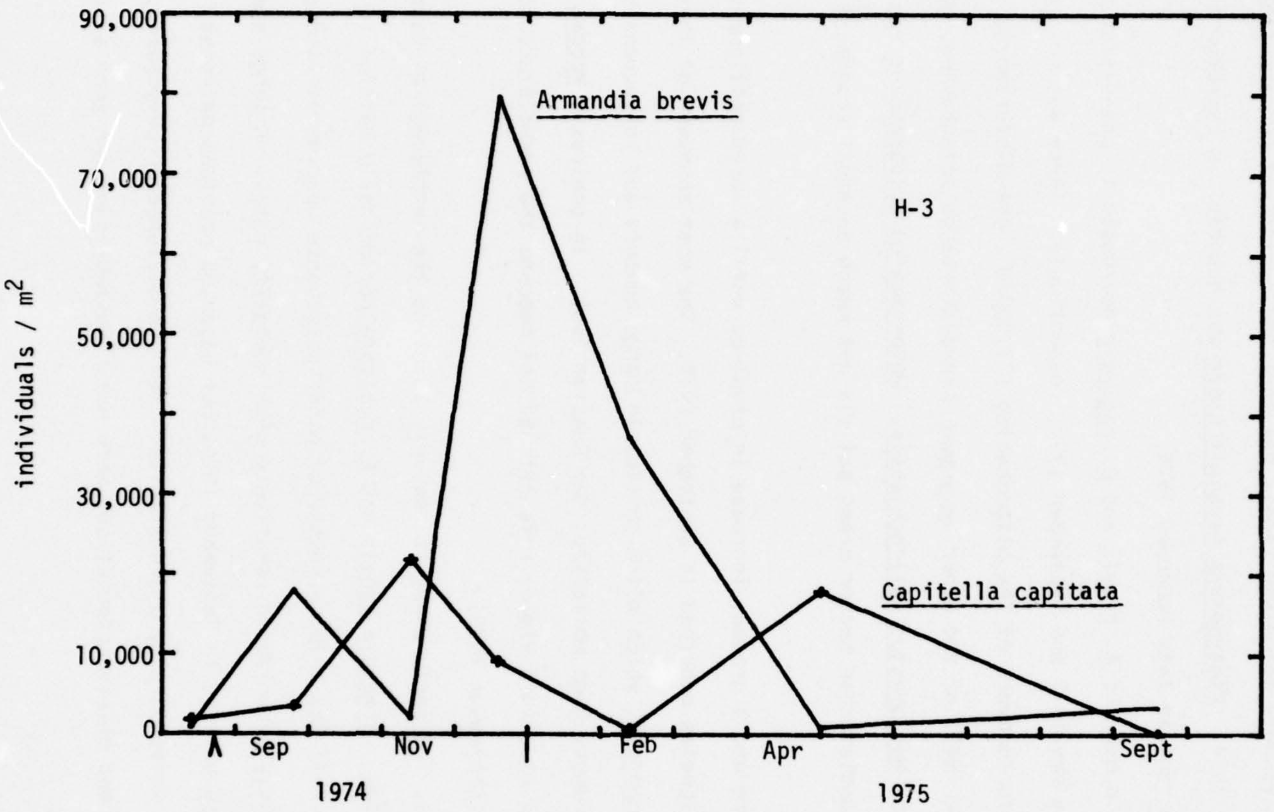

Figure 84. Variations in the abundance of *Armandia brevis* and *Capitella capitata* at H-3. Arrow indicates disturbance.

Variations in the number of species were dominated by the polychaetes. The slight increase from May to September 1975 was due to the bivalves (Figure 85). Species diversity or heterogeneity (H') and species equitability or evenness (J) experienced a large decrease after the disturbance due to numerical domination by a few species. Both generally increased with time but failed to reach pre-disturbance levels (Figure 86).

1974 Disturbance (H-2)

The pre-disturbance fauna at H-2 was similar to H-3 with regard to some polychaetes. The capitellids, Heteromastus filobranchus and Mediomastus californiensis, were the most abundant species. Oligochaetes and bivalves were rare; the nematode density was lower (H-3:9,000/m^2; H-2:2,000/m^2).

The dredging at this station was not as complete as that at H-3; therefore, animal survival was higher and more patchy. Nevertheless, the early phase of succession was similar to H-3 and the variations in the total number of individuals (PCM) were again due primarily to the polychaetes, especially Capitella capitata and Armandia brevis (Figure 87). The largest peak in density was in February 1975, when both of these species were most abundant. Capitella capitata was always more abundant than A. brevis. The latter decreased to a very low population size in May and the former reached a similar low by September 1975. This pattern of decline was identical to that at H-3. However, the larger density peaks in both species occurred earlier and A. brevis was always the numerical dominant at H-3. Furthermore, Nephtys cornuta, Eumida tubiformis and Gyptis brevipalpa had distinct abundance peaks in February 1975, rather than in December as they did at H-3.

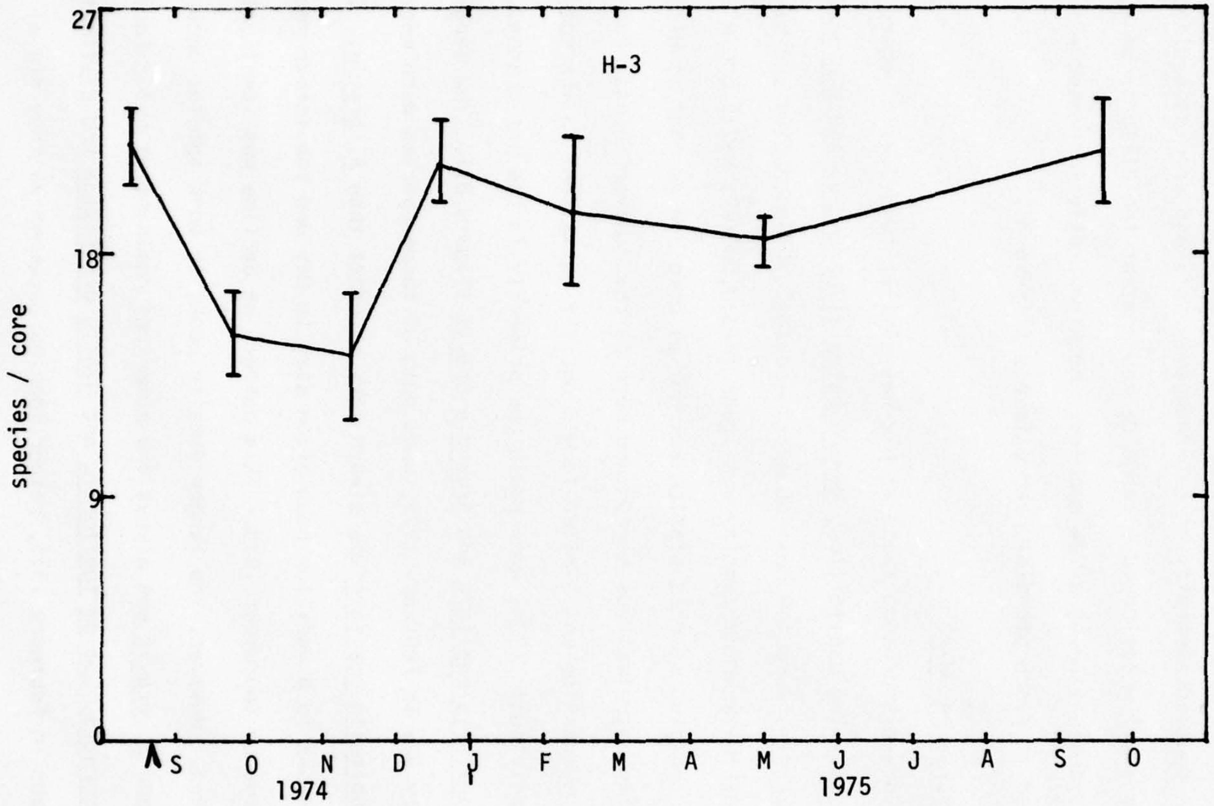

Figure 85. Variation in abundance of species of PCM at H-3 (mean and standard deviation of the mean). Arrow indicates disturbance.

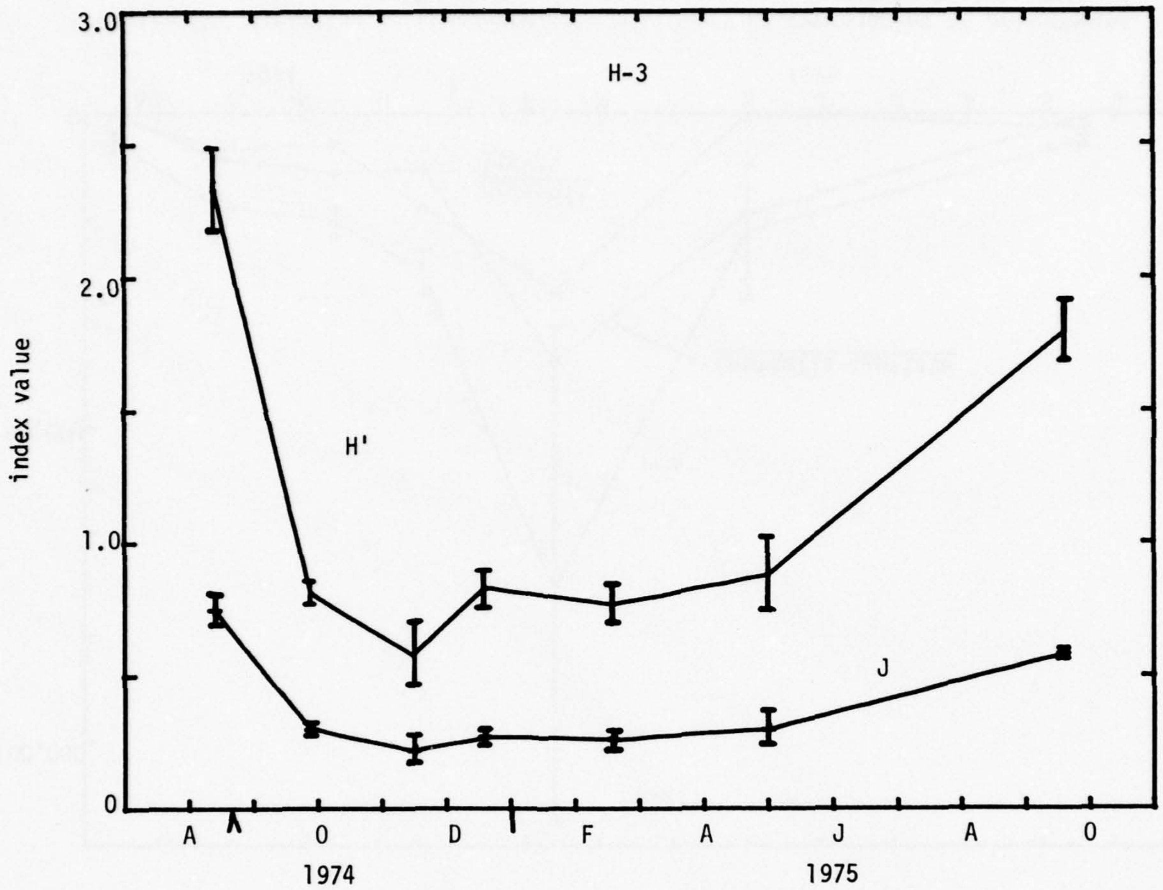

Figure 86. Variations in species diversity or heterogeneity (H') based on the Shannon-Weaver index and species equitability or evenness (J) based on the Pielou method at H-3. Arrow indicates disturbance.

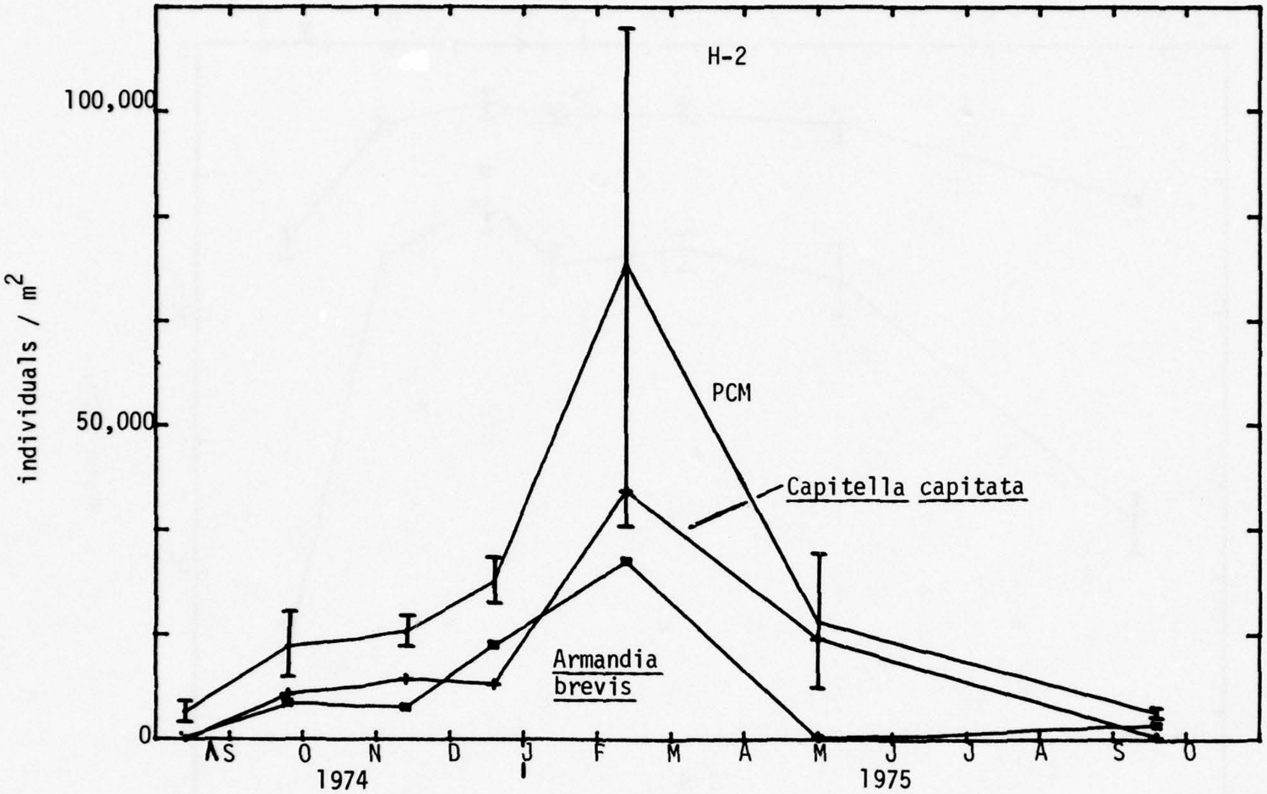

Figure 87. Variation in abundance of individuals of two species of polychaetes compared to PCM at H-2 (mean and standard deviation of the mean). Arrow indicates disturbance.

In contrast, the abundance peaks of Platynereis bicanaliculata were the same at both stations.

Because of the patchiness of the initial dredging disturbance, a fair number of large H. filobranchus were present in the first post-dredging samples and, within several months, they reached their pre-disturbance density. The main polychaete fauna at H-2 was essentially re-established between May and September 1975.

Settlement of several species of bivalves in September 1975 involved about 1/10th as many individuals as the corresponding H-3 settlement. Probably few of these animals survived. The mud at H-2 is too soft to support the weight of most adult bivalves.

Variations in the total species (PCM) were primarily due to the polychaete species, except in September 1975, when a large number of bivalve species settled (Figure 88). Species diversity or heterogeneity (H') and species equitability or evenness (J) did not follow any simple trend that could be easily related to the general pattern of succession (Figure 89). The low value in May was due to a very large number of C. capitata in one core; the high in September 1975 was caused by a decrease in polychaete numerical dominants and the settlement of several bivalves in low numbers.

The early phase of succession involved the same species of polychaetes at both H-2 and H-3 (Table 14). A later settlement of bivalves also occurred at both stations, though it was much reduced at H-2. However, in contrast to H-3, the pre-disturbance assemblage at H-2 had basically recovered between May and September 1975.

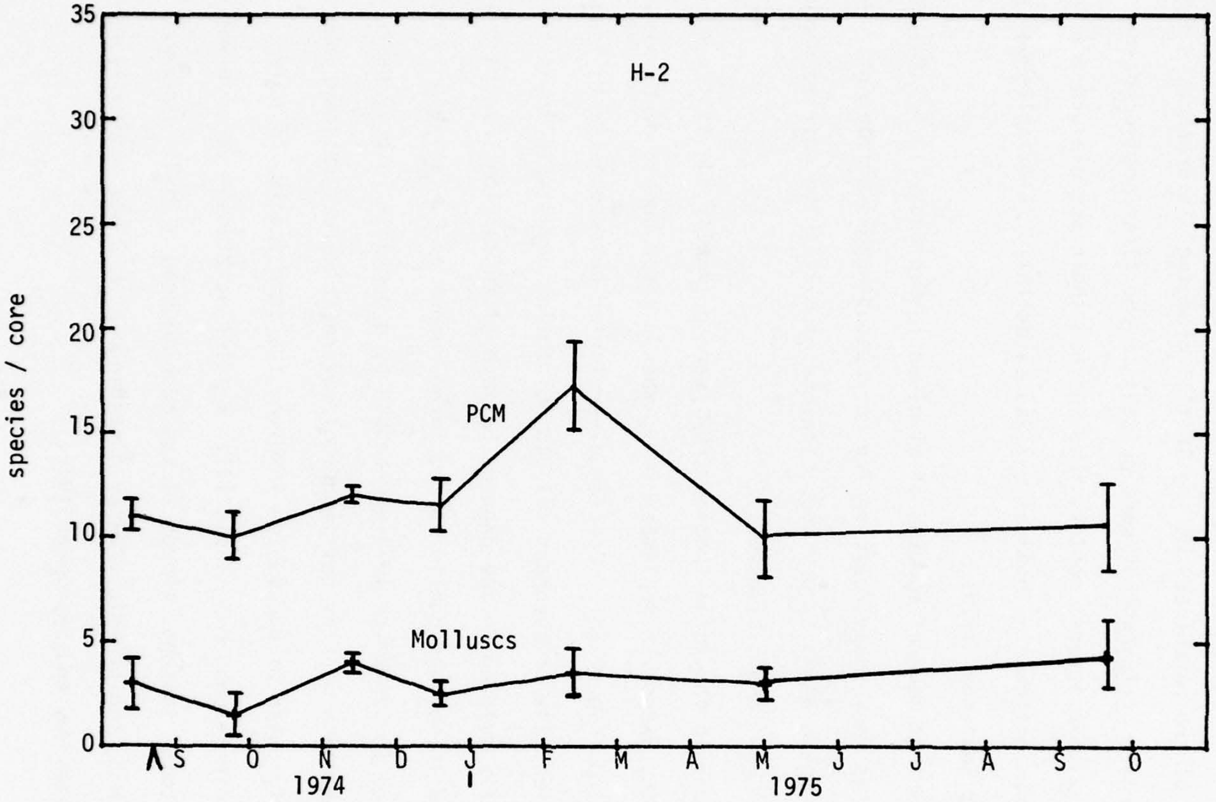

Figure 88. Variation in abundance of species of PCM compared to species of molluscs (mean and standard deviation of the mean). Arrow indicates disturbance.

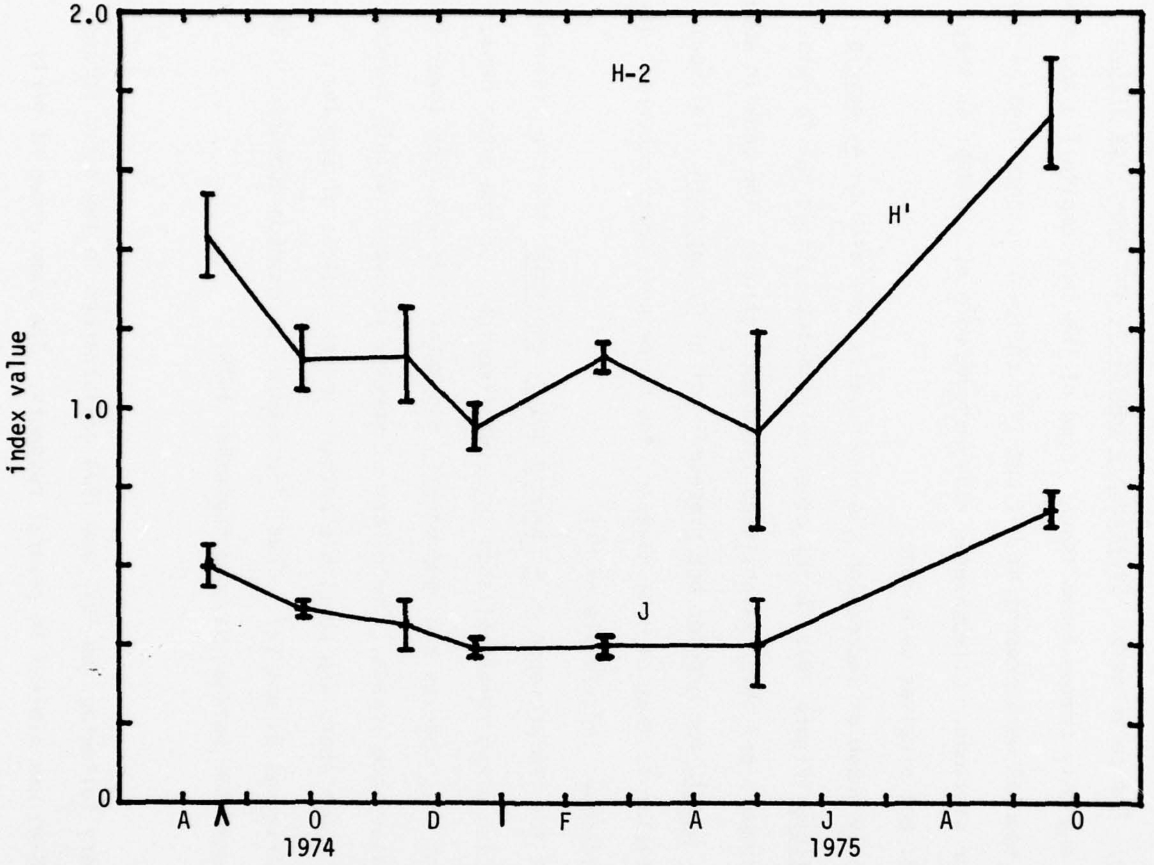

Figure 89. Variations in species diversity or heterogeneity (H') based on the Shannon-Weaver index and species equitability or evenness (J) based on the Pielou method at H-2. Arrow indicates disturbance.

1974 Disturbance (H-1)

The back harbor area (H-1) had the least complex bottom community prior to dredging. The polychaetes, *Streblospio benedicti* and *Dorvillea articulata*, were the only common forms there. Some of the same capitellid and other polychaete species were present at H-1 but in much lower numbers than at the other harbor stations. Oligochaetes and nematodes were as abundant as they were at H-3, but bivalves were rare.

The early phase of succession was numerically dominated by *A. brevis* and *C. capitata* (Figure 90). A few other polychaetes settled but in relatively low numbers and never established large populations. The peak in abundance of *A. brevis* was greater and preceded that of *C. capitata*. This pattern was similar to that at H-3; however, the major settlement occurred later and involved fewer individuals at H-1.

Except for the presence of *A. brevis* and *C. capitata*, the pre-disturbance polychaete fauna was re-established in several months. On the other hand, the abundance of oligochaetes and nematodes in September 1975 was much lower than the pre-disturbance levels. The number of species recovered within several months, although there was no simple pattern in the indices of species diversity (Figures 91 and 92). Thus, the general succession appeared to be completed sometime between May and September 1975.

Discussion

Recovery following the 1971 and 1974 disturbances in the outer harbor (H-3 and HS-8) was similar in several respects. The same group of early polychaete colonists characterized each succession, although their order of

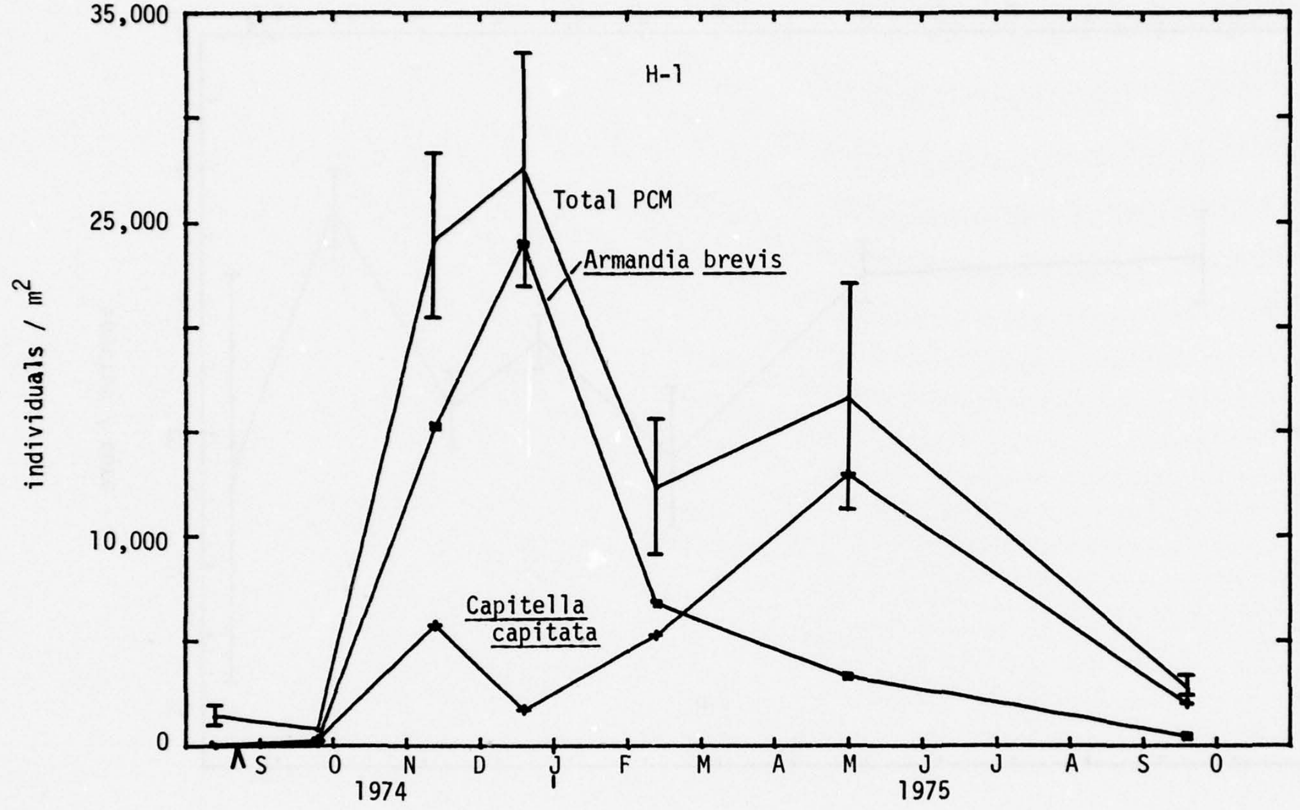

Figure 90. Variation in abundance of individuals of two species of polychaetes compared to PCM at H-1 (mean and standard deviation of the mean). Arrow indicates disturbance.

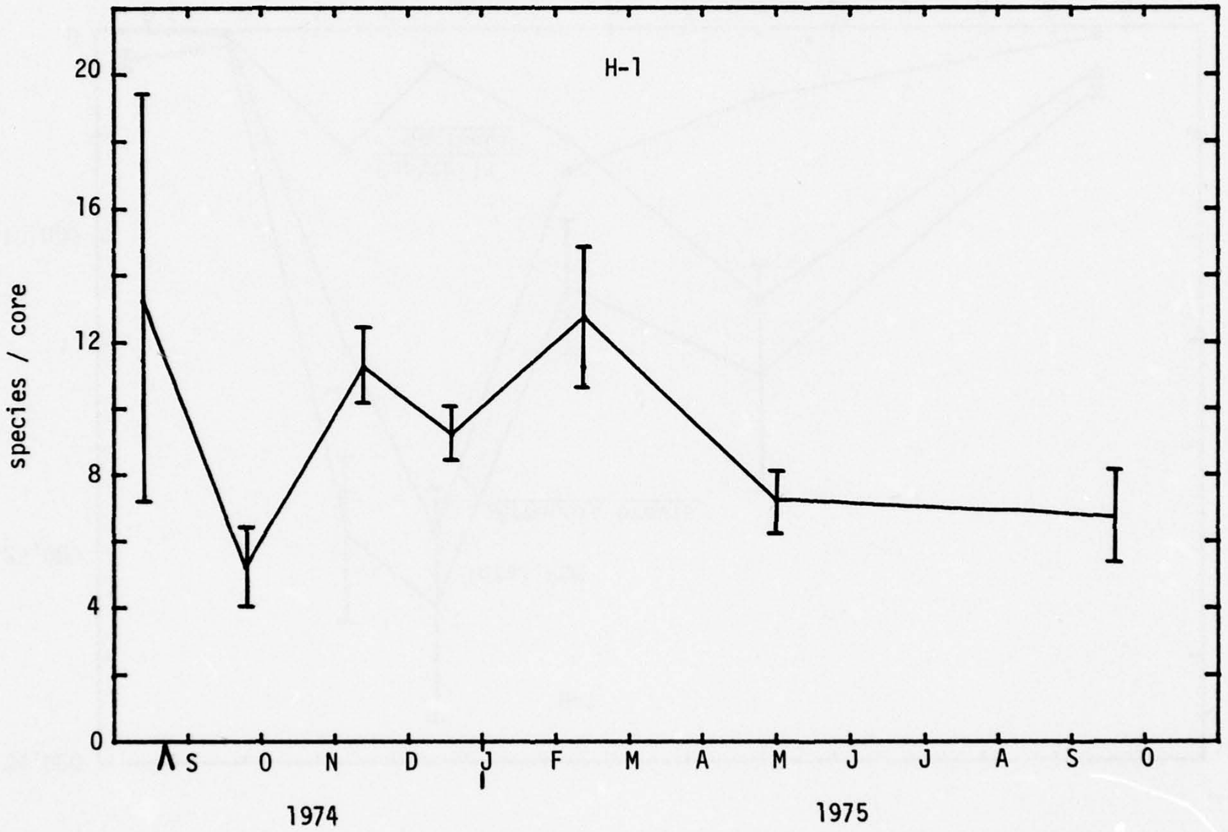

Figure 91. Variation in abundance of species of PCM at H-1 (mean and standard deviation of the mean). Arrow indicates disturbance.

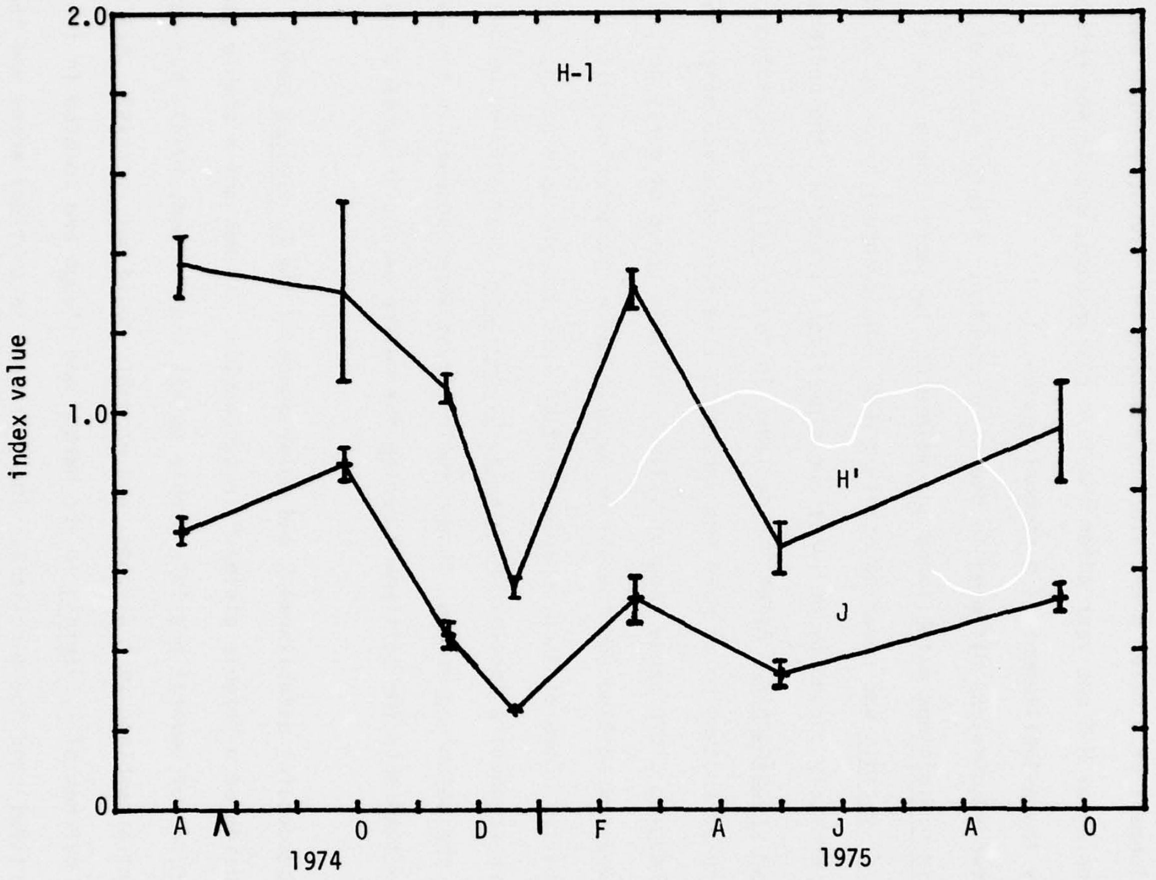

Figure 92. Variations in species diversity or heterogeneity (H') based on the Shannon-Weaver index and species equitability or evenness (J) based on the Pielou method at H-l. Arrow indicates disturbance.

occurrence and subsequent mortality rates were somewhat different (Table 14). In addition, the pattern of settlement and subsequent high mortality of most bivalve species was similar. Finally, the later recovery phase involved the re-establishment of similar pre-disturbance dominants. The late phase was only beginning at H-3 one year after the 1974 disturbance, and it was retarded at HS-8 by the establishment of a phoronid patch.

The two successions differed in one major concern. A large patch of Phoronopsis viridis was established and maintained for more than a year at HS-8, but P. viridis was never abundant at H-3. The eventual break up of the patch was probably caused by at least one significant predator, the nudibranch Hermissenda crassicornis. After the decline in the P. viridis population, the pattern of succession at HS-8 was very much like that observed after the initial dredging disturbance (August 1971). The same group of early polychaete colonists settled and thereafter experienced a characteristically high mortality. Some of these species settled into the phoronid patch, but the most opportunistic species (A. brevis, C. capitata) only settled before and after the patch's presence, though their larvae were abundant in the water column and available for settlement during the entire period (Figures 93 and 94).

The successful establishment and maintenance of the P. viridis patch may be considered a "stable plateau" in succession. It was not a stable end state, nor one of several possible stable points (Sutherland, 1974), but rather a transient assemblage that did not, and probably could not, persist. All of the dense patches of P. viridis in the harbor and slough are located in the high intertidal sand and mud flats. Their absence in subtidal areas and the nudibranch feeding observations suggest that predators restrict dense popula-

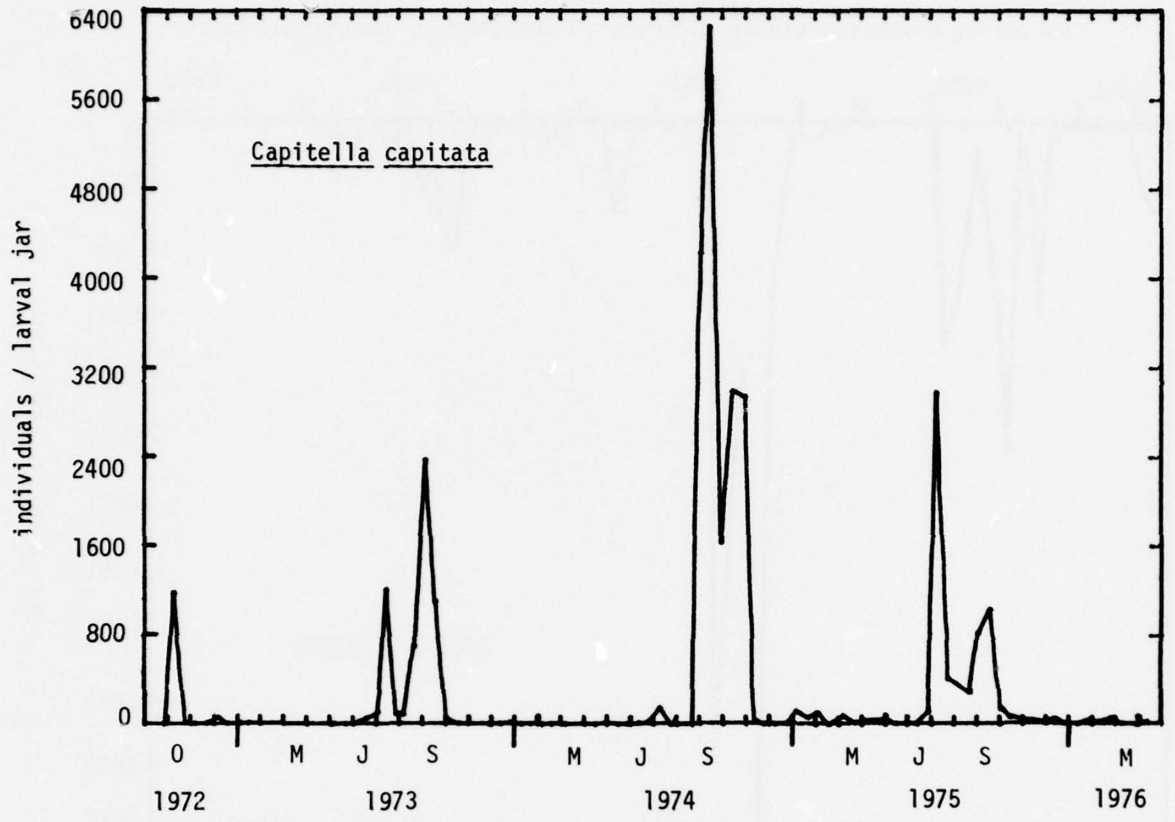

Figure 93. Number of post-larval Capitella capitata collected in larval settling jars per 14-day exposure.

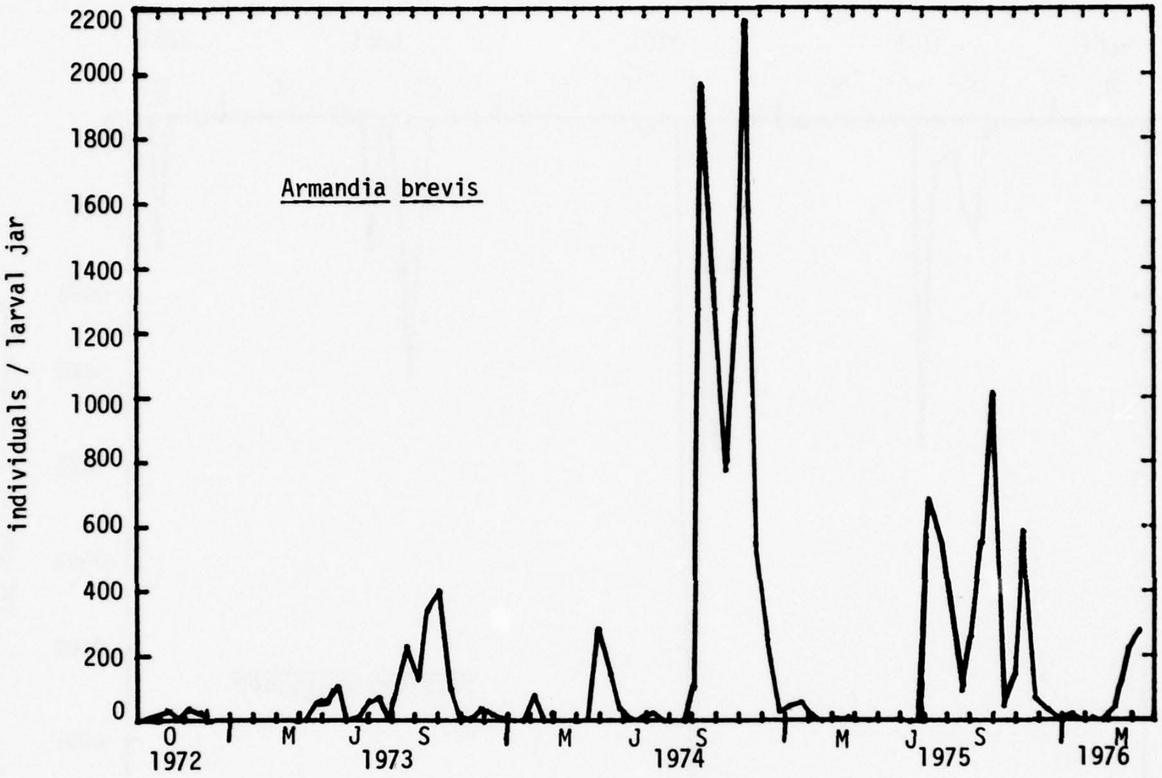

Figure 94. Number of post-larval <u>Armandia brevis</u> collected in larval settling jars per 14-day exposure.

tions to high intertidal refugia. Nevertheless, this "stable plateau" effectively prevented the re-establishment of pre-disturbance infauna and thereby slowed the rate of recovery. The pre-disturbance populations had essentially recovered by March or September 1974; therefore, succession took three years to complete at HS-8.

It is not known why a dense patch of phoronids did not form at H-3 in 1975, but it may have been related to differences in the initial disturbance. The 1974 excavated site (at H-3) was smaller and closer to undredged areas of potential slumping than at HS-8. *Phoronopsis viridis* may prefer not to settle in locations where large deposit feeders are nearby. In contrast, at HS-8 a large area was essentially defaunated and the only animals present were small surface deposit feeders. The absence of *P. viridis* at H-3 may also have been related to the proximity of industrial water intake pumps. Their net effect might be to isolate this area from the central slough where most of the phoronid larvae originate. On the other hand, HS-8 is located in the entrance channel, which is simply a continuation of Elkhorn Slough (Figure 2).

In summary, the successional patterns after both the 1971 and 1974 experimental disturbances involved many of the same species but were grossly dissimilar because of the recruitment and survival of a dense population of *P. viridis*. Early polychaete colonists responded to the break up of the phoronid patch as if it were a disturbance and the rate of recovery of the pre-disturbance infauna was much longer in the presence of *P. viridis* (HS-8, three years; H-3, probably two years).

Interpretation of the successional pattern following the 1974 dredging was complicated by differential disturbance. The outer harbor (H-3) and back harbor (H-1) stations were dredged relatively clean but not so well as

HS-8. H-2 was dredged most unevenly and many more large animals were present after the dredging, probably because of slumping. Nevertheless, the main hypothesis could still be tested. It predicted that the rate of community succession (i.e., recovery from disturbance) or community resilience (i.e., rate of rebound) increases with increasing environmental variability or physical stress. The two inner harbor stations recovered at the same rate; however, H-2 was less disturbed than H-1. If the disturbance at H-2 had been more complete, the authors predict that H-2 would have taken longer to recover. This is not an important point, since the dredging disturbance at H-3 and H-1 was similar and these stations are located at the extremes of the environmental gradient. The pre-disturbance fauna at H-3 was not re-established by the end of the study. By comparing HS-8 and H-3, it can be estimated that recovery at H-3 will be complete within two years. Thus, even by ignoring the H-2 station, the results support the hypothesis that community resilience and environmental variability are positively correlated.

The variations in the 1974 successional patterns along the southern channel were gradational. The inner harbor stations (H-1 and H-2) had few bivalves, and there was a gradient in their settlement along the channel. Only the most opportunistic polychaete species settled at H-1, but the general sequence was similar to H-3. Many of the same polychaetes colonized H-2 and H-3, and the pattern of succession was grossly similar at the two stations (Table 14). The variations in the peak abundance of Capitella capitata and Armandia brevis could not be explained by variations in the availability of larvae above the bottom. Larval jars were positioned at each station and the pattern of settlement into these was quite similar. It is suspected that some of the variation among stations was related to uneven digging and small-scale slumping during the dredging. However, larvae can also respond to differences in sediment size, deposition or scouring and other factors.

The large settlement of Armandia brevis at HS-8 in December 1973 and 1974 may be related to mild sedimentation at that time. Suspended solids were very high during the winter runoff period and reduced currents near the channel edge may have resulted in periodic deposition at HS-8. Armandia brevis generally preferred to settle in experimental containers that allowed a high rate of deposition of suspended particulates (Table 10) and may settle on the bottom if a thin layer of new deposit is present. In contrast, C. capitata probably prefers even more disturbed habitats and thus settled only in low numbers after the phoronid patch break up. In fact, the results from larval settlement experiments suggest that the larvae of more opportunistic species (i.e., early colonists) select disturbed habitats. In these experiments, azoic, air-dried sediment was heat treated (130° C for five hours) and placed in the larval settlement containers with an azoic, air-dried sediment that was not heat treated. The results showed that C. capitata had a strong preference for the heat-treated sediment; A. brevis had a slight preference for the air-dried sediment; and Polydora socialis showed no preference (Table 15). Heat treatment was a further disturbance of the sediment, but it was not clear how it related to the C. capitata preference. One hypothesis is that this particular opportunistic species is very selective for "disturbed" habitats. This experiment is not presented as a test of this hypothesis but rather as a highly suggestive, preliminary result that may prove to have general implications.

CHAPTER SIX

GENERAL DISCUSSION

Natural disturbances of marine bottom communities are common and can have a profound effect on community organization. A primarily unidirectional disturbance (i.e., wave-induced substrate motion) appears to be a major cause of shallow water zonation patterns along the open coast of western North America (Oliver et al., M.S.). Periodic occurrences of storm waves, variations in wave length and direction of arrival and strong long-shore and rip currents affect zonal patterns on several scales (e.g., seaward and shoreward migrations of Dendraster and amphipods, periodic recruitment of larvae followed by high mortality, holes ripped in Dendraster beds, extensive bottom erosion to depths greater than 10 m, etc). Regions near the heads of submarine canyons that come close to shore are particularly dynamic environments. Accumulation and movement of sediment and other material are common. Topographic changes, including large slumps, occur over short time periods and result in high benthic animal mortality (Chapter 4). Although physical disturbances are usually more widespread, biological disturbances have also been recognized (e.g., Fager, 1964).

Physical disturbances of marine bottom communities are not unique to temperate coasts. Anchor ice formation and uplift, slumping of steep submarine slopes and iceberg scouring are known to disturb shallow water marine communities in the Antarctic (Dayton, 1972; Dayton et al., 1969, 1970, 1974; Oliver et al., 1976). These disturbances result in distinct faunal zones that are both perpendicular (depth profile) and parallel to the shoreline. Iceberg scouring may also be common in certain shallow water locations in the

Arctic (A. Carey, Oregon State University, personal communication).

The general successional patterns following the various natural and experimental disturbances in Monterey Bay were primarily dependent upon the nature of the adjacent, undisturbed communities (i.e., community structure and variability and environmental variability). Along the northern sand-flat, large megafaunal animals moved into the deeper disturbed areas within the first day (e.g., demersal fishes within minutes and starfish within hours). The early phase of macrofaunal recovery was characterized by the immigration of highly mobile groups of adult peracarid crustaceans and the settlement of the larvae of several species of polychaetes that have opportunistic life history patterns. In the canyon area and in the Moss Landing Harbor, peracarid crustaceans are much less abundant and, therefore, did not colonize the disturbed locations there. Thus, the early phase of succession only included the opportunistic polychaetes. There was no consistent replacement of general trophic groups during the various successions. The second phase usually involved a gradual recolonization by the species that occupied the area prior to the disturbance. These species were also abundant in adjacent undisturbed areas. In one case, a relatively unique assemblage formed a "stable plateau" that temporarily prevented the re-establishment of the pre-disturbance community and increased the total recovery time by at least a year.

Other workers have documented these same two major phases of benthic succession, although they were usually not identified as such (Saila et al., 1972; Rosenberg, 1972, 1973; Grassle and Grassle, 1974; Rhoads et al., 1975; McCall, 1975; Dauer and Simon, 1976). Saila et al. (1972) investigated the colonization of dredged material in Rhode Island Sound and observed large megafaunal animals and mobile peracarid crustaceans as well as the more opportunistic polychaetes during the early phase of recovery. Dauer and Simon (1976) described the recovery of a sand flat area after defaunation by red tide and emphasized the role of adult migrations, but early succession was still characterized by the settlement of several, apparently more opportunistic, polychaetes. Grassle and Grassle (1974) identified a continuum of opportunistic polychaetes and McCall (1975) divided the polychaete colonists into three major groups. The authors chose to distinguish only two phases of succession to emphasize the difference between many early and late colonists. In particular, the early colonists responded readily to disturbances but were rare in the undisturbed or re-established assemblages. It is interesting that even in relatively remote Antarctic soft-bottom communities, the early phase of colonization of experimental azoic substrata and natural bottom areas scoured by icebergs was also characterized by mobile peracarids and opportunistic polychaetes (personal data).

Plankton tows, funnel trap data and morphological characters indicate that the early peracarid crustacean colonists are relatively active swimmers. The first polychaete colonists are characterized by high larval availability (frequent and abundant in larval jars), short generation time and high natural mortality rates. There is also a tendency toward smaller clutch size or lower fecundity per generation, smaller animal size and higher incidence of known brooding behavior within this group of early polychaete colonists. There is a positive correlation between the order in which polychaete species colonized a disturbed area and their rank order as determined by several of these life history parameters. Grassle and Grassle (1974) and McCall (1975) documented a similar relationship involving some of the same species in protected bays on the eastern coast of North America. Connell (1972) reviewed the process of community development or succession in marine rocky intertidal communities and concluded that the sequence of recolonization is mainly a reflection of the life history characteristics of the colonists. Foster (1975) came to the same basic conclusion but, in particular, emphasized differences in generation time and growth rates in experimental studies of algal succession in a subtidal kelp bed. Fugitive or opportunistic species were the first colonists in areas cleared by Dayton (1975) in a similar system. Thus, the sequence of succession is highly dependent upon the life history characteristics of the colonists in most marine communities which have been studied. This is probably also true for many terrestrial plant communities (Horn, 1975).

The lack of information about animal interactions in soft-bottom communities severely limits an assessment of their role in succession. Competition and predation are known to affect the pattern of succession after various experimental perturbations in rocky intertidal communities (e.g., Dayton, 1971). Predation by a nudibranch caused a major change in succession after the establishment and successful maintenance of a large patch of a phoronid worm in one harbor area (HS-8). Phoronids are tube-dwelling, suspension feeders which probably limit the activities and, thus, the numbers of mobile deposit feeders by monopolizing available space (Woodin, 1974). This was further evidenced by the increase in density and biomass of deposit feeders after the phoronid patch was destroyed. There are undoubtedly many obligate interactions that become increasingly important later in succession. One well-known example of this sort of interaction is the dependence of small sabellid polychaetes on the relatively stable mounds produced by a large deposit-feeding holothuroid (Rhoads and Young, 1971). As expected, the number of known commensal forms increased with time during all the local successions. It is also often presumed, but still undocumented, that the reduction in abundance of early colonists is related to inter-specific competition with later colonists. Thus, though few direct observations of animal interactions are available, they are probably quite important in determining benthic succession patterns.

Another biological phenomenon about which very little is known but which is the subject of formidable speculation (Wilson, 1958; Thorson, 1966; Woodin, 1976) is the recruitment of marine soft-bottom invertebrate larvae. The larval choice experiments in this study helped explain certain variations in larval settlement patterns during succession. In particular, Capitella capitata was conspicuously absent along the offshore disturbance gradients, while present at the canyon and harbor sites and abundant in the water column. Both C. capitata and Armandia brevis showed a distinct preference for fine sediment in choice experiments but a much higher proportion of the latter settled in the coarse, shifting sediment as compared to the former. Consequently, A. brevis settled along the offshore disturbance gradients and its settlement pattern could be explained by larval substrate preferences. The successful maintenance of the patch of Phoronopsis viridis at HS-8 was probably achieved by the gregarious settlement behavior of their larvae. Finally, the results of one series of larval selectivity experiments suggested the hypothesis that the larvae of some opportunistic polychaetes may be highly selective for disturbed substrates. More experiments need to be performed to document the generality of this pattern; however, if the hypothesis is correct, larval settlement behavior is much more important in determining benthic successional patterns than has been previously suspected.

This study has established that natural disturbances are common in nature and that the pattern of benthic succession (i.e., recovery from disturbance) can be divided into two general phases. This gross pattern is primarily determined by the mobility patterns of the crustaceans (when present) and by the life history characteristics of the polychaete colonists. There is also good evidence that animal interactions and larval recruitment patterns are important during succession. Rhoads et al. (1975) discussed the effect that physical and chemical changes in the sediment have on benthic succession in a muddy habitat. Their results are undoubtedly relevant to the protected back harbor areas but are probably unimportant in the shifting, relatively clean sand bottoms offshore.

Grassle and Grassle (1974) found that the level of opportunism of the polychaete colonists (determined by relative mortality rates) was related to their occurrence in bottom areas that were differentially disturbed by an oil spill. The most opportunistic species were found in the most disturbed areas (lowest diversity); intermediate opportunists on the less disturbed bottoms, and so on. As noted earlier, this pattern may be highly dependent upon larval substrate selectivity. A similar relation was observed between the sequence of succession and the distribution of species along the offshore gradients of natural environmental variability. Polychaete and crustacean species characteristic of the more variable end of the gradient occurred first in many successions. Those species characteristic of less variable environments (deeper water) occurred later. Variations in succession along the within depth experimental disturbance gradients were more complicated. Nevertheless, species occurrence in succession and species distribution along a natural gradient of environmental variability were interrelated.

Many ecologists have speculated about the relationship between species diversity and community stability (e.g., see the Brookhaven Symposia No. 22). Community stability is generally defined as the ability of a community to resist or rebound after a perturbation. In this discussion, community stability, community resilience and rate of succession or recovery from disturbance are equated. The diversity-stability hypothesis predicts that more diverse communities are more stable and thus, more resilient. Goodman (1975) reviewed the evidence that supports and refutes the hypothesis and concluded that there is "no simple relationship between diversity and stability in ecological systems." On the contrary, community resilience may actually decrease with increasing diversity, especially after a relatively severe disturbance like dredging or disposal (Watt, 1964; Dayton, 1972; May, 1973; Holling, 1973; Goodman, 1975). In fact, the authors found a positive correlation between community resilience, environmental stress and decreasing community complexity (a qualitative measure of species-species interactions based upon many components of community structure). Hence, communities living in a highly stressed and variable physical environment (e.g., shallow water offshore and the back harbor) were less complex and recovered more quickly from experimental disturbance than those in more benign and less variable areas (e.g., deeper water and outer harbor). In particular, wave-induced movement of shallow water sediments is intense and highly variable and potentially disruptive to bottom communities. Communities inhabiting these sediments are composed of species that can establish and maintain populations when the frequency and magnitude of natural disturbance are high. The community is dominated by early successional species because succession is continually interrupted by physical disturbance. Since these species must contend with a high level of natural disturbance and also represent an early successional group, community recovery (resilience) from the experimental disposal was rapid, relative to deeper water communities.

Finally, the following general ecological information should be considered prior to the initiation of a local dredging operation. At present, limitations on disposal are largely consigned by the physical and chemical characteristics of the dredged material. The nature of marine bottom communities is often not considered in the management process. Since the natural disturbance regime appears to be very important in determining the ability of a benthic marine community to persist or rebound from a relatively severe disturbance, it is recommended that an analysis of the environmental impact of a local dredging operation consider the nature of the physical environment and its relation to marine bottom communities. For example, it has been suggested that dredged material should be taken beyond the 100-fathom depth contour if certain physical and chemical "criteria" are above a predetermined level. Yet, bottom communities in these areas are probably adapted to a rather low level of environmental variation or disturbance and, therefore, may be unable to tolerate and readily recover from a disposal-related perturbation. This 100-fathom "rule" has also been applied for the "sake of consistency" in situations where there is relatively good evidence that disposal in shallower water might be less disruptive to the bottom communities. In particular, the head of the Monterey Submarine Canyon is known to experience large topographic changes and to support a relatively sparse fauna that is adapted to an unstable substrate. In contrast, knowledge of the benthic fauna in deeper water (greater than 100 fathoms) is sparse, being limited to information on some fishes, including a population of rare eelpouts (Maynea californica). Clearly, within the confines of present knowledge, it seems more desirable to place the dredged material in the shallower regions of the canyon where it will be channeled into deeper water via a natural sedimentary system.

The type of disposal method, water depth, currents and many other factors difficult to quantify will affect the physical and chemical characteristics of the bottom disturbance (see Inman and Brush, 1973). However, estimates of these factors allow a prediction of the degree of bottom disturbance. Once the estimate is available, the natural disturbance regime of a proposed disposal site and the nature of the associated bottom communities should be considered. This is a simple, preliminary requisite that is presently possible and should be a significant step toward a more sound ecological management process.

Some interesting work on the relationship between the disturbance characteristics of the environment and the structure of estuarine communities has been done in Coos Bay, Oregon, by Slotta et al. (1974). They asked somewhat different questions of a large estuarine system but concluded that the environmental disturbance regime has an important effect on bottom community structure and must be considered in any proposed modification of the system (e.g., dredging or disposal). The results of this study support their conclusion and extend them to the open coastal environment.

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TABLE I

Abundance of benthic and hyperbenthic animals captured by funnel traps in the crustacean zone (410 trap days).

(See Appendix for method discussion.)

Species	Number
AMPHIPODA	
Synchelidium shoemakeri	160
Paraphoxus daboius	79
Atylus tridens	66
Tiron biocellata	40
Monoculodes spinipes	40
Paraphoxus epistomus	11
Megaluropus longimerus	1
OSTRACODA	
Euphilomedes carcharodonta	12
Euphilomedes longiseta	7
Euphilomedes oblonga	5
CUMACEA	
Diastylopsis tenuis	57
Lamprops carinata	35
Hemilamprops californica	27
Mesolamprops dillonensis	25
Cyclaspis sp.	9
Anchicolurus occidentalis	4
MYSIDACEA	
Neomysis kadiakensis	550
Acanthomysis spp.	250
Other Mysids	50

TABLE 2

Mean abundance and temporal variation in abundance (as measured by the ANOVA test statistic) for the dominant species at M-4. (P) = polychaete; (C) = crustacean; (B) = bivalve.

Species	Number/ m^2	ANOVA test stat. value	Rank by abundance	Rank by ANOVA test stat.
Magelona sacculata (P)	1183.3	113	1	2
Tellina modesta (B)	727.8	121	2	1
Paraphoxus daboius (C)	405.6	57	3	11.5
Mediomastus californiensis (P)	333.3	50	4	15
Nothria elegans (P)	244.4	63	5	9.5
Prionospio pygmaea (P)	238.9	91	6	6
Lumbrineris luti (P)	227.8	43	7	16
Prionospio cirrifera (P)	194.4	56	8	13
Amaeana occidentalis (P)	138.9	54	9	14
Protothaca staminea (P)	105.6	105	10	4
*Nemertea**	105.6	-	-	-
Euphilomedes oblonga (C)	100.0	57	11	11.5
Siliqua spp. (B)	94.4	109	12	3
Edwardsia spp.	94.4	98	13	5
Euphilomedes carcharodonta (C)	83.3	89	14	7
Haploscoloplos pugettensis (P)	83.3	63	15	9.5
Nephtys cornuta (P)	77.8	68	16	8

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* not included in analysis (probably several species).

TABLE 3

Seasonal variations in the ANOVA test statistic at M-4.

Higher values indicate greater variability.

	ANOVA Test Statistic Value		
	Winter	Spring	Summer
Seasonal Breeders			
Magelona sacculata	12.4	19.3	17.6
Lumbrineris luti	1.7	1.5	13.4
Edwardsia spp.	3.4	18.1	10.8
Phoronopsis viridis	2.0	18.8	9.4
Paraphoxus daboius	1.65	12.5	13.0
Aseasonal Breeders			
Mediomastus californiensis	4.1	6.5	3.0
Prionospio pygmaea	13.0	18.7	13.0
Tellina modesta	18.24	18.8	17.0
Total Polychaeta	4.1	13.4	16.8
Total Crustacea	0.7	15.6	11.1
Total (PCM)	12.8	18.0	18.6

TABLE 4

Variations in the ANOVA test statistic with depth.

Higher values indicate greater variability.

	ANOVA Test Statistic Value		
	M-1 (6 m)	M-2 (9 m)	M-4 (18 m)
Polychaetes	86	72	103
Crustaceans	89	80	61
Molluscans	95	113	128
Total (PCM)	85	56	112
Species/Core	86	70	94
Shannon-Weaver Diversity Index (H')	62	65	79

TABLE 5

Variations in some physical properties of the sediment at the center of the disturbance (C) and the undisturbed site (A) at the offshore disposal sites.

		Pre-Disturbance	Post-Disturbance		
		Aug. 1974	Nov. 1974	Jan. 1975	Apr. 1975
N-2A	*Md	3.06	3.12	2.94	2.84
(9 m)	Sorting	0.52	0.30	0.43	0.38
	**% C	0.095	0.124	0.077	0.125
N-2C	Md		2.18	3.09	3.02
	Sorting		0.80	0.55	0.43
	% C		0.095	0.163	0.145
N-3A	Md	3.14	3.17	3.13	3.11
(18 m)	Sorting	0.43	0.40	0.43	0.41
	% C	0.193	0.134	0.125	0.114
N-3C	Md		1.95	1.90	3.08
	Sorting		0.79	1.06	.46
	% C		0.091	0.154	0.100
N-4A	Md	3.01	3.10	3.06	3.10
(24 m)	Sorting	0.74	0.39	0.48	0.41
	% C	0.115	0.086	0.115	0.135
N-4C	Md		2.10	--	2.80
	Sorting		1.13	--	0.51
	% C		0.159	--	0.096

*Median diameter in phi units
**Percent by weight of carbon

TABLE 6

The total number and frequency of polychaete species* caught during 14-day periods in larval jars collected from September 1972 to July 1975 (see Appendix).

Species	Total Number	Percent Frequency	(#) (F)
Capitella capitata	25,717	0.59	15,173
Armandia brevis	11,104	0.68	7,550
Nephtys cornuta	487	0.55	267
Harmothoe spp.	217	0.48	104
Nothria elegans	197	0.52	102
Prionospio cirrifera	155	0.39	60
Prionospio pygmaea	61	0.41	25
Polydora socialis	90	0.19	17
Amaeana occidentalis	50	0.32	16
Magelona sacculata	70	0.19	13
Phoronopsis viridis*	75	0.16	12
Platynereis bicanaliculata	22	0.12	3

*Phoronoid worm; only non-polychaete.

TABLE 7

Life history parameters of selected polychaetes.

Species	Width:Length, Large Individual (mm)	Egg Size (Microns)	Clutch Size*	Generation Time* (Months)	Mobility Pattern
Capitella capitata	1.0:30	--	10-500	1-2	Tube
Armandia brevis	0.5:20	50	--	1-2	Mobile cropper
Polydora socialis	0.5:30	--	500-1,000	3	Tube
Platynereis bicanaliculata	2.0:50	--	--	6-12	Tube
Prionospio pygmaea	0.5:11	20-60	20-50	2-4	Tube
Prionospio cirrifera	0.5:13	30	20-50	2-4	Tube
Mediomastus californiensis	0.5:20	40-80	50-3,000	--	Mobile cropper
Magelona sacculata	0.6:50	65-130	200-6,000	6-12	Burrow
Nothria elegans	2.0:150	100-240	1,000-2,000	6-12	Tube
Amaeana occidentalis	4.5:100	50-210	7,000-21,000	6-12	Burrow
Lumbrineris luti	1.0:150	100	100-200	6-12	Mobile cropper

*Very preliminary estimates.

TABLE 8

Settlement of several polychaete species into coarse sand in tall (increased deposition), medium and short (increased scouring) experimental containers (mean values). (See Appendix for methods.)

Species	Short*	Medium*	Tall*
Capitella capitata	1	6	43
Armandia brevis	<1	1	2
Nothria elegans	1	2	>2

*n = 4

TABLE 9

Ratio of adult to juvenile *Amaeana occidentalis* along the two deeper disturbance gradients in January 1975.

	Number/m^2		
	A	B	C
N-3 (18 m)	257:569	0:220	0:129
N-4 (24 m)	73:700	0:184	0:0

TABLE 10

Settlement of several polychaete species into fine sand in tall (increased deposition) and short (increased scouring) experimental containers (mean values). (See Appendix for methods.)

	Exposure Period			
	1-8 July 1975		8-14 July 1975	
Species	Short*	Tall*	Short**	Tall**
Capitella capitata	111	150	17	141
Armandia brevis	46	29	22	59
Polydora socialis	230	156	10	8
Prionospio cirrifera	4	1	--	--
Magelona sacculata	15	5	1	2

*n = 3
**n = 4

TABLE II

Average physical characteristics of sediment at various harbor areas.

Station	Median Diameter (Phi)	Coefficient of Sorting*	Percent Sand	Percent Silt/Clay (<0.62 microns)
H-1	7.9	2.0	3	97
H-2	7.8	2.9	7	93
H-3	2.4	1.9	80	20
HS-8	3.0	1.0	87	13

*Folk and Ward (1957); large numbers = poor sorting.

TABLE 12

Variations in sediment properties at Canyon Head Disturbance Site (P-3).

	Median Diameter (Phi)	Coefficient of Sorting*	Percent Silt/ Clay	Percent Organic Carbon
August 1971	3.05	0.51	7.8	0.13
Disturbance				
September 1971	3.17	0.97	22.2	0.64
November 1971-September 1973	3.00	0.45	8.5	0.12
December 1973	2.91	0.48	4.4	0.11
August 1974	2.52	0.51	0.0	0.09
Disturbance				
September 1974	2.59	0.59	2.1	0.15
October 1974	2.70	0.48	2.1	0.15
December 1974	2.69	0.42	2.3	0.01
January 1975	2.73	0.38	0.0	0.08
April 1975	2.93	0.52	5.9	0.18

*Folk and Ward (1957); large number = poor sorting.

TABLE 13

Variations in physical environment at outer (H-3) and back (H-1) harbor stations (mean ± standard deviation of mean).

Station	Temp. (^{0} C)	Salinity (%^{0})	PO$_4$ (μg-A/liter)
H-1 Surface	13.5 ± .65	28.5 ± 2.0	10.3 ± 2.4
H-3 Surface	12.8 ± .58	32.8 ± .6	1.9 ± .4
H-1 Bottom	12.4 ± .53	33.4 ± .08	4.18 ± 1.38
H-3 Bottom	12.5 ± .58	33.6 ± .08	1.05 ± .14
	Total DDT	Zn (ppb)	Oil & Grease (%)
H-1	174.7 ± 70	133 ± 10	0.2 ± .01
H-3	14.8 ± 9	25 ± 10	0.02 ± .01

TABLE 14

Early polychaete colonists ranked by their mortality rates and earliest peak abundance in succession at harbor stations.

	H-1		H-2		H-3		HS-8	
	Mortality	Successional Order	Mortality	Successional Order	Mortality	Successional Order	Mortality	Successional Order
Armandia brevis	1	1	1	1	1	1	2	2
Capitella capitata	2	2	2	2	2	2	1	1
Eumida tubiformis			3	6.5	3	5.5	-	-
Nephtys cornuta			4	6.5	4	5.5	7	5.5
Platynereis bicanaliculata			5	6.5	5	8	4	5.5
Gyptis brevipalpa			6	6.5	6	5.5	6	5.5
Prionospio cirrifera			7	4	7	5.5	3	5.5
Prionospio pygmaea			8	3	8	3	5	3

TABLE 15

Settlement of several polychaete species in differentially disturbed sediments (mean ± standard deviation of mean).

Species	Sediments Air-Dried and Heated to 130 °C*	Sediments Air-Dried Only**
Capitella capitata	50 ± 7	12 ± 3
Armandia brevis	67 ± 11	88 ± 15
Polydora socialis	35 ± 3	35 ± 3

*n = 15.
**n = 6.

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APPENDIX

A number of ancillary experiments were performed and various types of samples collected that are not discussed completely in the main text. Generally, the results are presented and interpreted with little or no consideration of the methods used to produce the data. These methods are outlined in this appendix rather than lengthen and possibly detract from the text.

Larval Jars

The larval jar setup consisted of a holding rack positioned 1 m above the bottom and attached to a vertical stake driven into the sediment. Widemouth (diameter 10 cm) gallon plastic jars were placed in separate rack compartments. Galvanized mesh (1.27-cm squares) was placed over the jar opening to prevent the entry of various fishes. The offshore rack was located at station M-4 (18 m) on the southern transect and the harbor racks at stations H-1, H-2 and H-3 (Figure 2). The main exposure interval was fourteen days, but sometimes jars were collected after only seven days or as many as twenty-eight days. The contents of each jar were washed over a mesh with 0.25-mm-square openings, preserved in 10% formalin and sorted to 70% ethanol. No sediment was added to the jars, but they collected a film of settled suspended materials within a day and an average of 1-2 cm in fourteen days. There was no indication of physical transport of juvenile forms from the bottom into the jars. Only a few larval forms and no bottom species that have pelagic larvae were caught in the funnel traps that collected animals swimming off the bottom. The traps did collect holoplankton and many active, swimming crustaceans. The larval jars did not trap swimming crustaceans or plankton, but these animals were occasionally retained within the jars. The jars did attract certain crustaceans, especially amphipods, that live on hard substrates or in association with attached epifauna.

A series of plankton tows were taken adjacent to the offshore larval rack (in May 1974) to compare the composition and relative abundances of the larvae in the plankton with the post-larval forms in the jars. A preliminary qualitative comparison indicated a high degree of similarity in species composition and a gross similarity in abundance patterns. Thus, the larval jars are a good index of larval availability (i.e., frequency and abundance of larvae in the water).

Larval Selectivity Experiments

Numerous experiments were performed to test hypotheses concerning larval substrate selectivity and early post-settlement survival patterns of soft-bottom invertebrates. Sediment was treated in various ways and placed in plastic freezer boxes (10x10 cm and 7, 9 or 13 cm tall). These were capped and transported to a holding rack at station M-5 (24 m) on the southern transect (Figure 2). The rack was 1 m above the sand bottom. It was constructed of galvanized sheet metal (40.6x50.8 cm) open at the top and bottom and held a maximum of twenty plastic boxes. The rack bottom consisted of a plastic grating and the top was either the same grating or a simple galvanized mesh to prevent the entry of fish. The plastic grating (1x1x1 cm) was used to reduce water motion. Reduced water motion resulted in increased sedimentation into the experimental boxes. A natural deposition/scouring cycle could be approximated by using the wire mesh top and varying the height of plastic containers. (However, even under these conditions, sedimentation was significantly higher in the rack corners; consequently, most experiments involved less than fifteen plastic boxes per rack and these were placed in the center of the rack.)

Many experiments required precise manipulation of the deposition/scour cycles. This was accomplished by exposing experimental substrata for short intervals (seven days) when hydrographic conditions were relatively calm and by using different container heights. The experimental setup was primarily developed by a trial-and-error procedure that included a considerable number of divers who visually compared the movement of bottom and experimental sediments under various environmental conditions. Therefore, a reasonable knowledge of the disturbance characteristics of the experimental apparatus is available.

To examine these characteristics even further, small plots of natural bottom sediment and associated fauna were carefully implaced into the plastic containers and then placed directly into the rack. This was all done underwater. Settlement into these treatments, azoic sediment and the natural, untransferred bottom provide a good index of the disturbance characteristics of the rack. This experiment has been performed, but the samples have not been completely processed. Nevertheless, a very preliminary examination indicated that settlement into the transferred and untransferred bottom sediments was similar and considerably less than that into the azoic sediment.

Funnel Traps

Funnel traps were used to catch mobile species swimming off the bottom. They were made with an inverted funnel (diameter 20 cm) with the spout leading into a removable holding jar. The traps were mounted on metal legs that allowed the open end of the funnel to be positioned parallel to and within several centimeters of the bottom. A small amount of sediment was placed in each trap as a refuge for confined individuals. Exposure intervals varied from one to four days.

Plankton samples were taken just above the bottom on several occasions and examined for benthic or near-bottom crustaceans. The species found in these samples were the same as those captured in the funnel traps. Thus, the traps allowed a relative measure of the mobility patterns of benthic crustaceans.

Breeding Cycles and Life Table Data

One author (Slattery) has carried out an extensive investigation of the breeding cycles of four abundant species of amphipods from several areas in Monterey Bay. The number of females, ovigerous females, males and immatures were recorded and measurements of clutch size, egg size and animal size were made.

Seven species of numerically important polychaetes were also measured (width of a given segment and length of a set number of segments) and examined for presence of eggs and number of eggs. Size frequency histograms were compiled for each sampling date for several stations. Histological sections of each species were prepared to study oogenesis and measure egg size. Finally, rough estimates of generation time (i.e., time to maturity) were made from monitoring local recruitment events in the field.

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