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NEW APPROACHES TO MONITORING AQUATIC ECOSYSTEMS

A symposium
sponsored by
ASTM Committee E-47
on Biological Effects
and Environmental Fate
and by the Ecological
Society of America
Minneapolis, MN, 17-21 June 1985

ASTM SPECIAL TECHNICAL PUBLICATION 940
Terence P. Boyle, National Park Service,
editor

ASTM Publication Code Number (PCN)
04-940000-16



1916 Race Street, Philadelphia, PA 19103

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Estuarine Invertebrates and Fish: Sampling Design and Constraints for Long-Term Measurements of Population Dynamics

REFERENCE: Hines, A. H., Haddon, P. J. Miklas, J. J., Wiechert, L. A., and Haddon, A. M., "Estuarine Invertebrates and Fish: Sampling Design and Constraints for Long-Term Measurements of Population Dynamics," *New Approaches to Monitoring Aquatic Ecosystems, ASTM STP 940*, T. P. Boyle, Ed., American Society for Testing and Materials, Philadelphia, 1987, pp. 140-164.

ABSTRACT: The first five to six years of a long-term data set are presented for invertebrates and fish representing an array of physiological tolerances, trophic levels, and life history strategies in a lower mesohaline subestuary of Chesapeake Bay. Population abundances were estimated for infaunal invertebrates with cores taken four to six times per year at five stations, for nearshore fish with seines taken once per year at 14 stations, and for epibenthic fish and crabs taken in trawls eight times per year at three stations. Physical/chemical parameters of estuarine water were monitored continuously. Analyses of variance and covariance were used to account for variation associated with seasonal cycles and to test for effects of year, station, and salinity on population abundances.

A 16-year record of meteorological and water parameters showed that the study period spanned a multiyear period of regional drought in the 1980s, which resulted in markedly increased salinities and reflected a greater deviation from the long-term average than reduced salinities during major storms of the 1970s. ANOVA and ANCOVA models accounted for 12 to 82% of the variation in population abundance, depending on the species. All but two species showed significant differences in population abundances among years in six years' data for 19 infaunal invertebrate species, six years for 18 species of nearshore fish, and five years for five species of epibenthic fish and crabs. Most species exhibited severalfold differences in abundance among years. About half of the infaunal species, several of the nearshore fish, and four epibenthic species showed significant responses to elevated salinities. However, despite the overall importance of salinity on estuarine systems, only a small fraction (1 to 6%) of the variation in any one species was explained by salinity changes. Failure to account for more of the population

variation by salinity resulted from: (1) the significant spatial (station) variation and the significant interaction of time and spatial variation in nearly all species; (2) the importance of other meteorological and water quality parameters in regulating populations; (3) salinity being important primarily during a critical period (for example, during spring recruitment) because other factors (for example, predation) may override the controlling influence of salinity during other seasons; (4) the spatial scale of the study area being too small to exhibit major shifts in species abundance across the major salinity zones of the estuarine gradient; (5) the location of the study area at the low end of the mesohaline zone means that high salinities dominating the study period are unlikely to affect euryhaline species as much as low salinities; and (6) possible biases of short-term variation since most years of the study period were characterized by unusually high salinity.

KEYWORDS: Chesapeake Bay, estuary, fish, infaunal invertebrates, long-term monitoring, population dynamics

Temporal change is an important aspect of ecological processes, yet we know little about the appropriate time scale involved in many population measures [1]. In estuarine systems, stochastic variability through time and large coefficients of variation characterize most populations of invertebrates and fish [2-4]. Recent attention [5,6] to the need for long-term measurements of ecologically important variables stems from the recognition of three major problems in population biology especially applicable to estuarine systems.

First, many species have life cycles that are sufficiently long and complicated that their population fluctuations can only be interpreted with long-term studies (for example, red-spotted newts) [7]. Most estuarine species of invertebrates and fish have complex life cycles involving larval stages or migratory behavior or both. Although the generation time of most estuarine invertebrates is short, some mollusks (for example, oysters) [8] and many estuarine fishes (for example, striped bass, yellow perch, white perch, shad) [9] live for at least five to ten years. These life spans and complex life histories require several years to evaluate effects resulting from time lags in environmental factors on population changes [10].

Second, certain rare or infrequent events occur at long enough intervals that it is generally impossible to measure biological responses with short studies unless an existing long-term monitoring program is already in effect before, during, and after the event. Examples of such rare or infrequent events in estuarine ecosystems include storms (for example, Tropical Storm Agnes in Chesapeake Bay) [11], population declines associated with disease [12,13], and the reproductive dynamics of some populations with dominant year classes (for example, striped bass) [14]. Moreover, meteorological fluctuations are tightly coupled drivers of estuarine ecosystems because they directly regulate salinities, vertical stratification, nutrient input, carbon budget, and sedimentation rates [15,16]. This tight coupling is manifested in the high disturbance regimes of estuarine systems. Understanding estuarine ecosystems requires long-term measurements of their responses to these meteorological fluctuations, particularly changes in freshwater inflow during irregular storms and droughts [17].

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Third, many aspects of environmental degradation can only be detected and assessed accurately when there is sufficient data to reveal long-term trends compared to the "noise" of short-term fluctuations [4]. Without long-term data, the inherent short-term variability of estuaries can mask the chronic and cumulative impacts of human activities, often until they reach critical levels. The best examples of long-term data indicating serious estuarine degradation against a background of high variability come from fisheries' catch statistics for species such as oyster, striped bass, and shad [10]. At the same time, there is a glaring lack of long-term data for species or variables which are not of direct commercial value but are important to the overall function of estuarine ecosystems (for example, benthic invertebrates). In some cases, such as the demise of submerged aquatic vegetation in Chesapeake Bay [18], the extremity of the change has been obvious, but the time course is poorly understood. Despite fears of catastrophe in other cases, such as pH of spawning areas of tributaries [19,20] or oxygen profiles of the deeper estuarine zones [21,22], the lack of long-term data can severely limit our evaluation of estuarine functions. Long-term population data for noncommercial estuarine species come primarily from community studies conducted by a few individual scientists [3,23,24] or by large environmental impact assessment programs, particularly for power plants [4].

The purpose of this paper is to present the first five to six years of a long-term data set for communities of invertebrates and fish species representing an array of physiological tolerances, trophic levels, and life history strategies in a subestuary of central Chesapeake Bay. We emphasize population responses of major species to salinity changes for two reasons. First, estuaries are, by definition, areas where fresh water mixes with the ocean [15], and the distribution of estuarine biota is generally restricted by salinity to zones along the estuarine gradient [2,25,26]. Second, at our study site salinity has been an obvious and major physical/chemical variable exhibiting year-to-year fluctuations over ranges known to influence abundances of estuarine biota [2,4,10]. Analysis of covariance of the population data is used both to remove the seasonal component of annual cycles and to test for species responses to salinity fluctuations. The analysis illustrates the power of long-term data in estimating interannual changes in population abundance and the difficulties of interpreting such changes. Although the difficulties may partly reflect the inherent variability of estuarine systems [25], the problems illustrated here are, first, the apparent lack of pattern in the abundant statistically significant fluctuations, and second, difficulties in interpreting statistically significant interactions among independent variables.

Study Site and Methods

This study was conducted at the Rhode River (38°51' north latitude, 76°32' west longitude), a 485 ha subestuary in the lower mesohaline zone of central Chesapeake Bay (Fig. 1). Salinity, temperature, and dissolved oxygen were

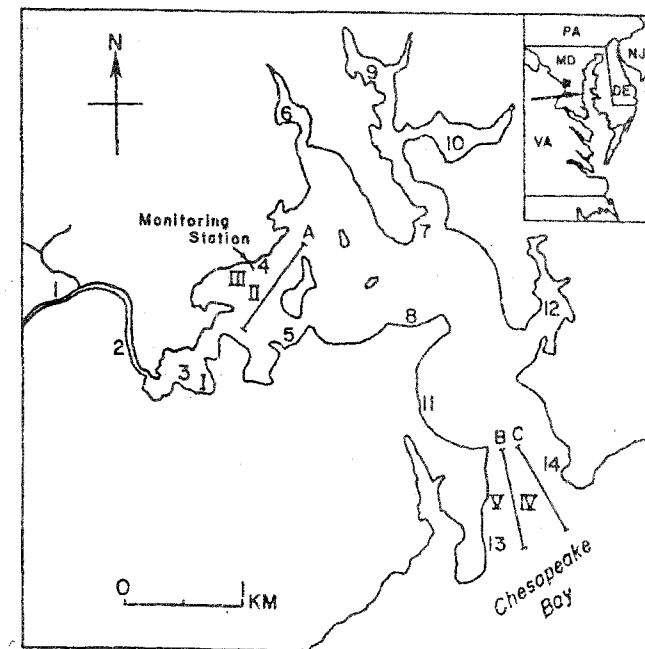


FIG. 1—Map of Rhode River subestuary showing locations of sampling stations. Physical/chemical variables were monitored continuously at the Smithsonian dock. Infaunal invertebrates were sampled at five stations indicated by Roman numerals: mud flat (I); dock mud (II); dock sand (III); river mouth mud (IV); and river mouth sand (V). Nearshore fishes were seined at 14 stations indicated by Arabic numerals. Epibenthic fishes and crabs were trawled along three station lines indicated by letters; dock mud (A); river mouth sand (B); and river mouth mud (C).

measured continuously from April 1970 to November 1985 1 m below the water surface at the Smithsonian dock with a Honeywell, Inc. water quality monitoring system which employs a thermocouple and a temperature-compensated conductance cell for salinity. Vertical profiles of temperature, conductivity, and dissolved oxygen at 0.5-m increments from surface to bottom were also taken irregularly during the biological sampling period from 1979 to 1985 using a Beckman Model RS5-3 electrodeless induction salinometer and a YSI Model 54 oxygen meter.

From October 1979 to April 1985, infaunal invertebrate communities were sampled about six times per year at about bimonthly intervals from late March through early December, except in 1984 when samples were taken only in late spring, summer, fall, and early winter. Infaunal samples were taken in a stratified random design at five stations located in mud and sand sediments at three regions of the subestuary (Fig. 1). The mud flat region had only a mud (10% sand, 90% silt and clay) station located in shallow water (0.5 to 1.0 m), but it was exposed to air on low tides on rare occasions (seven tides in five years).

The remaining stations were subtidal. The dock region had a sand (65% sand, 22% gravel, 13% silt and clay) station located near shore at 1.3 to 1.5 m depth and a mud (1% sand, 99% silt and clay) station at 1.8 to 2.3 m depth. The river mouth region had a sand (73% sand, 27% silt and clay) station at 2.0 to 2.5 m depth and a mud (5% sand, 95% silt and clay) station at 3.0 to 4.0 m depth.

At each station in each sampling period, ten core samples were taken haphazardly within a fixed 900-m² area. Ten cores were more than adequate to sample the infauna, because preliminary analysis during high infaunal densities in spring 1980 determined that 95% of the species present at a station were sampled by the seventh replicate core. From October 1979 to October 1980, a 0.025-m² box core attached to a pole with a remote trigger was used. The core was pushed by the pole into the sediment to a depth of 35 cm in mud and 15 to 20 cm in sand before triggering the jaws. From November 1980 to September 1985, 0.08-m² pipe cores either attached to the end of a pole at mud stations or operated by a diver at sand stations were used. These pipe cores penetrated to a depth of 35 cm in all sediments. Comparison of infaunal densities in ten pairs of box and pipe cores showed no significant differences for any species in either mud or sand habitats (ANOVA, $p > 0.3$). A previous study of vertical stratification [28] indicated that only about 4% of organisms inhabited sediment depths greater than 20 cm. These deep burrowing forms primarily consisted of a small proportion of the polychaete *Heteromastus filiformis* and the clams *Macoma balthica* and *Mya arenaria*. Therefore, changes in sampling method during the study had little, if any, influence on estimates of infaunal density. All cores were sieved on 0.5-mm mesh screen, fixed in 10% formalin, and stained with Rose Bengal. All organisms except oligochaetes and chironomid insect larvae were identified to species and counted under a dissecting microscope. Oligochaetes were all of the genus *Tubificoides*, mostly *T. gabriellae*; but species identification of each individual was not attempted. Chironomid larvae were enumerated as a group.

The abundances of nearshore fish were estimated once per year from 1980 to 1985 on low tides in late June, when the spring reproductive period was completed and migrating juveniles had moved into the estuary. Fish were sampled with a 16-m-long minnow seine made of 7-mm mesh. Three replicate (adjacent) seines were pulled along the shore at 14 stations (Fig. 1). Each seine sampled 33 m of shoreline to a distance of about 10 m from shore. All fish caught were identified to species and counted.

Abundances of epibenthic crabs and fish were estimated monthly with otter trawls (3-m-wide mouth; 5-cm mesh net body; 7-mm mesh cod end liner; tickler chain) from April to November from August 1981 to November 1985. Trawls were pulled for a fixed distance of 900 m on three consecutive days at three stations: one in the dock region (mud bottom) and two at the river mouth (mud and sand bottoms) (Fig. 1). All fish and crabs caught were identified to species and counted.

Statistical analyses used computer software available in the Statistical Analysis System (1984 version). All data on species abundances were \log_{10} transformed

before analysis, but yearly least square means were back-transformed in graphical presentations. The effects of year, station, and year \times station on population abundances were partitioned by ANOVA (shoreline seining data) or ANCOVA (salinity, benthic infauna, and otter trawl data) following the statistical approach of Holland [4]. Seasonal cycles in the population and salinity data were partitioned using the trigonometric functions $\text{SIN}(ct)$, $\text{COS}(ct)$, $\text{SIN}(2ct)$, and $\text{COS}(2ct)$ as covariates, where $c = 2 \times 3.1417/12$ (that is, the constant for converting the time in months to radians) and $t =$ the number of the month of the sample. Patterns of variation between years of infaunal abundance for 1979 should be interpreted cautiously because only a single (fall) sample was taken in 1979. Use of trigonometric functions in ANCOVA adjusts for seasonal biases in the sampling between years; however, extrapolation from only a single sampling period in a year may lead to inaccurate estimates. The fraction of variance attributable to each dependent variable and covariate was determined from the ANCOVAs as the ratio of the Type III sums of squares to the corrected total sums of squares. The use of ANCOVA to test for the effect of salinity on abundances of infaunal and epibenthic organisms is not strictly correct, because monthly mean salinities were paired by month with the abundance samples instead of using independent salinity samples for each trawl or benthic core. However, we judge the short-term (that is, monthly) average salinity to be a better estimate of salinity effects on the biota than instantaneous measurements.

Results

Water Temperature, Dissolved Oxygen, and Salinity

Monthly mean water temperatures exhibited a seasonal cycle every year with a peak of 27 to 28°C in July and a low of 2 to 4°C in January, and differences in the cycle between years of the invertebrate and fish sampling were not significant (ANCOVA, $p > 0.05$) and judged not to be important for the fluctuations in the populations of major species. The shallow mud-flat station often experienced temperatures 2 to 3°C higher than the dock during summer; however, temperature at the river mouth stations did not deviate more than 1°C from that at the dock. A thermocline did not develop and the water column was generally well-mixed throughout the shallow subestuary, except during calm summer days when a continuous 1 to 2°C gradient developed from surface to bottom as surface water heated. Supersaturated oxygen concentrations occurred frequently during midday in summer, and all stations occasionally exhibited anaerobic conditions (1 ppm dissolved oxygen) lasting a few hours during early morning in summer. The daily, seasonal, and between-year variations in oxygen concentration from 1979 to 1985 were not obviously different from those reported for 1970–1978 [27].

Salinities cycled seasonally in a manner typical of lower mesohaline zones of temperate estuaries: the 16-year average monthly low salinity of 5.9 o/oo occurred in May and increased gradually in summer and fall to a 16-year average

monthly high of 11.9 o/oo in November. Seasonal fluctuations accounted for 37% of the total salinity variation. Salinities also differed significantly among years (ANCOVA, $p < 0.0001$). Regional drought during the 1980s resulted in unusually high salinities during the sampling period for invertebrates and fish (Fig. 2). Salinities increased from late fall 1980 to highs of about 16 o/oo in 1981 and a spring monthly low of about 10 o/oo, and elevated salinities persisted until late spring 1983. Salinities in 1984 were near the long-term average, but very high salinities occurred again in 1985. Annual mean salinities for 1981 and 1985 were significantly higher at about 13 o/oo than other years, and 1980, 1982, and 1983 also had significantly higher salinities at about 10 o/oo than other years (Table 1). Lowest salinity years occurred in 1979, 1975, and 1972 in association with tropical storms. Salinity deviation from long-term averages (that is, residuals of the ANCOVA) during the drought period was of the same

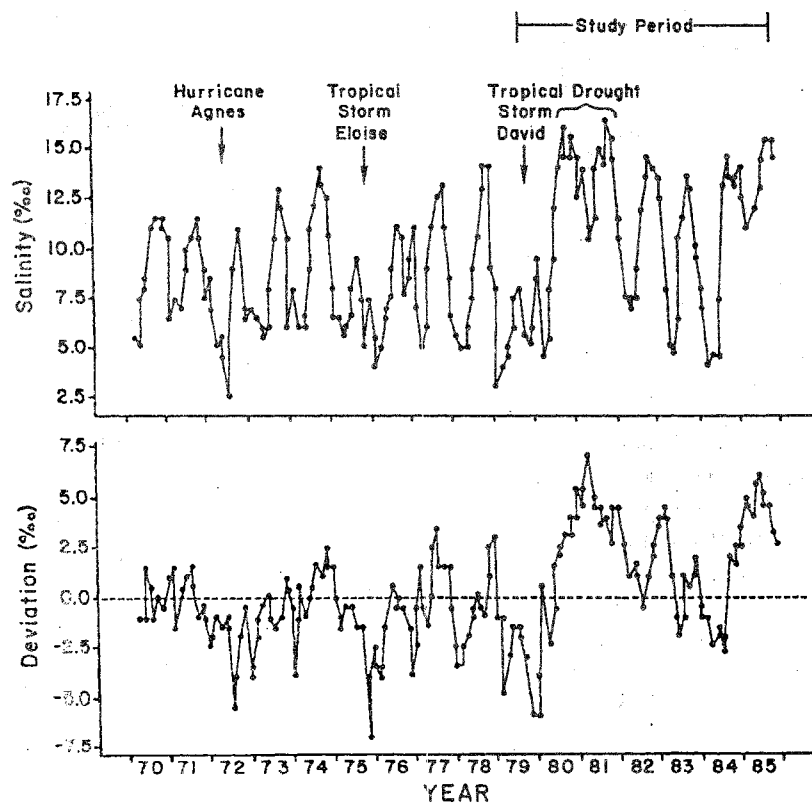


FIG. 2.—Long-term salinity fluctuations in the Rhode River subestuary. Top axis shows mean monthly salinities from April 1970 through April 1985. Bottom axis shows deviations in mean monthly salinity from the long-term season cycle described by trigonometric functions (see Study Site and Methods). Major deviations in salinity are indicated, as is the study period for sampling invertebrates and fish populations.

TABLE 1.—Salinity variation among years from 1970 through April 1985 for the Rhode River subestuary. Yearly means are shown. Horizontal lines indicate means which are not significantly different by Duncan's multiple range test.

Year	1981	1982	1983	1984	1985	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979
Mean salinity (o/oo)	13.7	10.8	10.1	8.6	13.5	8.9	9.1	7.0	8.2	9.3	7.2	7.4	9.6	8.4	5.9

magnitude and much greater duration than the low salinities following the tropical storms (Fig. 2).

Infaunal Invertebrate Populations

Infaunal invertebrate communities were composed of about 40 species (Table 2 and see Ref. 28); however, analysis was restricted to 19 abundant taxa: three clams, eight polychaetes, one oligochaete genus, one nemertean, three amphipods, two isopods, and one insect family. The remaining species occurred so rarely and sporadically that no patterns in their abundance were discerned.

Many species (for example, *Scolecoplepides viridis*, Fig. 3) had seasonal cycles characterized by spring recruitment pulses followed by rapid declines in density during summer as predatory fish and crabs consumed new recruits [29]. Other species (for example, *Polydora ligni*, Fig. 4) showed no predictable seasonal pattern in their population fluctuations. Many species (for example, *Heteromastus filiformis*, Fig. 5) showed large increases in abundance during the drought period from fall 1980 to spring 1983 at some stations but not at others. However, *H. filiformis* and most of the species showing increases in 1981 did not increase during the high salinity period of 1985. Population densities of all the abundant

TABLE 2—Infaunal species list. All species were collected in routine benthic core samples during 1979–1985.

Mollusca	Nemertinea
<i>Congeria leucohaeta</i>	<i>Carinoma tremaphoros</i>
<i>Doridella obscura</i>	
<i>Gemma gemma</i>	Platyhelminthes
<i>Hydrobia minuta</i>	<i>Stylochus ellipticus</i>
<i>Ischadium recurvum</i>	
<i>Macoma balthica</i>	Arthropoda
<i>Macoma mitchelli</i>	<i>Almyracuma proximoculi</i>
<i>Mulinia lateralis</i>	Chironomid spp.
<i>Musculum transversum</i>	<i>Chiridotea almyra</i>
<i>Mya arenaria</i>	<i>Cyathura polita</i>
<i>Tagelus plebeius</i>	<i>Corophium lacustre</i>
	<i>Corophium simile</i>
Annelida	<i>Edotea triloba</i>
<i>Branchiura sowerbyi</i>	<i>Gammarus daiberi</i>
<i>Eteone heteropoda</i>	<i>Gammarus mucronatus</i>
<i>Hellobdella elongata</i>	<i>Leptocheirus plumulosus</i>
<i>Heteromastus filiformis</i>	<i>Melita netida</i>
<i>Hobsonia florida</i>	<i>Monoculodes</i> sp.
<i>Laeonereis culveri</i>	<i>Mysidopsis bigelowi</i>
<i>Nereis succinea</i>	<i>Rhithropanopeus harrisi</i>
<i>Polydora ligni</i>	
<i>Scolecoplepides viridis</i>	
<i>Scoloplos fragilis</i>	
<i>Streblospio benedicti</i>	
<i>Tubificoides gabriellae</i>	

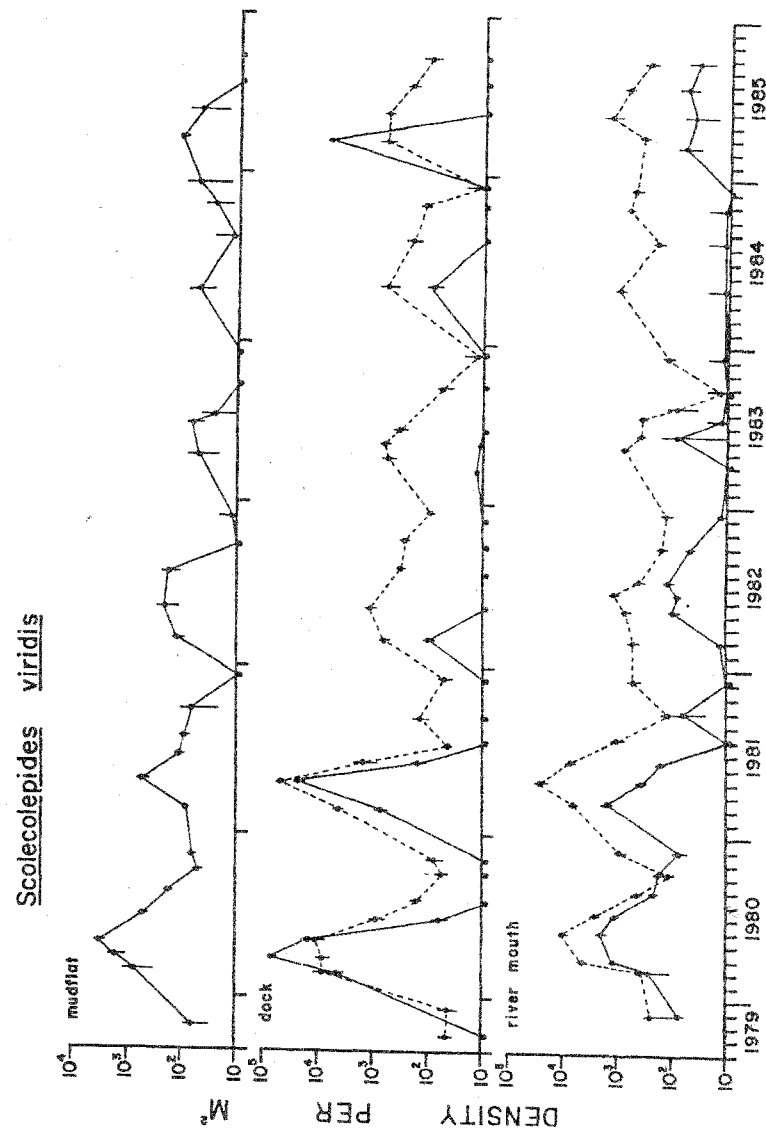


FIG. 3—Population fluctuations of the spionid polychaete *Scolecoplepides viridis*. This is an example of an infaunal species with strong seasonal cycles of abundance. Dashed and solid lines indicate sand and mud stations, respectively.

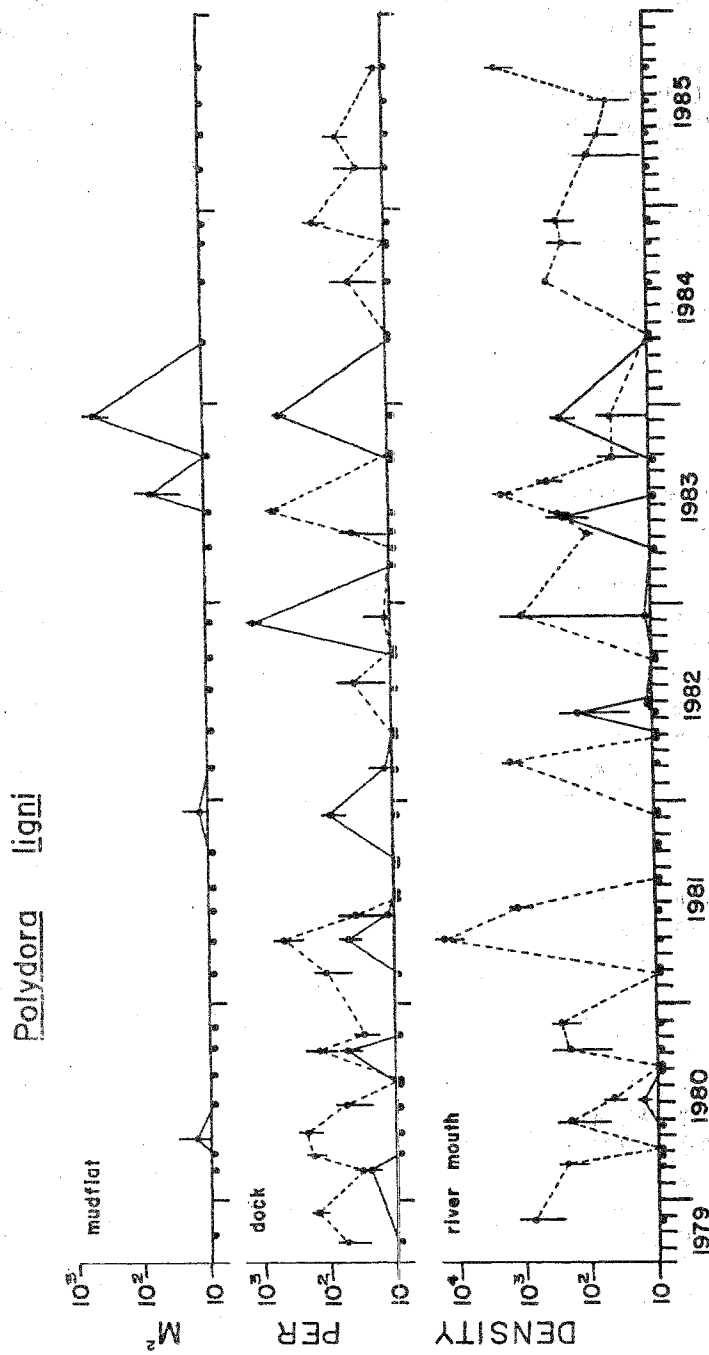


FIG. 4—Population fluctuations of the spionid polychaete *Polydora ligni*. This is an example of an infaunal species without seasonal cycles of abundance. Dashed and solid lines indicate sand and mud stations, respectively.

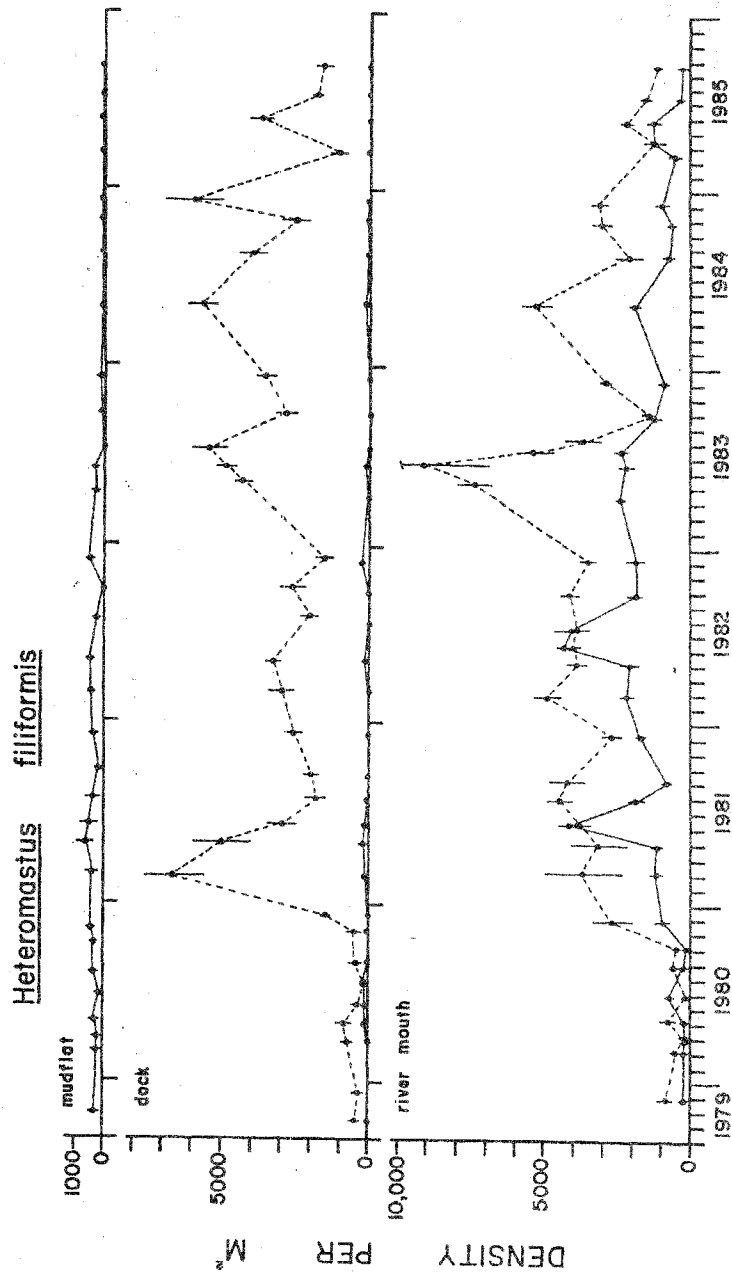


FIG. 5—Population fluctuations of the capitellid polychaete *Heteromastus filiformis*. This is an example of an infaunal species which increased in abundance at some stations but not others during the period of elevated salinities. Dashed and solid lines indicate sand and mud stations, respectively.

species exhibited significant effects of year and station, and all but one species had significant year \times station interactions (ANCOVA, $p < 0.05$; Table 3). In addition, the covariates of the seasonal (trigonometric) cycles were significant for most species (ANCOVA, $p < 0.05$; Table 3). Depending on the species, the ANCOVA models accounted for 12 to 83% (mean = 43%) of the variance in species density (Table 3). However, individual factors only accounted for up to 37% of the variance [for example, effect of station for the polychaete *Heteromastus filiformis* (Table 3)]. The seasonal cycle covariates only accounted for less than 10% of the variance. ANCOVA on each species at each station separately did not account for more of the variance in the data, and there were no obvious patterns in population changes associated with station depth, substrate, or location along the gradient from the river mouth to the mud flat. That is, when seasonal cycles in abundance were partitioned, each station appeared to be independent of the others. Nevertheless, there were marked differences in overall species abundances between years (Fig. 6).

Salinity was a significant covariate in ten of the species and was not significant for nine others, nor for the total abundance of infaunal organisms (Table 3). However, the salinity covariate accounted for at most 5% of the variation in abundance of any species. Many species appeared to increase in abundance during the period of elevated salinity during 1980 to 1983, with a few (for example, *Scolecoides viridis*) showing declines (Fig. 6). However, only *Streblospio benedicti* and *Gammarus tigrinus* showed significant positive and significant negative correlations, respectively, between annual mean abundance and annual mean salinity (Spearman rank correlation on the annual least squares means for species abundance and for salinity adjusted by the ANCOVA models, $p < 0.05$). Analysis of infaunal populations at each station separately did not reveal any consistent spatial or temporal patterns with respect to salinity.

Nearshore Fish Populations

Thirty-three species of fish were caught in the annual shoreline seining surveys from 1980 to 1984 (Fig. 7). Nearly half were rare and sampled only at one or two stations in a single year. Yearly variations in abundance of 16 of the most common species are presented here (Fig. 8). Abundances of all of these species exhibited significant variation among stations across the range of sediment types, shoreline vegetation, and proximity to the Bay (ANOVA, $p < 0.01$). All but one species (*Gobiosoma bosci*) had significant differences among years (ANOVA, $p < 0.01$). All the species except *G. bosci* had significant year \times station interactions (ANOVA, $p < 0.01$), making interpretation of the differences between years difficult. Canonical discriminant analysis (not shown) indicated that stations located in the freshwater creeks tended to be separated from other stations by having greater abundances of freshwater and oligohaline species, but there was extensive overlap of all 14 stations. The four most abundant species (Atlantic silversides, mummichog, spot, and menhaden) in 1980 had

TABLE 3—Fraction of variance (R^2) in infaunal species abundance accounted for by ANCOVA. Year and station are main effects; seasonal cycle and salinity are covariates. All variables are significant ($p < 0.05$), except where indicated by NS.

Species	Model	Seasonal Cycle	Salinity	Station	Year	Year \times Station Interaction
Mollusca						
<i>Macoma bathica</i>	0.55	0.08	NS	0.06	0.21	0.07
<i>Macoma mitchelli</i>	0.32	0.02	NS	0.10	0.01	0.10
<i>Mya arenaria</i>	0.36	0.03	0.01	0.06	0.05	0.10
Annelida						
<i>Eteone heteropoda</i>	0.25	0.06	0.01	0.03	0.05	0.05
<i>Heteromastus filiformis</i>	0.83	0.01	0.01	0.37	0.08	0.09
<i>Hobsonia florida</i>	0.31	0.02	0.01	0.10	0.03	0.10
<i>Laeonereis culveri</i>	0.65	NS	NS	0.34	0.03	0.12
<i>Nereis succinea</i>	0.50	0.01	0.01	0.15	0.04	0.17
<i>Polydora ligni</i>	0.18	NS	NS	0.08	0.02	0.03
<i>Scolecoides viridis</i>	0.58	0.09	NS	0.08	0.10	0.04
<i>Streblospio benedicti</i>	0.28	0.07	0.05	0.02	0.06	0.10
<i>Tubificoides</i> spp.	0.42	0.02	0.01	0.11	0.06	0.10
Nemertinea						
<i>Carinoma tremaphorus</i>	0.43	0.01	0.01	0.16	0.05	0.12
Crustacea						
<i>Cyathura polita</i>	0.50	0.01	NS	0.22	0.02	0.07
<i>Edotea triloba</i>	0.12	NS	NS	0.04	NS	0.03
<i>Corophium lacustre</i>	0.38	0.03	NS	0.09	0.06	0.04
<i>Gammarus tigrinus</i>	0.19	0.03	0.02	0.02	0.03	0.04
<i>Leptocheirus plumulosus</i>	0.66	0.06	NS	0.15	0.05	0.11
Insecta						
Chironomid spp.	0.55	0.03	0.01	0.08	0.10	0.14
Total Organisms	0.59	0.05	NS	0.19	0.07	0.04

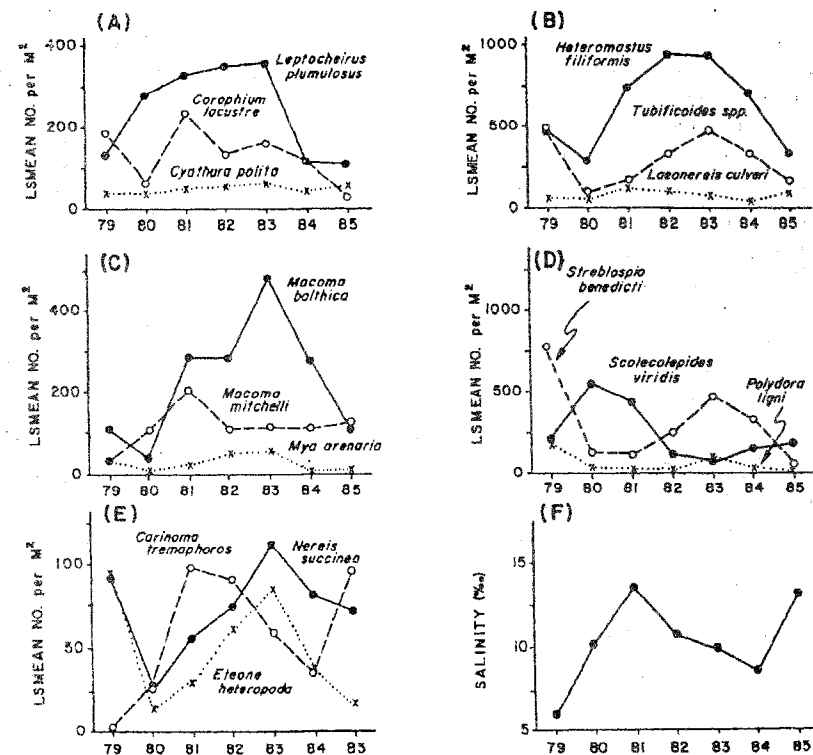


FIG. 6—Interannual changes in population abundances of major infaunal species. Least square means computed by ANCOVA for all stations are plotted for each year. Species are grouped: A = small crustaceans; B = deposit-feeding polychaetes; C = clams; D = spionid polychaetes; E = predatory worms; and F shows mean annual salinity.

significantly different abundances in subsequent years, but they did not appear to show any significant pattern of annual variation with respect to years of elevated salinities. However, chain pickerel (*Esox niger*), a freshwater species which was ranked fifth in abundance in 1980 and present in every seine taken that year, disappeared in 1981 during the high salinity period and did not return in subsequent years. *Fundulus diaphanus* (an oligohaline killifish) and *Anguilla rostrata* (American eel) also declined during the high salinity years. However, while other freshwater and oligohaline species (for example, the sunfish *Lepomis gibbosus* and *L. macrochirus*) showed significant reductions in one or more years, there was no consistent pattern of change with respect to salinity. Only the killifish (*Fundulus heteroclitus* and *F. majalis*) showed trends of increasing abundance from 1980 to 1985.

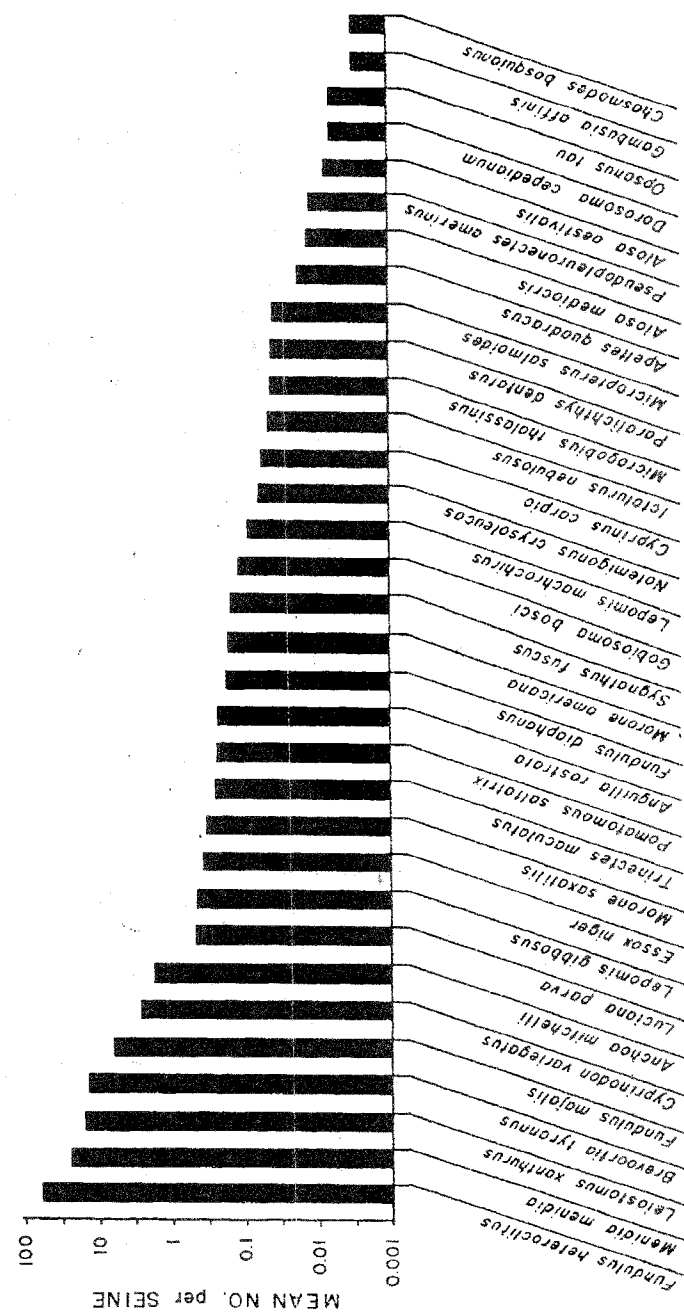


FIG. 7—Species composition of nearshore fish caught in seines during June from 1980 to 1985. Mean number caught per seine at all stations are plotted on a log scale.

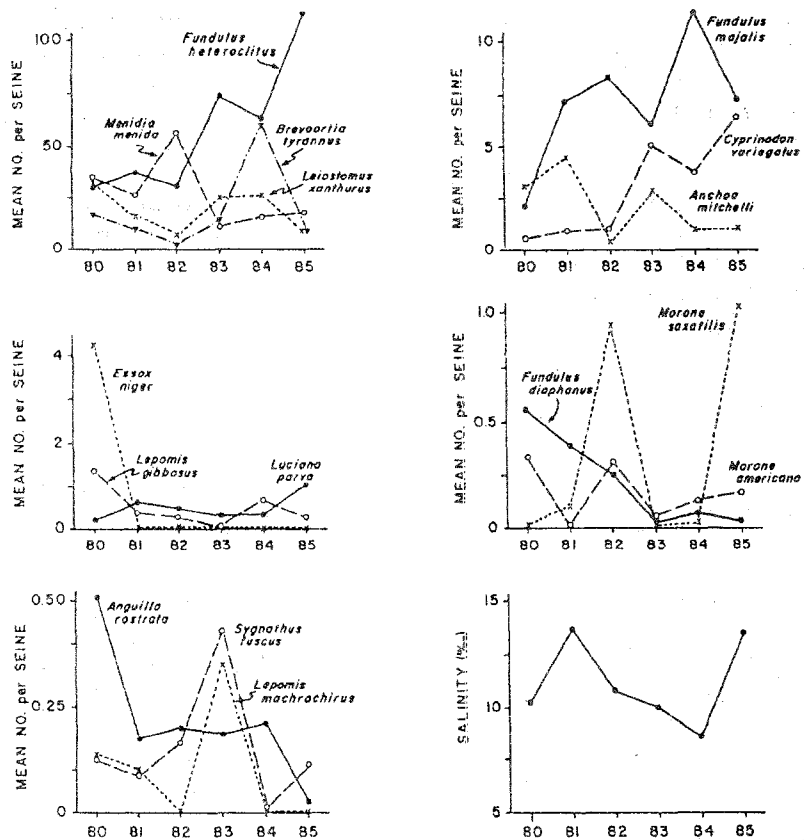


FIG. 8—Interannual changes in population abundances of 16 abundant species of nearshore fish. Mean number per seine for all 14 stations are plotted for each year. Species are grouped by similar abundances. Mean annual salinity is shown in the lower right axis.

Epibenthic Crabs and Fishes

Twenty species of fish and decapod crustaceans were caught in otter trawls from 1981 to 1985. All but five species were rare and occurred only in a few sampling periods. The five common species always comprised at least 90% of the organisms caught per trawl, and four of these species (*Leiostomus xanthurus*, *Micropogonius undulatus*, *Trinectes maculatus*, and *Callinectes sapidus*) comprise the dominant predators on the infaunal community [29]. The catch of epibenthic fish and crabs was highly seasonal (Fig. 9), and seasonal cycle covariates accounted for up to 25% of the variance in catch of individual species (Table 4). There were significant differences among stations in numbers of organisms caught (ANCOVA, $P < 0.01$; Fig. 9), with the dock mud station having consistently lower abundances than the two river mouth stations.

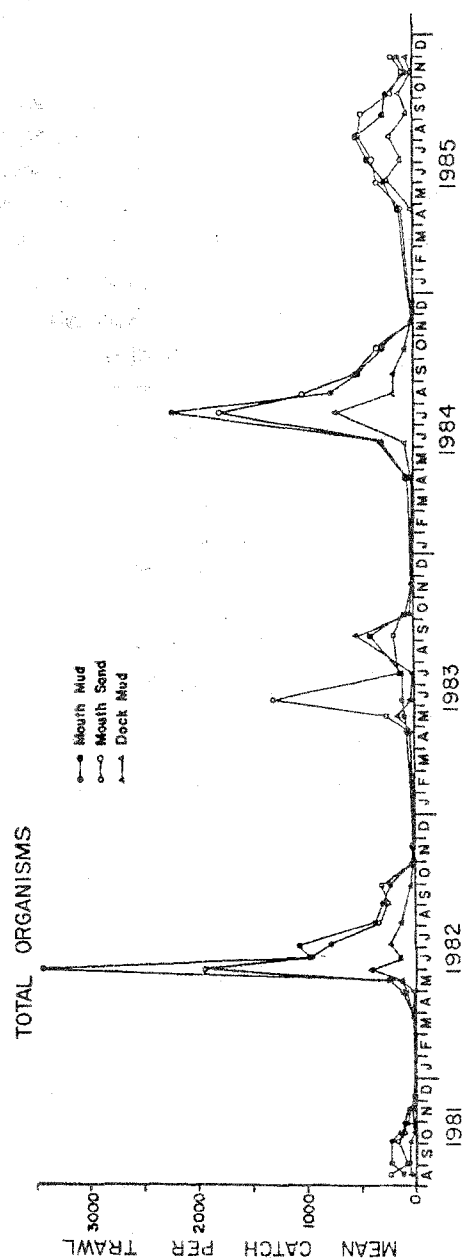


FIG. 9—Annual cycles in abundance of all epibenthic fish and crabs. Mean total numbers of organisms caught per otter trawl at three stations are plotted.

TABLE 4.—Fraction of variance (R^2) in otter trawl catch accounted for by ANCOVA. Year and station are main effects; seasonal cycle and salinity are covariates. All variables are significant ($p < 0.05$) except where indicated by NS.

Species	Model	Seasonal Cycle	Salinity	Year	Station	Year × Station
<i>Leiostomus xanthurus</i>	0.63	0.25	0.01	0.15	0.03	0.01
<i>Trinectes maculatus</i>	0.59	0.08	0.03	0.13	0.31	0.02
<i>Callinectes sapidus</i>	0.64	0.14	NS	0.22	0.17	0.03
<i>Anchoa mitchelli</i>	0.37	0.18	0.06	0.05	0.01	0.02
<i>Microgogonius undulatus</i>	0.59	0.03	0.03	0.42	0.02	0.03
Other species	0.40	NS	NS	0.29	0.02	0.03

Interannual variation in abundance of epibenthic predators was large (Fig. 10). The abundance of spot in 1984 was about five times that in 1981 and about twice that in 1982. The major decrease in spot abundance in 1983 was correlated by an increase in the abundance of croaker (*M. undulatus*), another sciaenid with similar feeding biology, and spot abundance was also relatively low in 1985 when croaker were again common. The abundance of hogchokers (*Trinectes maculatus*) declined from 1981 to 1984, but it rose markedly again in 1985. Blue crabs (*Callinectes sapidus*) exhibited a trend of increasing abundance throughout the study period, whereas abundances of anchovies and "other species" as a group showed no consistent pattern among years. All five main species exhibited highly significant differences among years (ANCOVA, $p < 0.001$; Table 4). All but blue crabs had significant effects of salinity, with salinity accounting for 1 to 6% of the variance in their abundance (Table 4).

Discussion

Population abundances of estuarine animals (infaunal invertebrates, nearshore fish, and epibenthic fish and crabs) in the Rhode River subestuary are extremely variable through time, with most species having severalfold differences among

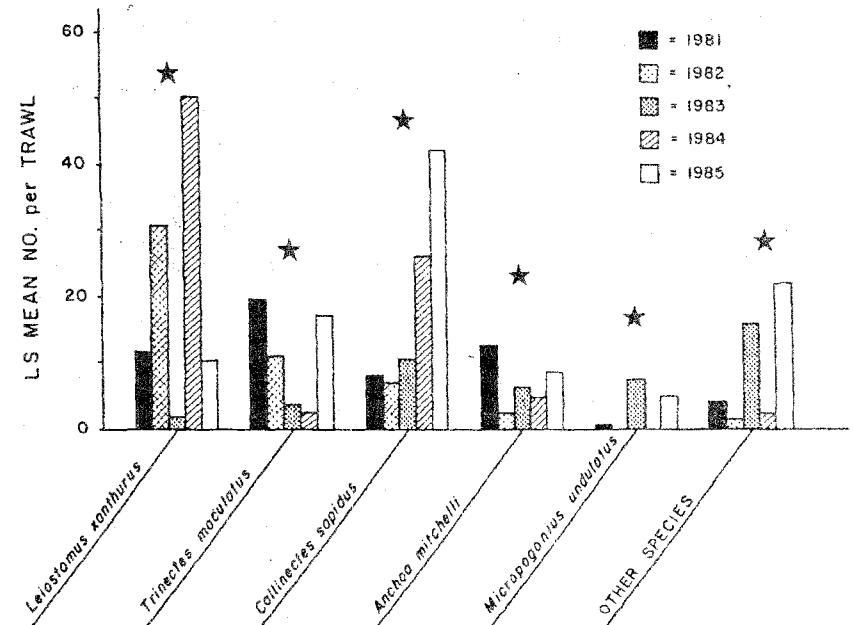


FIG. 10.—Interannual variation in abundance of five major species of epibenthic fish and crabs. Least squares means computed by ANCOVA for all stations are plotted for each year. Stars indicate significant differences in abundance among years (ANCOVA, $p < 0.05$).

years. Only two species (*Edotea triloba* and *Gobiosoma bosci*) did not show significant differences in population abundances among years. Annual variations in population abundances of many estuarine finfish and shellfish are correlated with fluctuations in precipitation and freshwater runoff [4,10,17,30,31]. Measurements of the effects of changes in freshwater inflow have focused primarily on reduced salinities during major storms [11,32,33], whereas the responses of estuarine communities to increased salinities during drought are not as well documented (Ref. 34–36 are exceptions). In our study, half of the infaunal species, several of the nearshore fishes, and four of five epibenthic species showed significant responses to elevated salinities. Nevertheless, our analysis indicated that only a small fraction of variation in any species was explained by salinity changes. Thus, we have the ability to detect significant changes in populations among years, but the remaining problem is to determine the patterns and, ultimately, the causes of these population fluctuations.

Failure to account for more of the population variation by salinity stems from several constraints on our data set. First, temporal variation was confounded by significant, large effects of spatial (station) variation in nearly all of the species. Recently, Holland [4] described long-term responses of many of the same infaunal species in a higher mesohaline zone of Chesapeake Bay about 80 km downbay from our site. Even among stations stratified by depth, sediment type, and salinity zone in a much larger sampling program than ours, he measured significant spatial variation. Thus, the spatial variability observed in our study may not be simply a limitation of the scale of our sampling program, but may be real and typical of the estuarine system.

At the same time, the geographic scale of our sampling was not extensive enough to average out local variation the way regional fishery catch statistics do [37]. Moreover, our study area did not cover a large enough area to reflect distributional shifts in species along a salinity gradient during changes among years in the salinity regime [2]. These distributional shifts may be a major cause of the significant year \times station interactions observed in our study site; but without the ability to measure distributional shifts, it is very hard to interpret these interactions. Our study site is located near the lower boundary of the mesohaline zone (Fig. 11). Elevated salinities during the 1980s shifted the mesohaline zone further into our site (Fig. 11). Since most species occurring in the mesohaline zone are characteristically euryhaline [2,25], elevated salinities at our location appear to have little effect on their abundance. However, salinity reductions of corresponding magnitude would shift the oligohaline zone into our site, which would probably have much greater (especially negative) effects on abundances of many species at our location.

Thus, since most years of our study period were characterized by unusually high salinities, this study may still suffer from the biases of short-term variation. Having a greater sample of years, and especially having data for years in the other extreme of salinity, may add considerable power to regression and correlation analyses of species abundance versus salinity. Fisheries' catch

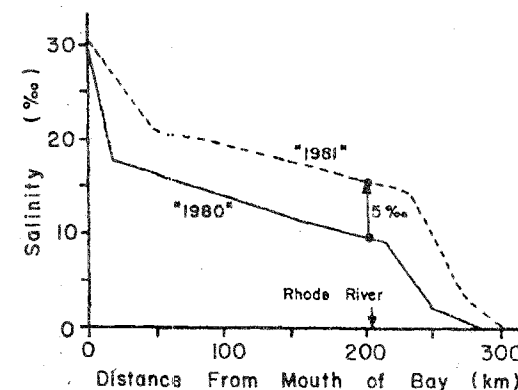


FIG. 11—Salinity profiles along a transect of the axis of Chesapeake Bay from the mouth to the Susquehanna River. The "1980" and "1981" profiles represent a typical summer profile and a profile of elevated salinities during drought, respectively, based on long-term measurements of Chesapeake Bay salinity profiles [39] and on the measured salinity increase at the Rhode River (see Fig. 2).

statistics often span several decades and provide some of the best data on long-term population dynamics of aquatic species. The duration of these data allows evaluation of lagged variables and correlative relationships with sufficient power that long-term trends can be detected and causal mechanisms can be inferred from very "noisy" data [10,37]. However, even data taken over a decade or more may not be long enough. The eleven years of data provided by Holland [4] for infaunal communities in the mesohaline zone of Chesapeake Bay span the extremes of salinity fluctuations in the 1970s and early 1980s illustrated by our Fig. 2, yet parallel statistical models for his longer data set do not explain much more of the variance in species abundances than our five- to six-year data.

Salinity is not the only environmental variable regulating estuarine populations, and our statistical models may be significantly improved by considering additional meteorological and water quality factors, as well as species interactions. Our ANOVA and ANCOVA models copy those of Holland [4], who also considered dissolved oxygen concentration and sedimentary silt-clay content. Although Holland [4] found that these additional factors had significant effects on infaunal populations, the amount of variance accounted for by his models was in the same range as ours (12 to 83%). Multiple regression analysis and stepwise regression analysis have proven to be useful tools in evaluating the importance of large numbers of environmental factors to population abundance. These models accounted for 18 to 83% of the variation in populations of common invertebrates and fishes in a Florida estuary [38] and were often very good at predicting regional population abundances of many species [10]. Even so, 50% or more of the variation of many common estuarine species remained unexplained

in analyses considering over a dozen major variables [38] or lagged variables [10].

One problem with these multivariate approaches is that while salinity is not the only important regulatory variable, it is probably the most important one because most others (for example, freshwater input, nutrients, organic loading, etc.) covary with salinity. Because they are not independent, adding these covariables may not account for much more variation in population abundance than indicated by salinity, although partial correlation analysis can assess the relative contribution of each covariable. Another problem with regression models is that they attempt to explain linear responses, whereas population fluctuations may be largely nonlinear responses to critical, threshold levels of an environmental variable. For salinity, population responses may be markedly nonlinear at around 5 o/oo, resulting in a distributional discontinuity in species distribution between the mesohaline and oligohaline zone. Salinity changes in this range will produce threshold-like responses in species abundance. Similarly, salinity or other variables may affect population abundances primarily during critical periods. Recruitment of sensitive larval stages may be the main determinant of population abundances of many invertebrates and fish [4], so that salinities and other variables are much more important in spring than other times of the year. Species, such as blue crabs (*Callinectes sapidus*) or spot (*Leiostomus xanthurus*), which spawn in the ocean and migrate into the estuary as small juveniles, are likely to be less susceptible to annual variations in estuarine conditions.

The range of fluctuations in estuarine populations indicate the importance of long-term studies for providing: (1) measures of the magnitude of natural variation; (2) measures of change associated with natural and man-made catastrophes and gradual trends; and (3) hypotheses of causal mechanisms controlling population abundances, based on correlative relationships with environmental variables. To be successful, the measurements must be made with consistent methods through time at spatial and temporal scales appropriate for the population dynamics of the species. The value of the data for estuarine communities lies in their contribution to understanding mechanisms of long-term fluctuations throughout the food web [3]. In ecosystems as variable as estuaries, data records spanning decades will probably be necessary to provide measures of change meaningful to managers.

Acknowledgments

We thank the following people for many hours of field assistance and sorting: Kathy Paige, Paul Seelbach, John Young, Martha Cousar, Craig Kelly, Mark Tedesco, Mark Haddon, James Schafer, and Romuald Lipcius. A. Fred Holland provided helpful advice on statistical approaches and valuable discussion about the problems of evaluating long-term data in estuarine ecosystems. A. Fred Holland, Kent Mountford, and an anonymous reviewer provided helpful comments on the manuscript. We are grateful to Terence Boyle for the opportunity

to present this paper. This work was funded in part by grants from the Smithsonian Environmental Sciences Program, Smithsonian Work/Learn Internship Program, Smithsonian Fluid Research Fund, and from the Maryland Department of Natural Resources.

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