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**Levin, Lisa Ann**

**THE ROLES OF LIFE HISTORY, DISPERSAL AND INTERFERENCE  
COMPETITION IN THE POPULATION AND COMMUNITY STRUCTURE OF  
A DENSE INFAUNAL POLYCHAETE ASSEMBLAGE**

*University of California, San Diego*

**PH.D. 1982**

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UNIVERSITY OF CALIFORNIA

San Diego

The Roles of Life History, Dispersal and Interference Competition  
in the Population and Community Structure of a  
Dense Infaunal Polychaete Assemblage

A dissertation submitted in partial satisfaction of the  
requirements for the degree Doctor of Philosophy  
in Oceanography

by

Lisa Ann Levin

Committee in charge:

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1982



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1982

Dedication

To my parents - Florence and Herb,  
for providing the building blocks  
of love and education.

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- "Drift tube studies of bay-ocean water exchange and implications for larval dispersal." *Estuaries*, 1982. (In Press)
- "Interference interactions among tube-building polychaetes in a dense infaunal assemblage." *J. Exp. Mar. Biol. Ecol.*, 1982. (In Press)
- "Bottom's up: juvenile terebellid polychaetes feeding in the water column." *Bull. So. Calif. Acad. Sci.* 80(3): 1982. (In Press) (with P.R. Greenblatt)
- "Do sea urchins and abalones compete in California kelp forest communities? International Echinoderm Conference, September 1981. (In Press) (with M.J. Tegner)

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ABSTRACT OF THE DISSERTATION

The Roles of Life History, Dispersal and Interference Competition  
in the Population and Community Structure  
of a Dense Infaunal Polychaete Assemblage

by

Lisa Ann Levin

Doctor of Philosophy in Oceanography

University of California, San Diego, 1982

Professor Paul K. Dayton, Chairman

The roles of life history and behavior in the dynamics of dispersal, recruitment and population maintenance were investigated for a dense infaunal polychaete assemblage on the Kendall-Frost mudflat in Mission Bay, California. Polychaete life history features provided the framework for investigations of (1) the relevant scales and mechanisms of dispersal, (2) response to disturbance, and (3) the spatial and

temporal predictability of species abundances in the plankton, during recruitment, and in the benthos. Field and laboratory studies of the Kendall-Frost polychaete species Pseudopolydora paucibranchiata Okuda, Polydora ligni Webster, Rhynchospio arenicola Hartman, Streblospio benedicti Webster, Exogone lourei Hartman, Fabricia limnicola Hartman and Capitella capitata Fabricius, revealed many shared life history traits which limit the spatial extent of dispersal. These include annual life cycles, small size, brood protection, small brood size and reduced or facultative planktonic larval stages.

Hydrographic studies and larval plankton distributions support the contention that dispersal is limited. Salinity and temperature gradients, and dye, drogue and drift tube trajectories demonstrated sluggish back-bay circulation. Most larvae released on the Kendall-Frost mudflat remain in the back of Mission Bay, where dispersal is constrained to small-scale oscillations in back waters or movements over the mudflat itself. Long distance transport between bays is minimal; drift tube releases and spionid larval distributions indicate a 3% probability of transport out to sea for planktotrophic larvae originating on the mudflat. However, larvae which do leave the bay may experience longshore transport 100 km or more to the north or south, particularly during winter storms.

Small-scale dispersal was examined by studying patterns of larval availability, recruitment into settling cartons and colonization of defaunated sediments. Polychaete distributions in the plankton and larval recruitment exhibited strong spatial and temporal variation including seasonal, lunar and diel cycles. Small-scale disturbance, commonly

generated on the mudflat by ray foraging and human activities, was studied by artificially defaunating small ( $< 1 \text{ m}^2$ ) sediment patches; a severe storm and consequent raw sewage spill created an episodic large-scale perturbation. Analyses of species' responses revealed colonization ability to be distinct from dispersal ability. Rates and mechanisms of colonization were governed by larval development, settlement and mobility patterns and varied with the scale of perturbation. For Streblospio, Exogone and Fabricia, factors such as brood protection, reduced or flexible pelagic larval phases, and post-larval movements, particularly by brooding adults, confer small-scale dispersal abilities which permit rapid colonization of disturbed patches and result in maintenance of high infaunal densities (over  $200,000/\text{m}^2$ ). Pseudopolydora and Polydora possess planktotrophic, long-lived larvae whose planktonic abundances are highly seasonal and variable from year to year. The timing of disturbance must coincide with periods of peak larval availability for successful colonization by these species. In general, the annual life cycles and flexible small-scale mobilities of most species confer substantial community resilience.

Within the dense assemblage, intra- and interspecific behavioral interactions appear to mediate spatial pattern and influence the relative success of surface feeding species. The presence of dense Pseudopolydora or Fabricia tubes inhibits recruitment of Pseudopolydora larvae. Intraspecific territoriality in Pseudopolydora, manifested as uniform tube spacing and aggressive palp contact, is initiated during settlement and enhanced during subsequent interaction. Interspecific

interference by Pseudopolydora causes withdrawal and loss of foraging time in Streblospio and Fabricia.

These findings demonstrate that interference competition, life histories and dispersal influence population and community structure in Mission Bay and are probably of general ecological and evolutionary significance in most infaunal communities.

CHAPTER I  
INTRODUCTION

"Spatial heterogeneity and the potential for dispersal fundamentally alter species' interactions and dynamics and are essential considerations in the species' evolutionary relationships to the environment" (Levin, 1976). Though these concepts were clearly present in the thinking of Darwin and Wallace, their incorporation by ecologists into theoretical and field-oriented investigations is relatively recent. Marine systems played a leading role in development of these ideas as an early interest in the origins of spatial patchiness in oceanic plankton populations (Kierstead and Slobodkin, 1953; Hutchinson, 1963) grew into one of the central themes in biological oceanography today (Steele et al., 1978).

Marine scientists have understood for many years that benthic organisms live in a heterogeneous environment (Petersen, 1913) but the importance of dispersal within and between habitat patches has been largely ignored in field studies. (A notable exception to this is the work of Thorson (1946, 1950) ). This is surprising considering that benthic marine organisms possess complex life cycles often involving a planktonic larval stage with obligate dispersal. Theoretical ecologists commonly incorporate patch structure and dispersal in models investigating population stability (Roff, 1974), predator-prey interactions (Crowley, 1981), and competitive coexistence (Levins and Culver, 1971), while field ecologists have been slow to address the issue of dispersal. However, the slow realization that the mature stages are not necessarily those most critical in regulating populations or structuring communities

has spawned new interest in the roles of life history and dispersal in structuring benthic assemblages. The sequence of events associated with larval development, dispersal, habitat selection, settlement, metamorphosis and establishment of post-larvae, may dictate recruitment success and be the dominant factors structuring communities. The numerous recent symposia concerned with invertebrate reproduction and larval ecology (Crisp, 1971; Hrs-Brenko and Costlow, 1974; Chia and Rice, 1977; Stancyk, 1980; and Sulkin, 1981) attest to the growing emphasis on life histories.

### Dispersal

Cole, in 1954 states "... the way in which differences between the life histories of species may result in different characteristics of their populations has remained relatively unexplored." A generation later this remark remains true for life history traits affecting dispersal in marine organisms. My thesis addresses this problem in a comparative investigation of the role of life history and associated dispersal properties in the population maintenance and community patch dynamics of a dense infaunal polychaete assemblage.

The study of larval dispersal essentially began many years ago when Thorson pointed out the need to consider the reproductive and larval ecology of marine bottom invertebrates (1946) and their relation to ocean circulation (1961). Thorson's (1946) collections of invertebrate larvae in the North Atlantic and Johnson's (1939, 1960) surveys of crab and lobster larvae off southern California demonstrated the close association between larval distributions and current patterns. Scheltema's (1968, 1970, 1971a, 1974) collections of "teleplanic" (long distance)



larvae across the North and Equatorial Atlantic Ocean are among the geographically most extensive studies of this nature. Scheltema (1971b, 1974) compared larval distributions with drift bottle data for the same regions and was able to estimate rates of dispersal and consider the implications for population maintenance, gene flow and range extension. Investigations of invertebrate larvae in the Norwegian and Barents Sea (Mileikovsky, 1968) and fish larvae in the California Current (Parrish et al., 1981) also suggest an important role for large-scale current and surface drift patterns in larval transport.

In situations where larval distributions in the plankton are not known, studies of larval development have been matched with knowledge of advection and diffusion of ocean water to infer dispersal potential (Efford, 1970; Jackson and Strathmann, 1981). The extension and establishment of coastal populations of intertidal species have sometimes been attributed to coastal currents, as is the case for the molluscs Littorina littorea (Kraeuter, 1974), Littorina saxatilis and Mytilus edulis (Wells and Gray, 1960).

Many of the studies mentioned above have shown that larvae may remain viable in the plankton for long periods and are capable of dispersing over great distances. The advantages of such teleplanic, or long-distance dispersal have been treated theoretically (often speculatively) in considerations of energetic (Chia, 1971, 1974; Crisp, 1974; Strathmann, 1977; Vance, 1973), genetic (Crisp, 1979; Scheltema, 1971b, 1975; Strathmann, 1974), evolutionary (Hansen, 1978; Scheltema, 1977, 1978; Shuto, 1974), and ecological (Obrebski, 1980; Palmer and Strathmann, 1981; Scheltema, 1977; Strathmann, 1974; Strathmann and Vedder, 1977, 1981; and Vance, 1976) implications. These investigations lead to

the conclusion that long-distance dispersal may be rendered highly adaptive by a variety of environmental or genetic conditions associated with habitat heterogeneity or instability, resource competition and genetic mixing. However, in its present state, dispersal theory cannot yet explain the variation in dispersal abilities among benthic marine organisms.

Estuarine studies have been among the most successful attempts to associate larval dispersal with population maintenance. These investigations are often related to management of commercially valuable species (Sandifer, 1975; Seliger et al., 1982) and include synoptic studies of physical and biological factors influencing larval dispersal (Seliger et al., 1982). Carriker (1951) was one of the first to make extensive field studies of larval distributions in relation to bay circulation, but he was not able to link dispersal to maintenance of bivalve populations. However, Ayers' study (1956) of clam populations in Massachusetts does define the role of larval dynamics in population maintenance. He concluded, from a model based on bay flushing rates and postulated larval survivorship, that the Mya arenaria population in Barnstable Harbor loses most of its larvae to the open ocean and is dependent on larval immigration from nearby harbors for recruitment.

Estuarine larvae, particularly long-lived feeding forms (like Mya in Ayer's study), are subject to transport out to sea by tidal or river flushing. Numerous investigators have invoked larval behavior to explain larval retention in estuaries (see Sulkin, 1981 for a symposium devoted to the topic). Larval retention by behavioral regulation of vertical distribution in the estuarine water column has been documented for barnacle larvae (Bousefield, 1955), bivalve larvae (Wood and Hargis,

1971), polychaete larvae (Daro, 1977), crab larvae (Foreward and Cronin, 1980; McConaugha et al. 1981; Sandifer, 1975; Stancyk and Christy, 1981) and fish larvae (Edmands, 1981). Larvae adjust their vertical position relative to vertically stratified water masses and tidal oscillations with the effect of influencing local dispersal while avoiding transport out to sea. Behavioral retention mechanisms have also been described for dinoflagellate (Tayler and Seliger, 1978) and copepod (Trinast, 1975) populations in estuaries.

Passive mechanisms utilizing hydrographic features have been proposed to retain both mero- and holoplanktonic forms in estuaries. DeWolf (1973, 1974) explains retention of barnacle cyprids by mechanical density differences between larvae and seawater. In considerations of tidal flushing, Ketchum (1954) defines estuarine exchange ratios which permit passive maintenance of phytoplankton populations growing at a specified rate, and Miller (1982) describes estuarine null points behind which zooplankton populations are passively maintained. Like coastal systems, circulation may drive larval transport and subsequent recruitment in estuaries as well. Seliger et al. (1982) explain differences in oyster settlement in 2 tributaries of Chesapeake Bay by differential river flow. Estuarine water masses, isolated by sluggish circulation, will retain larvae and create distinct back-bay invertebrate assemblages, as was documented for polychaetes in the Elkhorn Slough, California (Jong, 1980; Oliver and Jong, 1981). This mechanism also appears to operate in Mission Bay, California (Chapter II) where polychaete larvae oscillate with the tides in the back regions of the bay until settlement (Chapter III). It is likely that for many species both passive

and behavioral phenomena are involved in maintenance of estuarine populations (Jacobs, 1968).

Nearshore as well as estuarine species appear to actively facilitate retention near the parent population. Adult and larval behaviors which utilize tidal and gyral features to prevent dispersal offshore have been documented for coral reef fish (Johannes, 1979), fish in the California Current (Parrish et al., 1981) and reef zooplankton (Aldredge and Hamner, 1980; Hamner and Hauri, 1981).

Most dispersal studies consider fairly long-lived planktonic forms. Less attention has been directed towards the dynamics and adaptive significance of benthic and very short-lived planktonic larval stages, many of which involve brood protection. Both Pechenik (1979) and Caswell (1981) have attempted to model the existence of evolutionarily stable "mixed" life histories (those involving a brooded and pelagic stage). Species with considerable brood protection and short-lived larvae are often assumed to be poor dispersers. However, recent studies have demonstrated that species with mixed development are the best infaunal colonizers in many disturbed situations (Grassle and Grassle, 1974; Santos and Simon, 1980). This is also true of the Mission Bay polychaetes, all of which are small, annual species with mixed development.

Brooding and reduced dispersal ability have been repeatedly associated with very small organisms (Chia, 1974; Strathmann and Strathmann, 1982). This size trend has been demonstrated for meiofauna (Swedmark, 1964), asteroids, ophiuroids, bivalves, chitons, slipper limpets, octopuses (Strathmann and Strathmann, 1982), and polychaetes (pers. observation). Possible explanations for this pattern include

considerations of allometry, energetics of egg production and larval development, and implications for dispersal and recruitment.

The above discussion has reviewed important aspects of dispersal by larvae. However, it is important to note that post-larval movements in the plankton may result in significant small-scale dispersal for benthic organisms. Post-larval stages often adopt dispersive behavior when planktonic larval stages are reduced or absent, or when reproduction and larval development occur somewhere other than the adult habitat. This latter situation is seen in species of nearshore fish, shrimps and crabs whose juveniles develop in estuaries. As with larvae, post-larval juveniles and adult stages may actively swim up from the benthos into the water column or be passively resuspended by tidal scour or current action. Sometimes post-larval organisms attach themselves to surface films or floating objects and also are dispersed passively. This is known to occur in a variety of molluscs: Mytilus edulis (Nelson, 1928), other bivalves (Siggurdsson et al., 1970), Hydrobia ulvae (Levinton, 1979), and nudibranchs (Swennen, 1961). Fouling organisms on wood or ships are also dispersed in this manner.

#### Recruitment

Larval availability in the plankton does not ensure that the larvae are competent to or likely to settle at a given locale. Several conditions must be met before successful recruitment can occur. First, larvae must choose to settle. Many physical and biological factors influence larval habitat selection (see Scheltema, 1974; Crisp, 1974; and Campbell and Meadows, 1972 for reviews of the topic and Chia and Rice, 1977 for more recent work), and once substrates are chosen,

settlement may be thwarted by behavioral interference, predation, or structural interference from surface feeding species (Rhoads and Young, 1971; Woodin, 1976). Artificial settling containers provide a means to experimentally test for larval availability, habitat selection, recruitment success, and the life history stages active in small-scale colonization. Settling apparatus and defaunation studies have been used successfully to make inferences about larval movements in Elkhorn Slough (Hannan, 1981; Jong, 1980) and colonization abilities on the Florida coast (Dauer and Simon, 1976; Santos and Simon, 1980a, b).

#### Evolution and Population Genetics

The implications of dispersal for the evolutionary processes of differentiation, speciation, range extension and extinction are far-reaching. Hansen (1978), Scheltema (1977) and Shuto (1974) noted that in the paleontological record, species lacking planktonic larval stages have shorter geographic ranges and higher extinction rates. Population genetics and ecology have been combined in studies of extant species to identify the genetic consequences of different larval development modes and associated dispersal abilities. Dispersal potential on the appropriate scales does not assure that genetic exchange actually occurs among populations. Electrophoresis provides a method for assessing both the amount of larval exchange which does occur and its genetic consequences. Existing electrophoretic data suggest that the degree of population differentiation is inversely related to the length of pelagic larval life in benthic invertebrates (Burton and Feldman, 1981; Hedgecock, 1981). Benthic species with long-lived planktonic larvae such as Mytilus edulis (Milkman, 1971), Balanus

balanoides (Levin, 1974), Littorina littorea (Berger, 1973), Crepidula fornicata and C. plana (Ament, 1980) show considerable geographic uniformity, probably at least partially due to long-distance dispersal abilities. Species which brood their young and have reduced planktonic stages, such as Littorina obtusata, Littorina saxatilis (Berger, 1973), Schizoporella errata (Gooch and Schopf, 1971), Crepidula convexa (Ament, 1978) and Pileolaria pseudomilitaris (Beckwitt, 1981), exhibit strong geographic variation, implying low level dispersal.

Recent electrophoretic research suggests that gene frequencies of larvae may be compared to those of adult populations to identify larval origins and effects of selection (Gooch, 1978; Orr *et al.*, 1982). Despite these advances, electrophoretic techniques remain relatively unexploited in the study of dispersal.

#### Disturbance

Much of the spatial heterogeneity observed in marine systems is attributable to physically or biologically generated disturbance. Disturbance has been implicated as a major structuring agent in marine environments as diverse as the rocky intertidal (Dayton, 1971; Levin and Paine, 1974; Osman, 1977; Sousa, 1979), coral reefs (Connell, 1978; Vermeij, 1978), shallow sands and muds (Johnson, 1970; Pearson and Rosenberg, 1978; Oliver, 1979; and Brenchley, 1981), and the deep sea (Dayton and Hessler, 1971, but see Grassle and Sanders, 1973; Turner, 1977; Craig Smith, pers. comm.). Localized disturbance may create patches in which existing organisms are disrupted and temporal successional sequences are renewed. When such events are frequent, the habitat becomes a mosaic of patches in different successional stages with impor-

tant consequences for community equilibrium, species diversity, population persistence and life history and dispersal strategies.

Thistle (1981) and Dayton and Oliver (1980), in reviewing disturbance studies in soft sediments, emphasize the importance of scale (as does Jumars, 1978), particularly the aerial extent and the frequency of disturbance, in interpreting responses of communities and their component species. Large-scale, episodic disturbances, such as tropical storms (Boesch et al., 1976; Rees et al., 1977), cold kills (Dahlberg and Smith, 1970), anoxia (Edwards, 1979; Leppakoski, 1971; Santos and Simon, 1980b; Simon and Dauer, 1972), and oil spills (Grassle and Grassle, 1974; and Sanders et al., 1980) are known to alter infaunal community composition. Disturbance of lesser magnitude, e.g. deposition of dredge spoils (Oliver et al., 1980) or canyon slumps (Van Blaricom, 1978), and very localized perturbation, such as that generated by epibenthic foragers (Van Blaricom, 1978; Brenchley, 1981) or fecal mounds of subsurface burrowers (Thistle, 1980b; Ronan, 1975) may also structure infaunal assemblages and contribute to the mosaic nature of the habitat.

The scale on which disturbance is perceived, and therefore the response of organisms to perturbation, is dependent on the size and mobilities of the resident species. Grassle and Grassle (1974) found polychaete life histories to be the major determinant of success in recolonization of sediments following a devastating oil spill. In Sousa's (1980) study of algal succession in disturbed boulder fields, life histories again dictated species' response and tolerance to disturbance. In concurrence with these studies, my investigations in Mission Bay reveal that life histories conferring flexible dispersal abilities



over short distances permit many members of the Kendall-Frost polychaete assemblage to respond rapidly to small-scale sediment disruption.

#### The Thesis: Introductory Remarks

Ecologists have recognized the patchy and variable nature of marine assemblages for many years, but it is only recently that marine communities have been studied as dynamic rather than static systems. The preceding literature review was intended to survey investigations pointing to the mechanistic importance of life histories, dispersal and disturbance in structuring marine systems. The blending of techniques from oceanography, experimental ecology, ethology, developmental biology and population genetics offers a new, multidimensional view of these dynamic processes.

The polychaetes of the Kendall-Frost Reserve in Mission Bay, California present an optimal system for the study of life histories, dispersal and their implications. Polychaetes are the dominant intertidal taxon and are easily maintained in the laboratory. They represent a group of closely related co-occurring species which exhibit a wide spectrum of life history patterns. These species are survivors in a frequently disturbed, shrinking habitat which is isolated by coastline physiography from similar habitats and assemblages. The fine-grained patchiness of the sediments and large-scale isolation of the habitat permit the study of dispersal over several spatial scales.

This dissertation addresses 2 facets of structure in the Mission Bay infaunal polychaete assemblage: (1) the roles of life histories and associated dispersal properties in population maintenance and habitat patch dynamics and (2) effects of competitive interactions on community

composition and spatial structure (the literature relevant to this problem is reviewed in Chapter VI). Both of these features are essential to an understanding of the community dynamics of dense infaunal assemblages.

The first part of this dissertation (Chapters II through IV) presents information acquired to define the relevant time and space scales and mechanisms of dispersal for 7 polychaete species in the Kendall-Frost community. Chapter II introduces the history, geography, and hydrography of Mission Bay. It presents studies of water column structure, tidal circulation, flushing rates and ocean currents in Mission Bay and along the southern California coast. Salinity and temperature measurements, and drift tube, dye and drogue releases provide hydrographic information necessary to infer within and between bay dispersal potential for polychaete larvae originating on the Kendall-Frost mudflat. The latter part of Chapter II focuses on the Kendall-Frost habitat and its polychaete assemblage.

Chapter III presents plankton studies in Mission Bay. Larval distributions, used to verify dispersal trajectories suggested by hydrographic studies, are described from both large-scale plankton sampling conducted quarterly for 1 year throughout Mission Bay, and small-scale sampling in waters overlying the Kendall-Frost mudflat. This chapter also contains analyses of spatial and temporal (annual, seasonal, lunar and diel) distribution patterns for polychaete larvae and other meroplankton present in the mudflat water column.

Shifting from the water column to the sediments, Chapter IV describes laboratory and field studies of polychaete life histories, settlement, and colonization, as well as monthly surveys of recruitment

and benthic infaunal abundances. Laboratory rearing experiments were conducted to estimate larval development times in the plankton, larval behavior, duration of the competent (ready to settle) period, and more importantly, the variability in these traits. These results (presented in Chapter IV) are used to interpret hydrographic and larval distribution patterns and lead to the conclusion that for most polychaete species, dispersal is limited primarily to the Kendall-Frost mudflat itself. Electrophoretic studies, described in Appendix Four, were designed to examine the consequences of dispersal (or lack of it) for the genetic structure of southern California polychaete populations. These genetic investigations revealed a considerable lack of polymorphism in most species surveyed, preventing (between) species comparisons of population differentiation between bays.

Small-scale dispersal was investigated through studies of larval and adult availability in the Kendall-Frost plankton (Chapter III) and larval settling behavior, colonization patterns and benthic distributions on the mudflat (Chapter IV). Artificial settling tray and patch defaunation experiments revealed mechanisms of species' response to both fine-grained disturbance (such as that caused by ray feeding and human trampling) and a large-scale perturbation (a severe storm and sewage spill in early 1980). The different hydrographic, plankton and benthic investigations are drawn together in Chapter V to summarize species-specific life history and dispersal patterns and their implications for population and community dynamics.

Chapter VI addresses behavioral interactions among tube building, surface feeding polychaete species. The roles of settling behavior, territoriality, and interference interactions in defining

intra- and interspecific spatial structure are investigated using nearest-neighbor analysis, field experiments and quantitative behavioral observations made in the laboratory. These studies are presented as 2 separate papers in publication format.

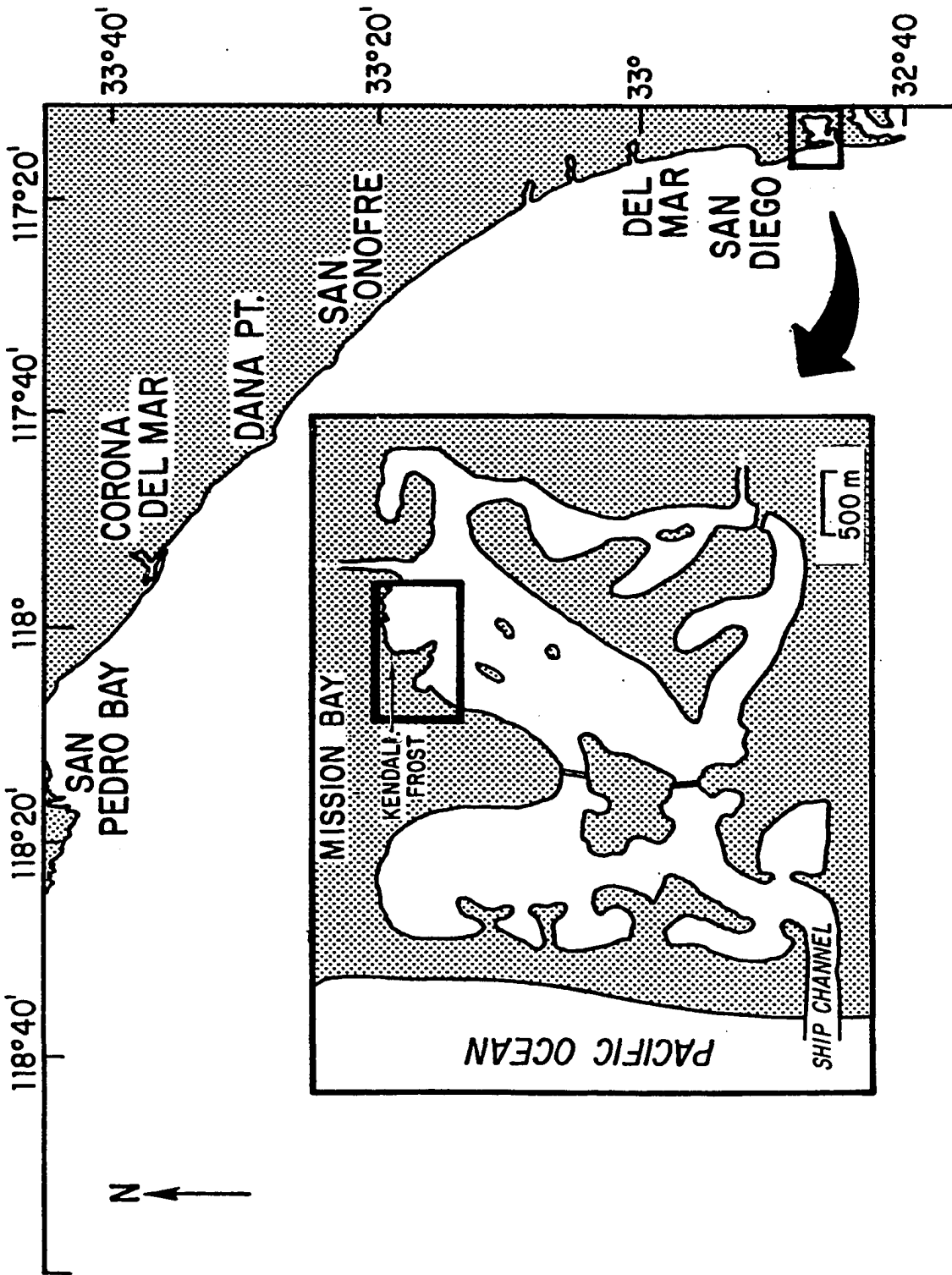
The final chapter, Chapter VII, summarizes the findings of this dissertation and their implications. I also consider the benefits and limitations of the approaches adopted in this study, and conclude with a synopsis.

CHAPTER II  
MISSION BAY DESCRIPTION

This chapter provides introductory information about the Mission Bay environment and the Kendall-Frost polychaete community, the subject of this thesis. In order to understand the various factors influencing the polychaete assemblage under investigation, it was necessary to first consider the history of Mission Bay and then the hydrographic features of the bay in its present configuration. The first section in this chapter introduces the general features of Mission Bay and discusses historic records of the human modifications of the bay physiography. The next section presents information about temperature, salinity, flushing and circulation patterns in Mission Bay. These data were collected over a three year period to assist in determining dispersal trajectories of polychaete larvae originating in the back reaches of Mission Bay. The final section introduces the Kendall-Frost Marsh Reserve, located in the back of the bay. I describe the general species composition of the mudflat infaunal community and the grain size and disturbance characteristics of the mudflat sediments. The seven polychaete species which dominate the infaunal community and form the basis of this investigation are introduced, with a detailed discussion of their life styles, feeding habits and geographic distributions.

Mission Bay is a well-mixed shallow estuary located in southern California, 14 miles north of the U.S. - Mexico border (Figure 1). The bay receives little fresh water input except during heavy rains (December - March). Rose Canyon Creek and Tecolote Creek are currently the only two sources of fresh water.

**Figure 1: Location of Mission Bay in southern California**



Circulation in the bay is driven by tides. Mean tidal excursion is 3.8 ft with extremes of -2.5 and +7.0 ft. Mean tidal height is +2.8 ft (Herron, 1972). Tides are mixed, semi-diurnal. Extreme low water occurs at night in summer and during daylight hours in fall and winter. Tidal fluctuations in Mission Bay resemble those along the open coast, with low tide occurring 12 minutes later at Crown Point than San Diego.

### History

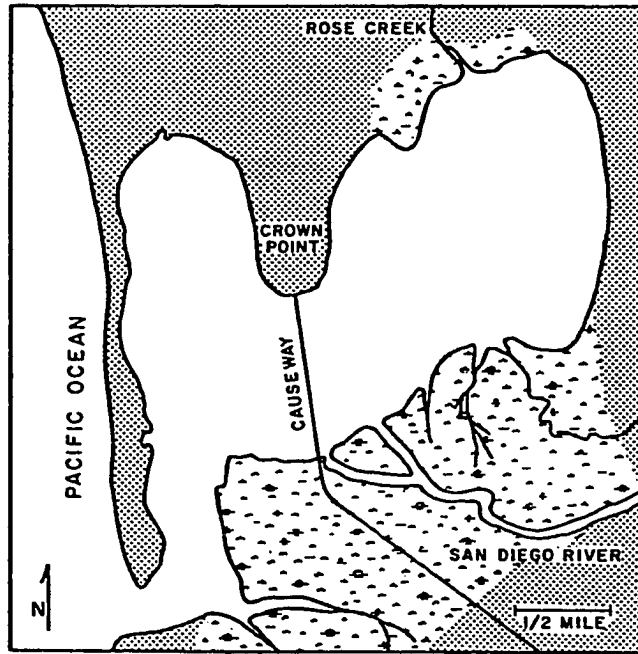
Mission Bay (formerly False Bay) is of structural origin and represents a submerged downwarped portion of the Soledad Mountain Block (Schubel, 1967). The first historical record of Mission Bay occurs in the diary of Sebastian Viscaïno, Nov. 10, 1692, who thought: "...that it was a good port, although it has at its entrance a bar of little more than 2 fathoms depth and that there was a very large grove at an estuary which extended into the land, and many Indians...." (Moriarty, 1974). The bay was originally a natural estuary of over 4,000 acres. The San Diego River which once drained into either Mission Bay or San Diego Bay was diverted to Mission Bay in 1876 and remained the major drainage feature in the bay until 1946. Historically, Mission Bay must have been quite deep—as Viscaïno reported the bay to be a good port. In the early 1900's most of Mission Bay was very shallow (<1 m) and contained extensive eel grass beds, mudflats and salt marshes. The bay contained a southern marsh covering almost 2 square miles. A smaller marsh (≈ 1/4 sq. mi.) was located in the northeastern corner of the bay and mudflats extended south along Crown Point (Figure 2) (Fry and Croker, 1933).

The construction of Mission Bay Park, begun in 1946 and completed in 1963, drastically altered the bay habitat. The San Diego

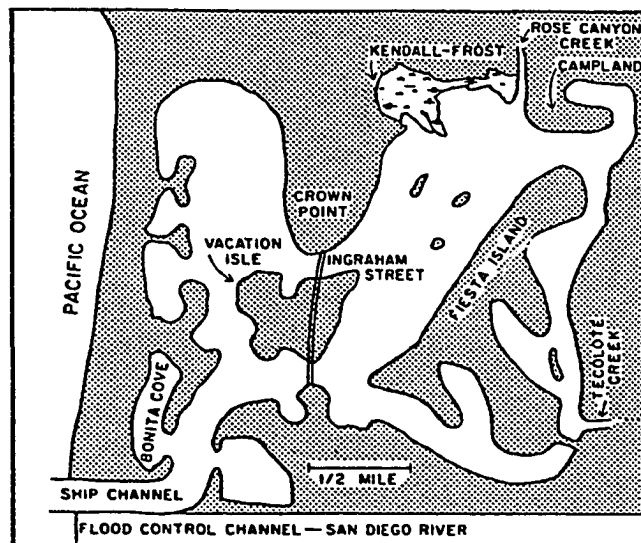


Figure 2: Mission Bay: 1933\* and 1980 (\*1933 map after Fry and Croaker, 1933)

### MISSION BAY – 1933



### MISSION BAY – 1980



River which flowed into the southern marsh was diverted to a flood control channel in 1945. Rose Canyon Creek, which formed the main channel of the northern marsh, was diverted in 1940 to its current course 2600 m east of the old channel.

Major portions of the bay were dredged to depths of 3 or more meters eliminating the entire southern marsh and most of the mudflats. Dredge spoils were dumped at numerous disposal sites, creating Vacation and Fiesta Islands. In the vicinity of the Kendall-Frost Reserve, Rose Creek inlet and an area immediately to the west were dredged and spoils were disposed of on Campland Beach. This must have resulted in substantial disturbance and siltation on the adjacent mudflat. Today street drainage from Pacific Beach flows into the mudflat.

Sand, brought in to form beaches along the eastern side of Crown Point, also eliminated extensive mudflat areas (Jim Lance, pers. comm.). Some of this sand has been transported eastward by water movement to form a spit extending into the upper portions of the west side of the mudflat (Figure 11). The influx of sand over the last 30 years has changed the character of the western mudflat sediments from very sticky mud high in silts and clays (still characteristic of the eastern portion) to a muddy sand, and has in the process influenced the faunal distribution. Modifications associated with Mission Bay Park and accompanying urban development have had an immense impact on the extent and nature of the wetland habitats remaining in Mission Bay. The organisms inhabiting these wetlands today are the survivors of a once extensive estuarine system.

### Hydrographic Studies

Information about longshore transport along the southern California coast, tidal circulation within Mission Bay, flushing rates and small-scale water movement over the Kendall-Frost mudflat, was sought in order to understand the trajectories of planktonic polychaete larvae originating on the Kendall-Frost mudflat. Circulation patterns were studied with temperature and salinity measurements, drift tubes, fluorescence dye and a surface drogue.

#### Methods

##### Temperature and Salinity Measurement

Surface water temperatures and salinity were monitored at 53 stations in Mission Bay (Figure 3) from an 18 ft skiff. Surface temperatures were measured with a bucket thermometer. Salinity samples were taken in citrate glass bottles and analyzed for conductivity in the laboratory on an Autolab inductive salinometer. Surface sampling was conducted on October 18, 1979, February 4, 1980, May 12, 1980 and August 25, 1980. On each date sampling was begun at high tide (Station 1) and completed at low tide (Station 53).

To obtain vertical profiles temperature was measured at 1 m depth intervals using a diver held bucket thermometer. Water samples for salinity analysis were collected in citrate glass bottles at the same depth intervals by divers. Six stations were sampled for vertical temperature profiles (Figure 4) on October 27, 1981. Sampling was done from 0900 (high tide) through 1230 (mid ebb tide) with approximately half-hour intervals between stations. Vertical sampling stations

**Figure 3: Hydrographic sampling stations in Mission Bay**

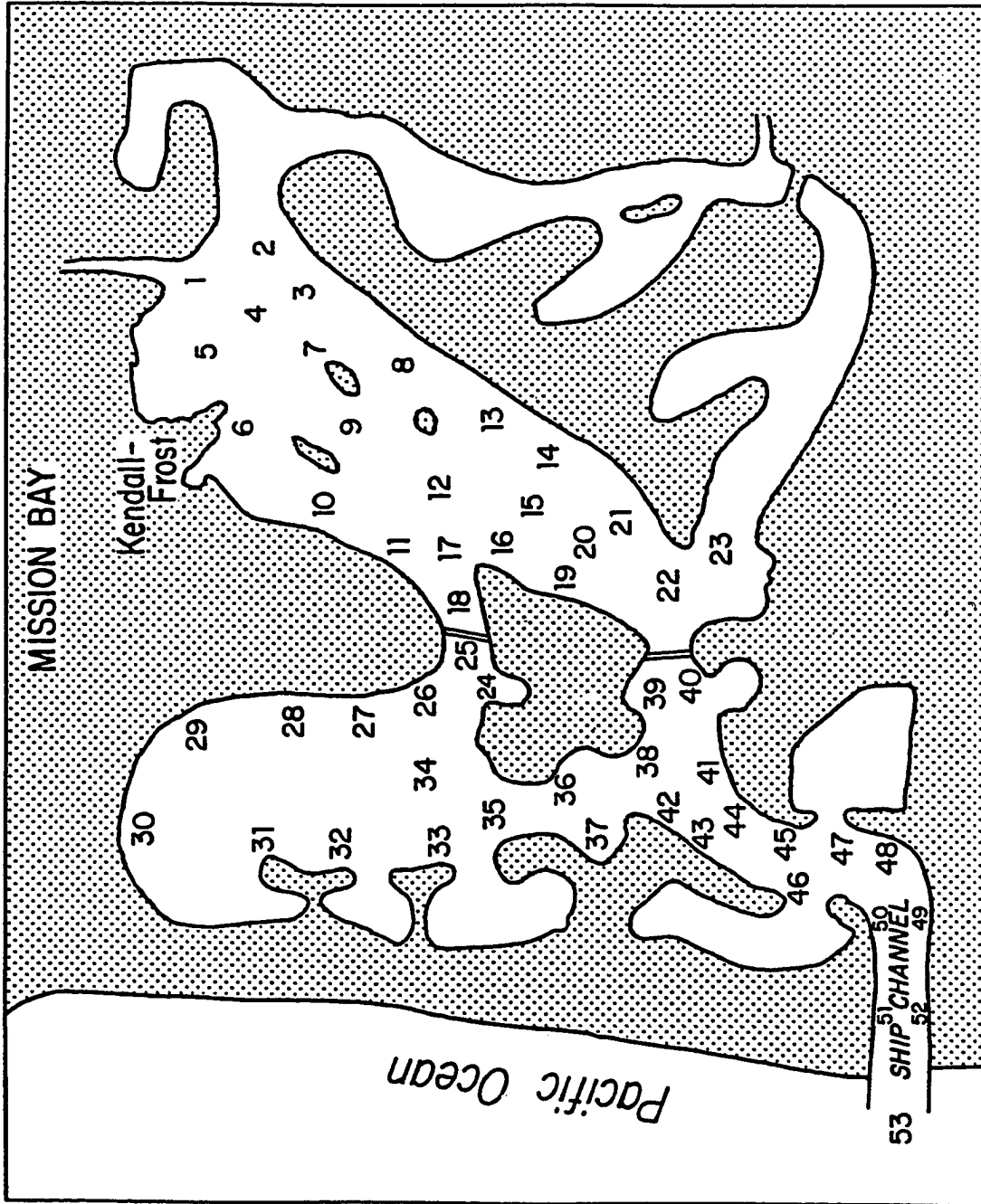
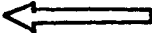

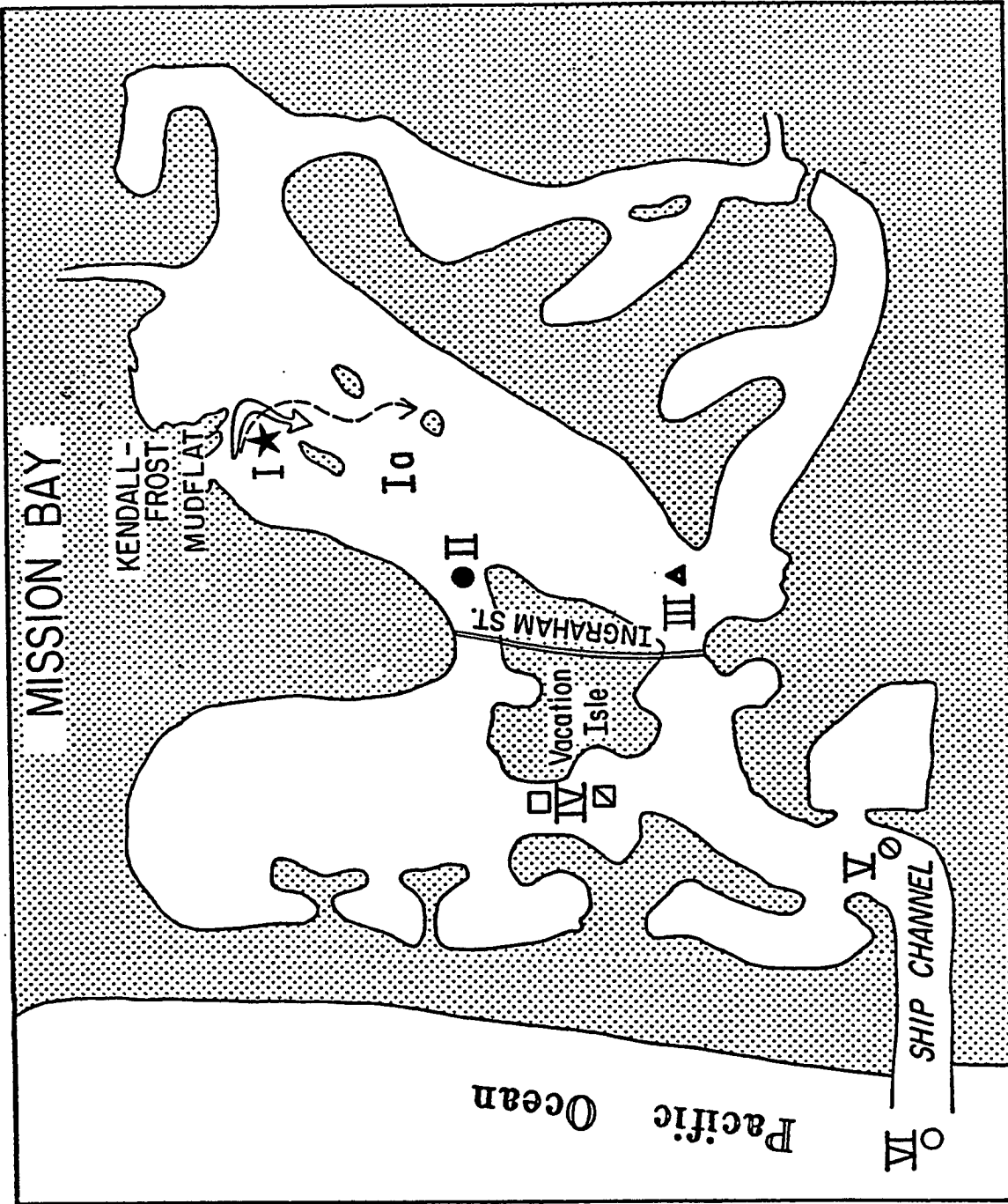


Figure 4: Drift tube release sites. Slashed symbols represent releases on flood tides. All others were ebb tide releases.

 Continuous release dye path (6/26/80)  
during 2 ft tidal excursion

 Surface drogue track (4/5/81) during 3 ft  
tidal excursion





correspond to surface sampling stations (Figure 3) as follows:

I = 4, Ia = 12, II = 18, III = 22, IV = 36, V = 41-42, VI = 53.

#### Drift Tube Studies

Disposable, clear plastic test tubes (Falcon 2045), 15 cm long by 1.6 cm wide with screw-on caps, were employed as drifters. They were stuffed with stamped, addressed postcards requesting the time, date and exact site of tube recovery. The tubes were ballasted with coarse sand, so as to float upright in seawater with the cap protruding < 2 mm above the water surface. The caps were sealed with paraffin and the tubes were painted bright orange and labeled "OPEN ME."

Drift tubes were released on four dates over a one year period: November 5, 1979, February 14, 1980, May 12, 1980 and August 25, 1980. Batches of 25-50 tubes were dropped from a small boat at stations I through VI in Mission Bay (Figure 4). A total of 200-250 tubes were released on each date. Releases were made during ebb and flood spring tides to allow for maximum transport into or out of the bay. Tidal excursions for the 7-hour period following each drift tube release were 8.0 ft, 8.2 ft, 5.0 ft and 4.2 ft for November, February, May and August, respectively.

#### Water Movement over the Kendall-Frost Mudflat

Fluorescene dye was employed by mixing a single packet (standard navy signal size) with one gallon of water and releasing this at one spot on the Kendall-Frost mudflat 2-1/2 hours after high tide. Some of the poorly mixed powder fell to the mud surface and resulted in continuous release of dye during the 2 hours of observation. Photographs of the dye track were taken from a sand dune near the mudflat. A surface

drogue constructed from a weighted bleach jug was used in a similar manner on the mudflat during ebb tide. The drogue was tracked by a person in a skiff.

## Results

### Temperature and Salinity

Temperature and salinity measurements indicate Mission Bay is a fairly well mixed coastal lagoon with little freshwater input except during rains.

The horizontal temperature and salinity patterns are summarized in Figures 5 and 6. Actual values for each station are given in Appendices One and Two). Temperatures ranged from 15.50 to 17.28°C in February, 15.78 to 18.40°C in May, 20.90 to 23.65°C in August and 18.25 to 21.42°C in October. There seems to be a temperature gradient of  $\leq 3$  °C from the back of the bay to the ocean entrance. Salinities ranged from 2.5 to 31.3 o/oo in February, 32.15 to 32.16 o/oo in May, 33.35 to 33.67 o/oo in August and 33.48 to 33.73 o/oo in October. In the absence of rain (which occurred prior to and during the February sampling), there is a salinity gradient of  $\leq 0.5\%$  within Mission Bay. The strongest temperature and salinity gradients occur in the back of Mission Bay nearest the Kendall-Frost mudflat, indicating sluggish water movement and less mixing in the region east of the Ingraham Street bridges.

Vertical temperature and salinity profiles (Figure 7) indicate that Mission Bay is vertically well-mixed. Horizontal temperature and salinity gradients seen at these six stations (on October 27, 1981) were similar to those observed in October 1979. There was a 0.3 o/oo decrease in salinity and a 1.1°C decrease in temperature from the back of the bay to the Ship Channel.

Figure 5: Mission Bay temperature contours Nov. 1979 - Aug. 1980

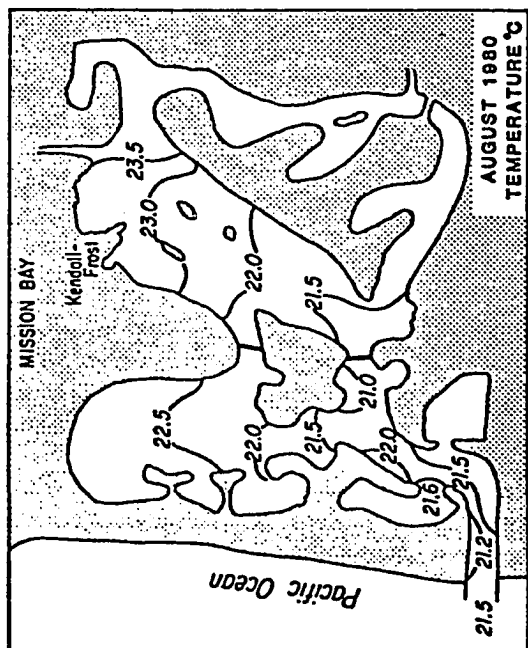
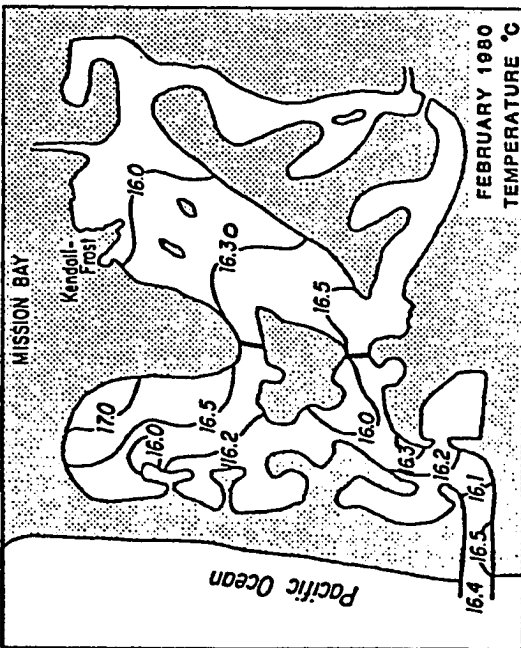
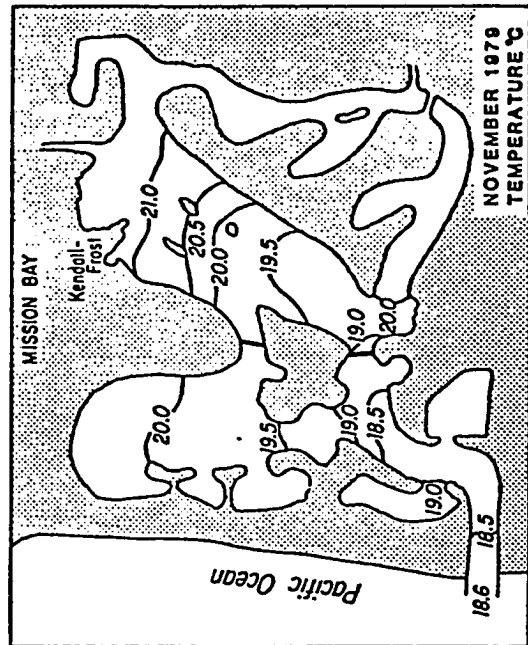
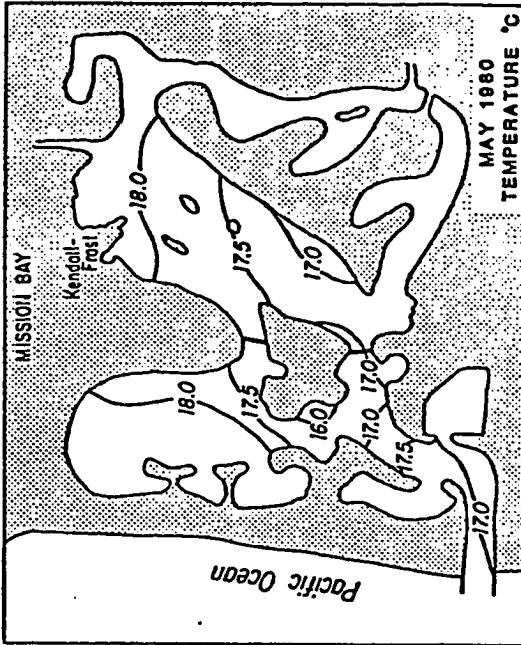


Figure 6: Mission Bay salinity contours Nov. 1979 - Aug. 1980

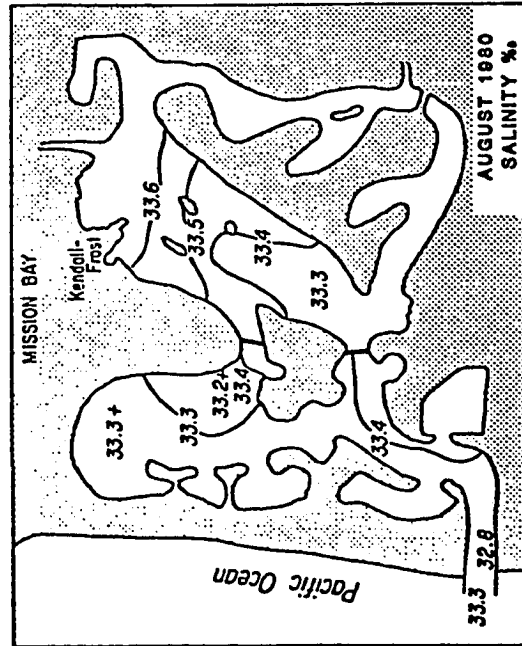
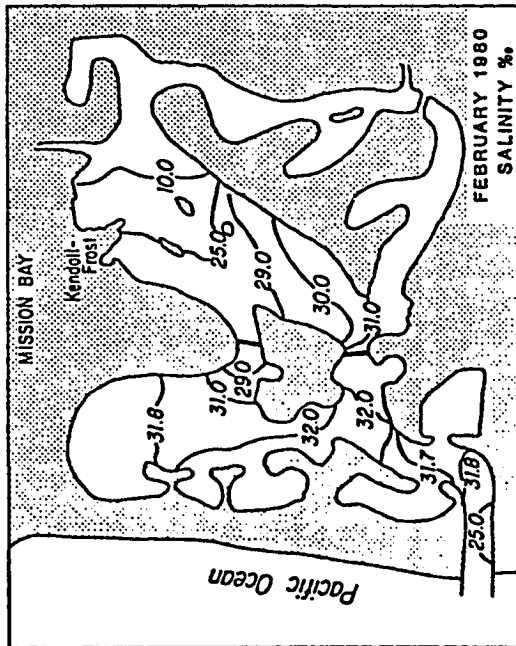
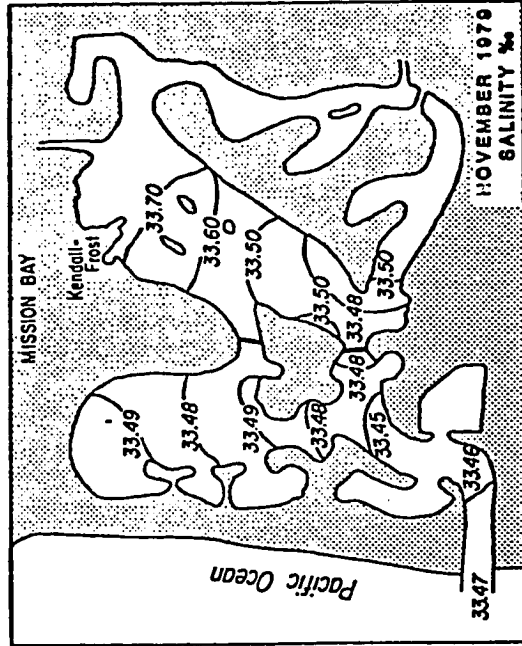
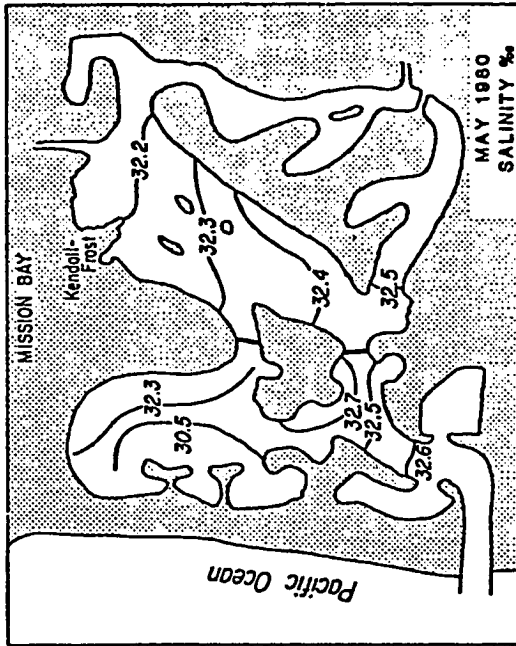
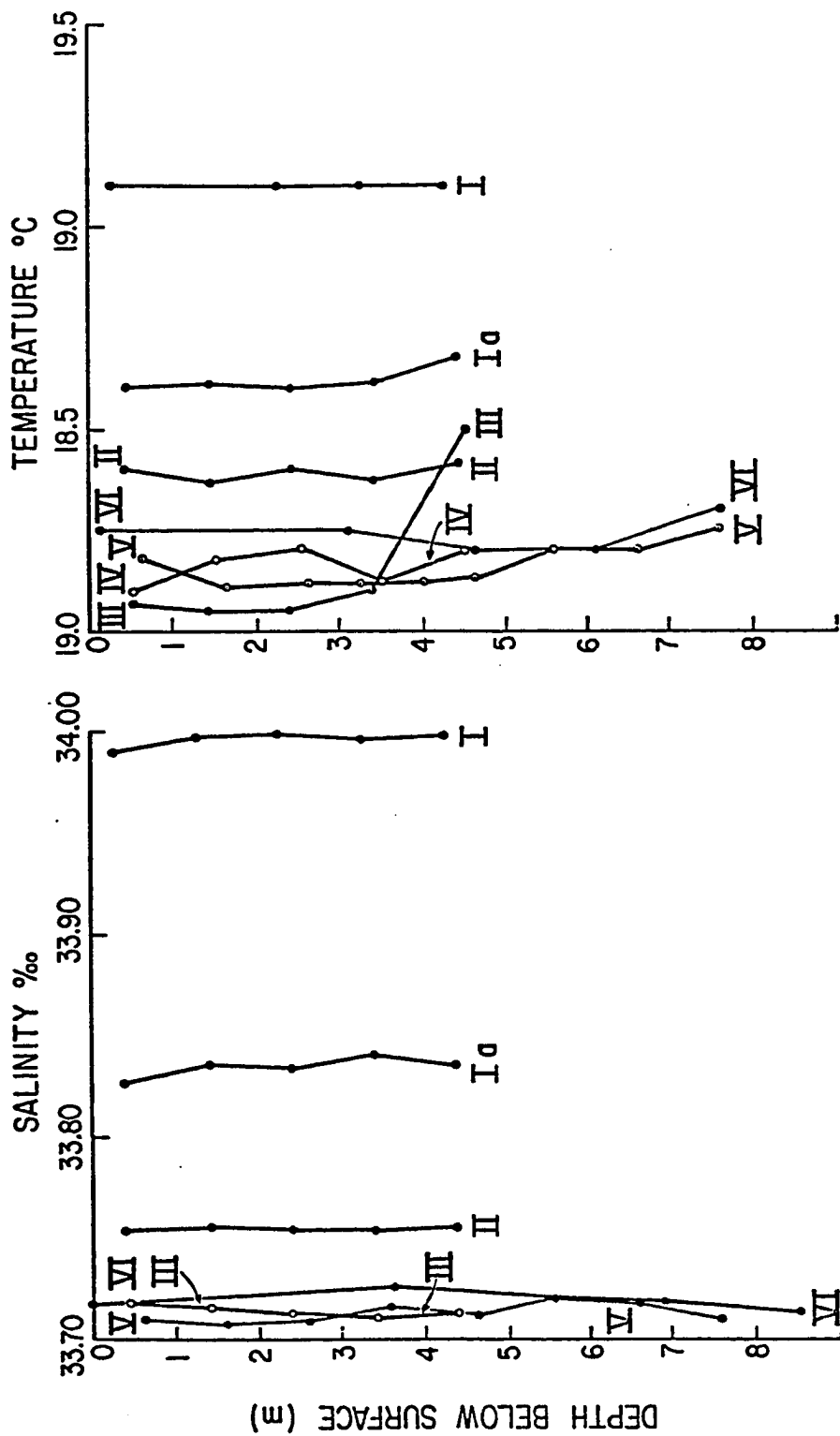


Figure 7: Mission Bay vertical salinity and temperature profiles  
October 1981





## Drift Tube Studies

### Recovery

Drift tube recovery rates were high, 35.6% for the entire study. This rate is similar to the 44% and 39% recovery rates reported for drift card releases close to shore in Puget Sound and the Strait of Juan de Fuca (Kopinski, 1981), but is much higher than the 3.4% (Crowe and Schwartzlose, 1972) and 5.7% (Squire, 1977) return rates in southern California studies where drift bottles and cards were released further offshore. Several thousand drift tubes, identical to those used in this study, were released by M. J. Tegner along the southern California coast and near the Channel Islands. Recovery rates were 30% for the June release and 11% for the October release (M. J. Tegner, pers. comm.). Recovery rates in the Mission Bay study varied with season and site of release (Table 1). Recoveries were greatest in May (49%) and lowest in February (19%). High recovery rates corresponded to dates and release site with minimal transport. The release sites with the greatest rate of recovery were back bay locations (Sites I, II).

Over 80% of the drift tubes recovered were picked up within one week of release in the November, May and August drops. The February tubes were released in the middle of a two week storm and returns were slower. 81.4% of all tubes recovered in this study were found within two weeks of release. Only tubes found within this two week period were considered in calculations of longshore transport.

### Transport Inside Mission Bay and Probability of Exit

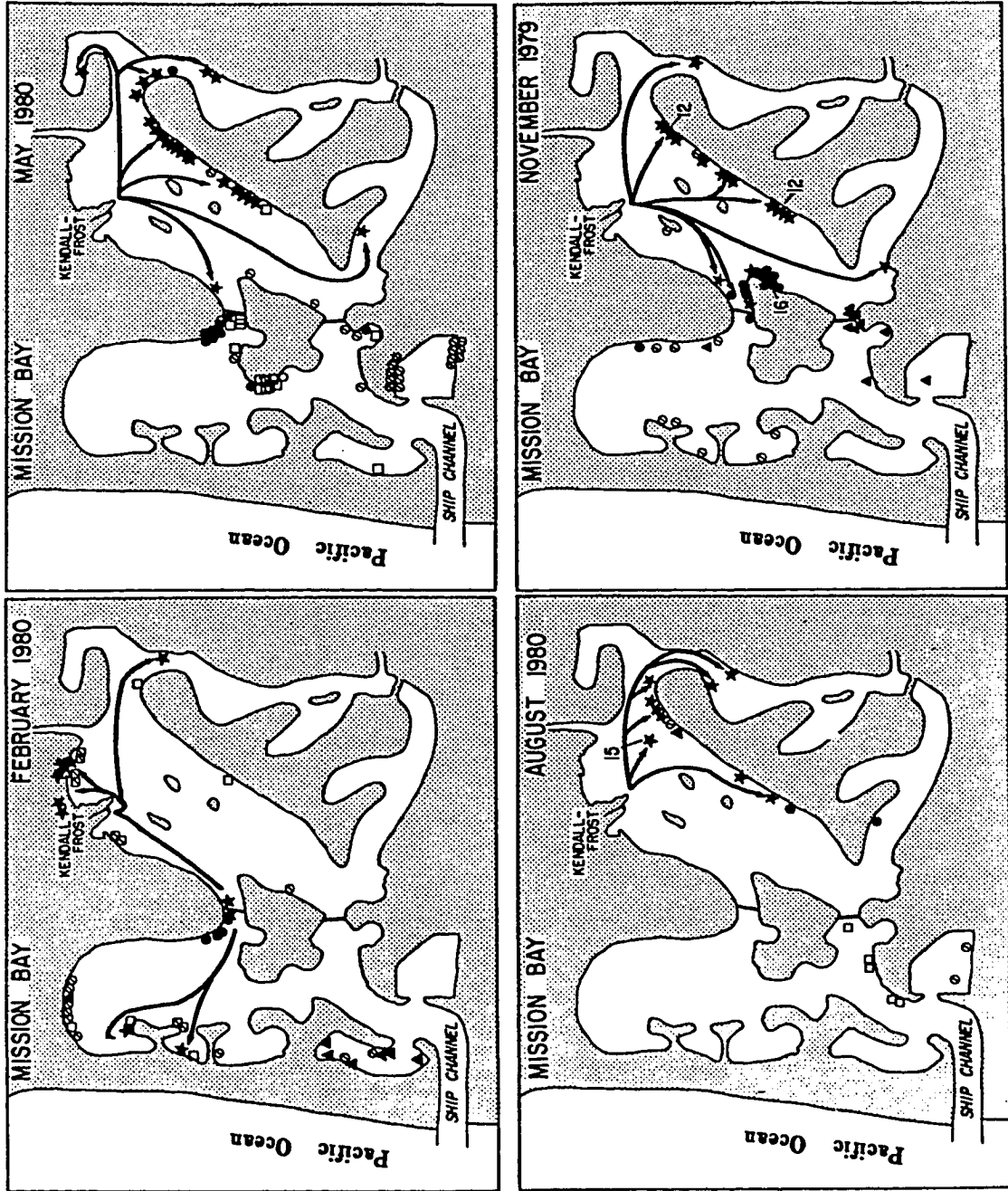
Figure 8 depicts the location of drift tubes recovered inside Mission Bay. The probability a tube will leave Mission Bay varies with

Table 1

<u>Release Date</u>	<u>Percent Recovery</u>	<u>Percent Recovered on the Outer Coast</u>	
		<u>Released Front-Bay</u>	<u>Released Back-Bay</u>
February 1980	19.2% (48/250)	27.0% (7/26)	0.0% (0/16)
May 1980	48.8% (122/250)	32.7% (18/55)	4.9% (2/41)
August 1980	27.9% (53/190)	53.8% (7/13)	3.7% (1/27)
November 1979	47.0% (94/200)	26.6% (4/15)	3.1% (2/63)
<u>Release Site*</u>			
I. Kendall-Frost	47.4% (83/175)	-	1.2% (1/83)
II. Ingraham Br. N.	45.0% (45/100)	-	4.4% (2/45)
III. Ingraham Br. S.	26.7% (20/75)	-	10.0% (2/20)
IV. Vacation Isle	32.0% (56/175)	44.6% (25/56)	-
V. Inner Ship Channel	27.9% (53/190)	17.0% (9/53)	-
VI. Outer Ship Channel	30.5% (61/200)	98.4% (60/61)	-

\* All drift tubes were released during ebb tides except those from Station V which were released during flood tides.

Figure 8: Drift tube recoveries inside Mission Bay, Nov. 1979 -  
Aug. 1980. (See Figure 4 release sites). Dark symbols  
represent tubes released in the back bay on ebb tides.



its release site. Over 96% of recovered tubes released in the back-bay and 67% of tubes released in the front bay were recovered inside Mission Bay. The remainder were found along the outer coast. The probability of exiting Mission Bay seems to be consistent from season to season (Table 1) for each release site. Of the 175 tubes released during the study at site I (furthest back-bay), 90 were recovered. Only three tubes were found in the front bay and 1 tube was recovered outside the bay.

Drift tube recoveries on the outer coast underestimate probabilities of drift tubes or larvae exiting Mission Bay. Undoubtedly, many tubes leaving Mission Bay were never recovered. The 30% recovery rate of drift tubes released in the outer Ship Channel (Site VI - at the ocean entrance) suggests that this underestimation is substantial, as all but one of these were found along the outer coast. Assuming a 30% recovery rate for all tubes exiting Mission Bay in this study, as many as three times the number of drift tubes actually recovered (originating in the back-bay) may have left the bay. This would raise exit probabilities to 10% for the back bay as a whole and 3% for Site I, assuming a near perfect chance of discovery for tubes ending up inside the bay.

Previous measurements of tidal current velocities in Mission Bay (McNaboe et al., 1978) suggest that drifters (or larvae) originating in the back of the bay should be capable of exiting the bay in a single tidal cycle. Tidal currents attain velocities of 75 cm/sec in the front bay and 20 cm/sec in the back bay during spring tides.

### Back-bay Water Movement

Fluoroscene dye and a surface drogue were used to examine water movement over the Kendall-Frost mudflat during ebb tide. A single use of each method during periods of maximum tidal velocity (between 2.5 and 4.5 hrs after higher high tide) revealed only sluggish (10 cm/sec) water movement on and adjacent to the mudflat. Figure 9 depicts the dye path during ebb tide at 1/2 hr intervals beginning 2.5 hrs after higher high tide. The drogue followed a similar path (Figure 4). The drogue and dye observations plus the strong horizontal surface salinity and temperature gradients maintained in the upper reaches of the bay (Figures 5, 6) indicate little mixing with ocean waters. These observations are consistent with retention in the back bay of over 90% of the recovered drift tubes released at Sites I, II and III. The high probability of retention is emphasized by the fact that drift tubes were released during spring ebb tides which offer maximum transport potential.

Current measurements during spring flood tides (McNaboe et al., 1978) suggest tubes or larvae entering Mission Bay on a flood tide could reach the back half of the bay in a single tidal cycle. Drift tube recoveries are not numerous enough to verify this, but 15% of recovered tubes released near the bay entrance on a flood tide were recovered (within two weeks) in the back bay (Figure 8). Thus, larvae originating outside Mission Bay might eventually settle in the back-bay mudflats.

### Outer Coast Transport

Seventy-seven tubes were recovered along the exposed southern California coast within two weeks of their release inside Mission Bay. Figure 10 presents recovery sites of all tubes found outside Mission

Figure 9: Fluoroscene dye path photographed at half hour intervals from the Kendall-Frost mudflat. Release occurred on an ebb tide at 1030 on 6/26/80, 2½ hours after high tide (+5.2 ft)

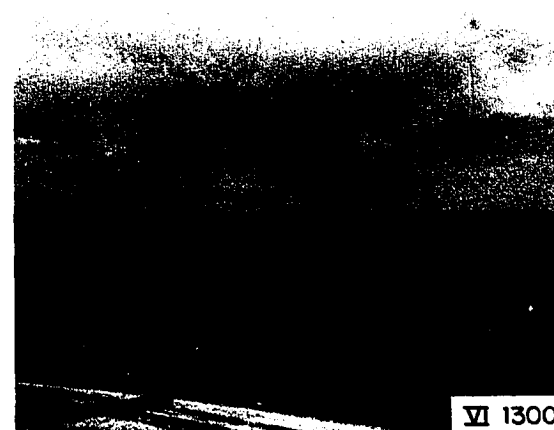
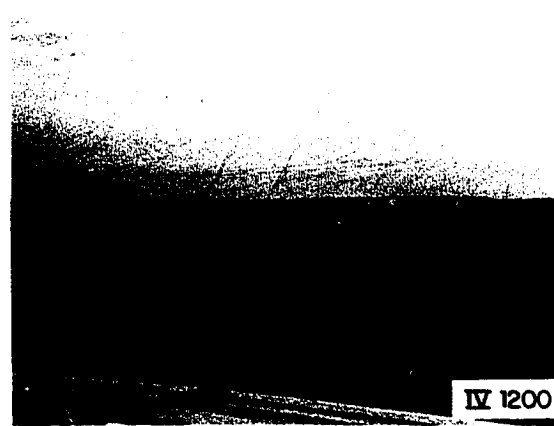
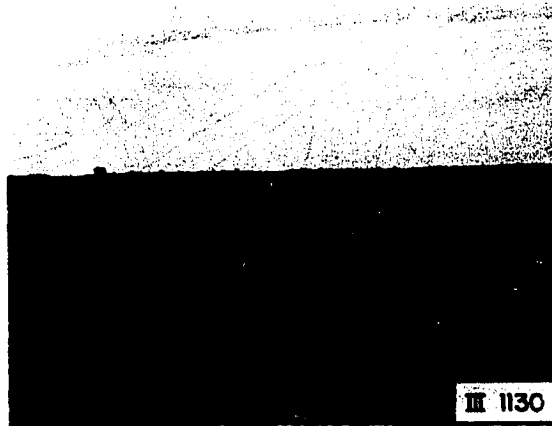
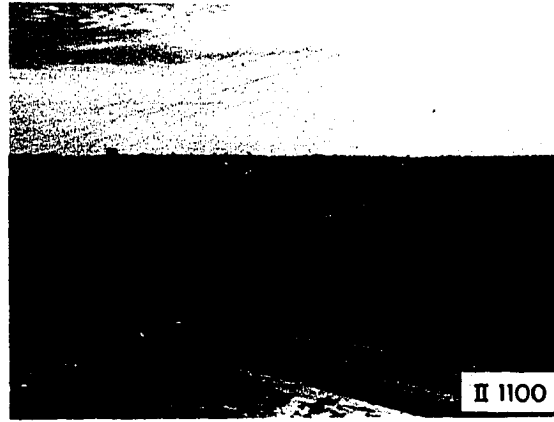
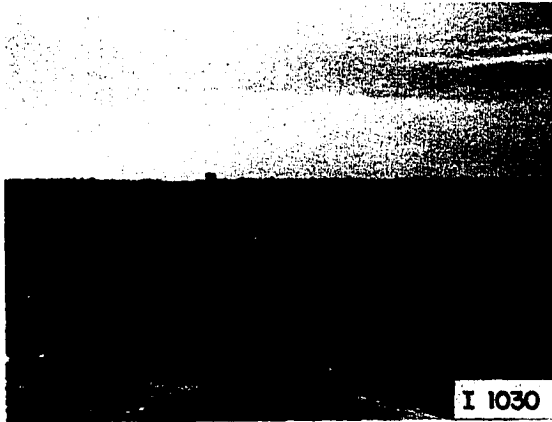
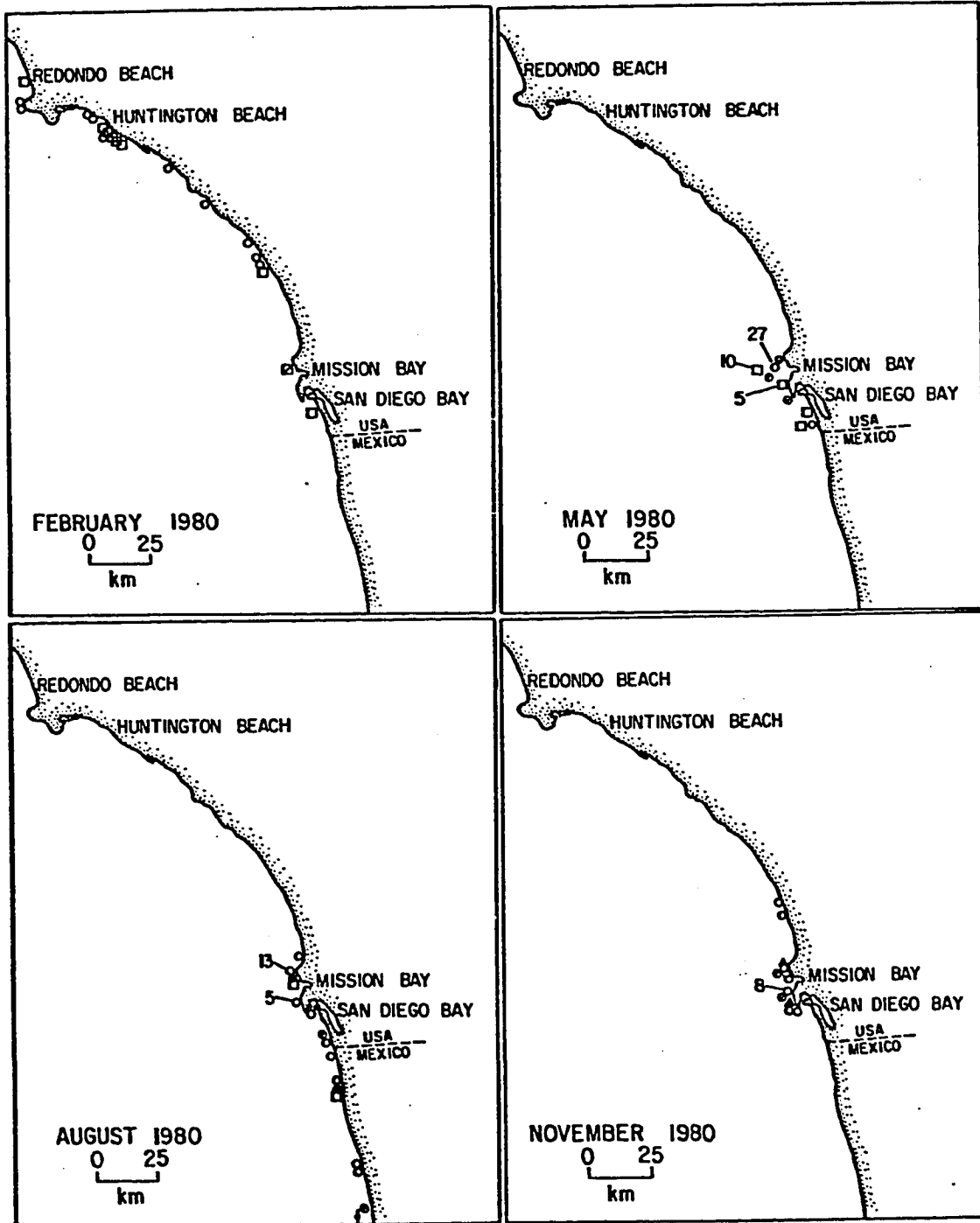




Figure 10: Outer coast drift tube recoveries, Nov. 1979 - Aug. 1980.  
Light symbols represent front-bay releases. Dark symbols  
represent back-bay releases. (See Figure 4 for release  
sites.)



Bay. These returns are used to determine direction and rates of longshore current transport. Transport was most consistently to the south (73% of the tubes traveled south) except during winter storms. This is indicative of the relatively permanent southerly flowing current reported by Schwartzlose (1964) off southern California and is consistent with seasonal records of longshore current velocities measured with current meters off Del Mar and San Onofre, California (Winant, 1980). In mid February a major storm traveled north along southern California. All tubes recovered within two weeks of the February release had traveled north of Mission Bay.

Table 2 presents the mean and maximum distances and rates recorded for drift tubes in each season. Winant and Bratkovitch (1981) report that mean seasonal current velocities recorded along the southern California coast always exceeded 1 cm/sec and that mean surface currents were greatest in summer (6.15 cm/sec) and smallest in the fall (2 cm/sec). These current speeds are consistent with the August and November drift tube transport rates. Of interest is the mean rate (24.1 cm/sec) and low standard deviation (9.2 cm/sec) observed for the 10 drift tubes traveling north in February 1980. Similar transport rates (15-30 cm/sec) were reported for north traveling drift bottles released off central California in January 1958 and December 1959 (Schwartzlose and Reid, 1972). Storm systems traveling north along the narrow southern California shelf may induce strong local winds which drive surface waters northward. Sustained current velocities of over 50 cm/sec to the north were recorded off Del Mar during such an event in September 1978 (Winant, 1980). Storm induced winds, which attained speeds of 52 mph (2600 cm/sec) on February 14, 1980 and remained strong through the

Table 2

	February (1980)	May (1980)	August (1980)	November (1979)
Rate of Travel (cm/sec) (x 1. D.C.)	24.1 ± 9.2	3.9 ± 10.1	5.9 ± 4.1	1.1 ± 1.7
Distance Traveled (km) (x 1 S.D.)	125.7 ± 40.2	2.3 ± 4.3	19.8 ± 17.7	2.8 ± 3.2
<u>South</u>				
Maximum distance (km)	-	20	205 (16 da.)	11.7
Maximum rate* (cm/sec)	-	50.0	15.6	6.3
Number recovered	0	35	13	9
<u>North</u>				
Maximum distance (km)	173.3	1.7	1.7	1.7
Maximum rate (cm/sec)	36.1	4.2	0.3	0.3
Number recovered	10	8	1	2
<u>Wind Speed on Release Date**</u>				
Maximum (mph)	52	20	21	17
Average (mph)	16.1	8.2	10.1	5.6

Annual average for San Diego is 6.7 mph

\*Lags in drift tube recovery can only permit a minimum estimate of speed of travel. Here I give the largest of these estimates.

\*\*Recorded at San Diego International Airport (4 km from Mission Bay) by the National Weather Service

month, may account for the consistent and rapid transport of drift tubes to the north in February. The maximum tube transport rates attained in this study were 36 cm/sec to the north in February and 50 cm/sec to the south in May. The maximum distances traversed by drift tubes were 173 km to the north in February and 205 km to the south in August. Return postcards were not printed in Spanish and this, plus the small scattered population south of the U.S. border may have hindered recovery of tubes washing up in Baja California.

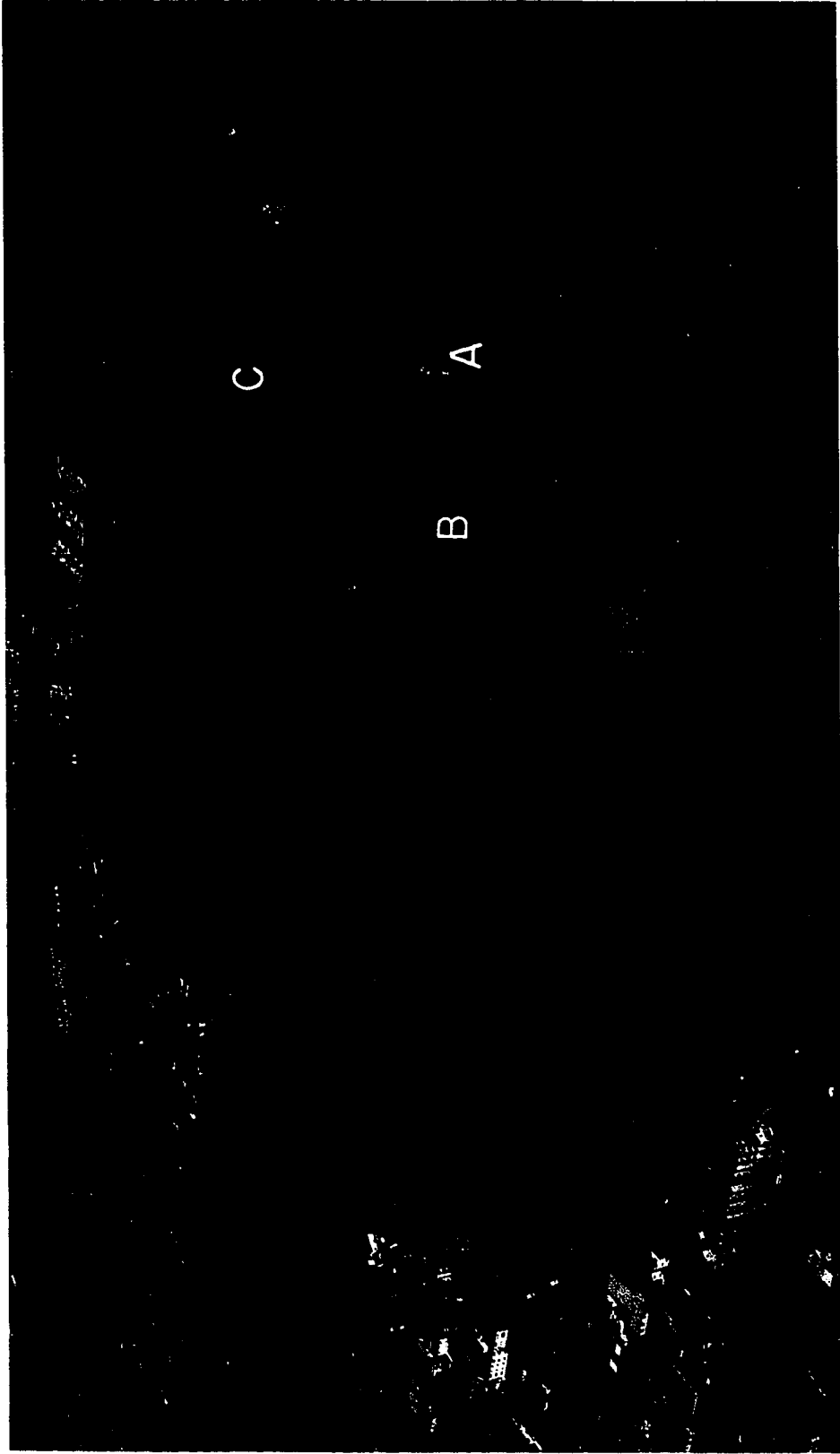
### Summary

Results of the drift tube, dye and drogue studies and the salinity and temperature gradients maintained in the back of Mission Bay all support the contention that water movement in the back-bay is sluggish. Very few of the drift tubes released in the back bay exited to the ocean and the dye and drogue tracks traveled only a few hundred meters from the Kendall-Frost mudflat. However, tidal currents in the narrow regions of the bay, particularly under bridges and in the Ship Channel, can reach up to 1.5 knots during spring tides (McNaboe *et al.*, 1978). Exchange with ocean waters is considerably greater in the front region of Mission Bay. Larvae reaching the front (west) half of the bay are more likely to be carried out to the ocean. Longshore transport to the north and south along the outer coast may be rapid (25 - 50 cm/sec), particularly during winter storms, providing larvae with access to many bay mouths.

### The Kendall-Frost Reserve

The Kendall-Frost Marsh Reserve and adjoining tidelands are located in the northeast corner of Mission Bay, California (Figure 1).

**Figure 11: Aerial photograph of the Kendall-Frost Reserve in  
Mission Bay, California and study Sites A, B and C.  
(Photograph taken by Larry Ford.)**



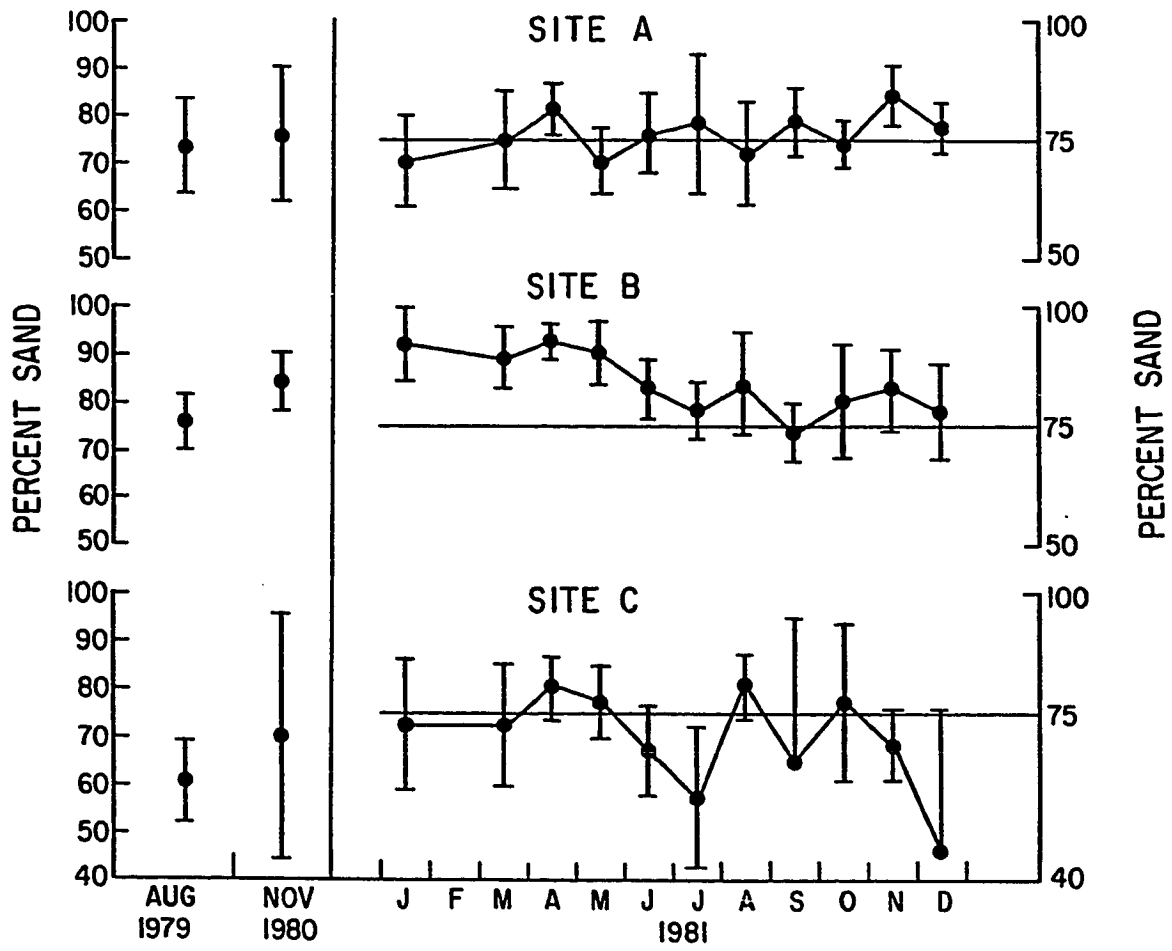
The Kendall-Frost Marsh Reserve was acquired by the University of California in 1952 and in 1972 was established as a Wildlife Sanctuary. The reserve is comprised of approximately 20 acres of marsh. Mudflats extending below 0.0 tide abut the marsh and are owned and protected by the City of San Diego. The wetland system ( $\approx$  50 acres) is composed of a typical (but small) southern California zoned salt marsh (see MacDonald, 1967 for a description of the salt marsh), mudflats dissected by numerous small channels, and a narrow band of eel grass occurring at approximately 0.0 tide level. An arm of the marsh, bisected by the main channel (formerly Rose Canyon Creek), extends bayward separating the mudflat into an extensive eastern and smaller western portion (Figure 11). Sediments in the western portion are sandy, due to current action and sand transport from Crown Point Beach. The eastern portion of the mudflat is quieter and contains a higher proportion of silts and clays.

#### Study Sites

Three regions of the Kendall-Frost mudflat were examined intensively during this study (Figure 11). Each was characterized by slightly different sediment characteristics, tidal heights and hydrographic conditions. Site A was a low intertidal site ( $\approx$  0.5 ft above MLLW) just above the eel grass bed and  $\approx$  50 m west of the marsh arm. Site B was located at  $\approx$  +2.5 ft above MLLW tide level, west of and adjacent to the central arm of the marsh. Site C was located at similar tide levels (+2.5 ft) 20 m to the east of the marsh arm. Figure 12 presents percent sand in sediments collected from each site during a one year period. Grain sizes were determined from 4 replicate cores (.001 m<sup>2</sup> x 2 cm depth) taken at each site at monthly intervals. Organics were



Figure 12: Percent sand ( $>62\mu$ ) (mean values  $\pm 2$  standard deviations,  $n = 4$ ) in sediments at Sites A, B and C on the Kendall-Frost mudflat.



dissolved in hydrogen peroxide for two days, then sediments were wet sieved, dried, and weighed to determine % sand ( $>62\mu$ ) versus % silt-clay ( $<62\mu$ ). Sediments are lower in sand ( $62\mu$ ) content at site C (40-80%) than at A or B (70-95%), however, grain sizes are highly variable over short distances (meters) and vary somewhat with season.

Species composition is fairly constant across the entire mudflat, but as with sediment characteristics, each site differs somewhat in faunal abundances (Appendix Three). Polychaetes and oligochaetes are the numerically dominant taxa in the surface (upper 7 cm) sediments. Phoronids, tanaids, amphipods, decapods, cephalaspidean gastropods and bivalves comprise the remainder of the infaunal community. Macroinfaunal densities in the assemblage commonly reach 100,000-200,000 individuals/m<sup>2</sup>. Major macrofaunal predators of these infauna are migratory shorebirds, bottom feeding fish, rays, skates and bait diggers.

#### Disturbance

Physical disturbance is a conspicuous feature of the Mission Bay intertidal habitat. Small rays feed on the mudflat at high tide, forming shallow pits in the sand. The ghost shrimp, Callianassa californiensis, creates numerous sediment mounds around its many burrow openings. Human disturbance is also frequent; foot traffic is heavy on some parts of the mudflat and fishermen dig deep pits to capture Callianassa for use as bait. These various forms of disturbance impart a mottled and pitted appearance to the mudflat surface.

The disturbance quantified in this study is that which is likely to influence surface feeding polychaetes. Surface sediment features were classified as puddles, mounds or undisturbed at 10 cm intervals

along 15 m transects. Puddles were depressed areas with standing water during low tide and mounds were regions elevated above undisturbed sediment, often with a grayish color. Mounds generally had a Callianassa burrow opening at their center. Transects were laid parallel to the water line at low (+0.5 ft), mid (+1.0-1.5 ft) and higher (+2.5 ft) tide levels. One meter square quadrats were photographed over a 1 month period and monitored for persistence of surface features. Three quadrats were marked with stakes in the lower left corner at each of the three tide levels mentioned above. Photographs were taken on days 1, 2, 3, 4, 7, 14 and 28 after the initiation of the survey. Slides were observed sequentially under a dissecting microscope and features were plotted and followed with a camera lucida.

Table 3 presents transect data for the frequency of surface sediment features on the Kendall-Frost mudflat. At all tide levels 40-60% of the sediment appears undisturbed to the naked eye. The remainder appears as mounds or puddles of standing water at low tide. Mounds, produced primarily by Callianassa burrowing activities, are almost twice as common at lower (16%) than higher (8%) tide levels. Puddles, generated by human and ray feeding activities, are more common higher in the mudflat (30-50% cover).

Many features on the sediment surface appear to persist for 2 weeks or more. One-third of the pits and mound followed in the low intertidal (n = 15) disappeared (became indistinguishable) within 1 week of observation, while only one-tenth did so at higher tide levels (n = 29). Larger features persisted longer. Algae and eel grass growing attached to the mud surface remained intact for the duration of the study (29 days).

Table 3  
Disturbance Studies on the Kendall Frost Mudflat  
October, 1981

<u>Tide Level</u>	<u>Puddles</u>	<u>Mounds</u>	<u>Undisturbed</u>
+ 0.5	28.9%	16.7%	53.9%
+ 0.5	29.3%	16.0%	54.7%
+ 1.5	51.3%	7.4%	41.3%
+ 1.5	32.0%	7.3%	60.7%
+ 2.5	44.7%	10.3%	45.0%
+ 2.5	45.7%	10.6%	43.7%
+ 2.5	48.0%	8.0%	44.0%

(Percent cover is given for features along two 15 m transects  
at each of 3 tide levels.)

## Polychaetes

The numerically dominant infaunal polychaetes in the Kendall Frost community are the spionids Pseudopolydora paucibranchiata (Okuda), Polydora ligni (Webster), Rhynchospio arenicola (Hartman), and Streblospio benedicti (Webster), the syllid Exogone lourei (Hartman), the sabellid Fabricia limnicola (Hartman) and the capitellid Capitella capitata (Fabricius, Mission Bay variety). These species comprise 50-90% of the infauna through most of the year and are the focus of the studies presented here. Their life habits and feeding modes (based on observations made in the laboratory between 1978 and 1981) and geographic range are described below.

### Pseudopolydora paucibranchiata

Pseudopolydora paucibranchiata constructs vertically oriented firm tubes (1 mm diameter) of silt in the upper centimeters of the sediment. Tubes open at the surface or may protrude up to 1 cm above the sediment surface. This seems to be a function of silt-clay content in the sediments and water motion. Tubes protrude higher in quieter waters. Tube construction is described by Blake and Woodwick (1975). Pseudopolydora paucibranchiata suspension feeds or surface-deposit feeds, depending on water motion. When current is rapid, the palps suspension feed in a spiralled configuration (Taghon et al., 1980, pers. observation). Flimsy rod-shaped fecal pellets are deposited outside the tube opening but break up quickly. Adult worms are 10-20 mm in length, palps may be extended to reach as far as 10 to 15 mm.

Pseudopolydora paucibranchiata, described originally from Japan, was first reported on the (E.) Pacific Coast of the U.S. in 1950 from

Los Angeles Harbor and Newport Bay. Introduction may have occurred with Japanese oysters or in ships' ballast water (Carlton, 1978). Today Pseudopolydora paucibranchiata is common intertidally and in shallow subtidal waters of many (but not all) bays along the E. Pacific from Washington south to Mission Bay. Extension of the species' range along this coast has probably been by unaided larval dispersal. This species attains extremely high densities in sandy mud sediments in Tomales Bay, Catalina Island, and Mission Bay. P. paucibranchiata was not reported in a 1971 study of the Kendall-Frost infauna (P. Jumars, unpublished data). This species may have been introduced to Mission Bay since that time or may have been experiencing an extremely poor year in 1971. Pseudopolydora is most dense at low tide levels (-1.0 to +1.0 ft) but extends to  $\approx$  +3.5 ft above MLLW and may be very abundant at mid tide levels during some years.

#### Polydora ligni

Polydora ligni is a slightly larger spionid which also constructs vertically oriented tubes of silt and sand in the upper few cm of sediment. It surface deposit feeds or suspension feeds depending on water motion and particulate load. Fecal material is released unconsolidated and swept out of the tube by the respiratory current. P. ligni adults attain lengths up to 30 mm and palps may be extended a comparable distance.

This is a cosmopolitan species and has been reported from estuarine habitats all over the world. It is considered indicative of polluted conditions (Pearson and Rosenberg, 1978) and sediments high in silt-clay content. There is some question as to the possible existence

of a Polydora ligni species complex, such as that found for Capitella capitata (Grassle and Grassle, 1976). Electrophoretic and morphological studies of P. ligni by Rice and Simon (1980) indicate at the very least, sibling species-level differences between southern California P. ligni and some Florida populations. P. ligni occurs intertidally and subtidally in fine sediments in Mission Bay.

#### Rhynchospio arenicola

Rhynchospio arenicola constructs flimsy, mucous lined tubes which open at the sediment surface. These tubes are not preserved during sample processing. Like the other spionids, this species is a facultative surface deposit and suspension feeder. Adults are small,  $\approx$  10 mm in length and palps are short (<5 mm). Rhynchospio occurs in bays along the E. Pacific Coast from British Columbia south to at least Mission Bay. In Mission Bay, it occurs intertidally in sandy muds and possibly in shallow subtidal mud, though it was not reported in Dexter's (1979) survey. This species was not present in my collections from the more southern bays, San Diego Bay, Tijuana Slough, Estero Bay and Bahia de San Quintin.

#### Streblospio benedicti

Streblospio benedicti builds flimsy, mucous lined tubes in the upper few centimeters of the sediment and feeds at the sediment surface. Individuals are facultative surface deposit feeders and suspension feeders, switching feeding modes according to water motion and particulate load. They deposit rodlike fecal pellets on the mud surface outside the tube opening. Adults are  $\approx$  10-20 mm in length and have relatively short palps which extend  $\approx$  5 mm. Streblospio occurs on the East



Pacific Coast from British Columbia south to Estero Bay, Baja California, on the Atlantic Coast from the Gulf of St. Lawrence south to the Gulf of Mexico, in northern Europe, the Mediterranean Sea, the Black Sea, and Venezuela (Carlton, 1978). Streblospio was first reported on the Pacific Coast from 1932 collections in San Francisco Bay. It was probably introduced earlier with importation of Atlantic oysters and possibly through ship fouling (Carlton, 1978). Today Streblospio is common in most muddy intertidal or estuarine habitats along the Pacific Coast. In Mission Bay this species is most abundant at mid tide levels +1 to +3 ft above MLLW, becomes rare in the low intertidal and is not reported subtidally (Dexter, 1979, this study).

#### Exogone lourei

Exogone lourei is a small ( $\approx 5$  mm) errant syllid (subfamily: Exogoninae) which lives and feeds just beneath the sediment surface. It is a deposit feeder, detritivore and possibly grazes on benthic diatoms. This species occurs in bays along the Pacific Coast from British Columbia south to Baja California (Bahia de San Quintin). It is limited to intertidal and shallow subtidal depths in Mission Bay.

#### Fabricia limnicola

Fabricia limnicola is a small ( $< 7$  mm) sabellid which builds sand tubes in the top centimeter of mid-intertidal sediments. This species often occurs at high densities ( $> 10^5/m^2$ ) and tubes may be glued to one another during construction, forming a tube mat over the mud surface. Fabricia limnicola is primarily a suspension feeder, filtering fine particles with radioli of its tentacular crown, however it may use two dark palps at the crown center to surface deposit feed. Fauchald and Jumars

(1979) suggest that members of the subfamily Fabriciinae (to which this species belongs) are secondarily becoming selective deposit feeders as adaptation to life in nutrient poor or physically unstable environments. Fecal material is "thrown off" the palps in small pellets (<100  $\mu$ ), which are readily carried away with the slightest water motion.

Fabricia limnicola has a very limited geographic range. It has been reported only from southern California (Anaheim Bay, Los Angeles Harbor, Newport Bay and Mission Bay), and Baja California (Bahia de San Quintin on the Pacific Coast and Bahia de Los Angeles in the Sea of Cortez) (Carlton, 1978). Carlton (pers. comm.) proposes that this distribution suggests either relict endemism or introduction via boat traffic from an unknown source.

#### Capitella capitata (Mission Bay Variety)

Capitella capitata is a subsurface, burrowing deposit-feeder. It constructs a tube of mucous bound sediment only during reproduction, and will remain in the tube until brooded larvae are released. Adults are quite small (<10 mm) relative to other varieties of Capitella capitata which have been described. Capitella is a cosmopolitan polychaete, reported around the world from the intertidal to the deep sea. It has become well known as a pollution indicator (Pearson and Rosenberg, 1978) and is a frequent colonizer of disturbed sediments.

Grassle and Grassle (1976) have found through electrophoretic analyses and life history studies that Capitella capitata is a species complex rather than a single species. They originally identified six sibling species from shallow waters in Massachusetts and have continued to find new species. Hartman (1968) describes several varieties of

Capitella capitata from California. The species described here appears to be a new variety and does not resemble electrophoretically any of those described by the Grassles (pers. comm.).

Collections in other southern California bays have yielded other varieties of Capitella capitata (some of which also occur in Mission Bay), but not the one reported here. It is possible that its distribution is limited to Mission Bay.

CHAPTER III  
MISSION BAY PLANKTON STUDIES

Introduction

The plankton studies conducted in Mission Bay were designed to furnish several types of information. A bay-wide survey, conducted quarterly for 1 year, was intended to (1) provide an overview of mero- and holoplankton distributions, and (2) describe the seasonal distributions of specific polychaete larvae. The survey of plankton distributions was intended to provide clues about within-bay circulation and plankton retention phenomena such as those described by Jacobs (1968), Trinast (1975) and Miller (in press). Counts of polychaete larvae were made to determine dilution rates of larvae from the back to the front bay and species-specific abilities for dispersal out of Mission Bay and along the open coast.

Larvae of the polychaete species considered originate from populations concentrated in the back bay. A small-scale plankton program was carried out in waters overlying the Kendall-Frost mudflat, to determine: (1) which benthic species are represented in the water column, (2) at what life history stage they are present in the plankton, (3) variations in distribution and abundances of early vs. competent larvae, (4) seasonal patterns and annual fluctuations in larval meroplankton availability, (5) spatial variation in availability over the mudflat, and (6) the relationship between larval availability, recruitment and benthic abundances of the dominant infaunal species. Monthly samples were collected at two sites over the Kendall-Frost mudflat during 1981. Intense sampling (every 1 1/2 hours) was carried out through several complete tidal

cycles to examine effects of lunar, diurnal and tidal cycles on plankton behavior and distributions.

### Methods

#### Bay-Wide Sampling

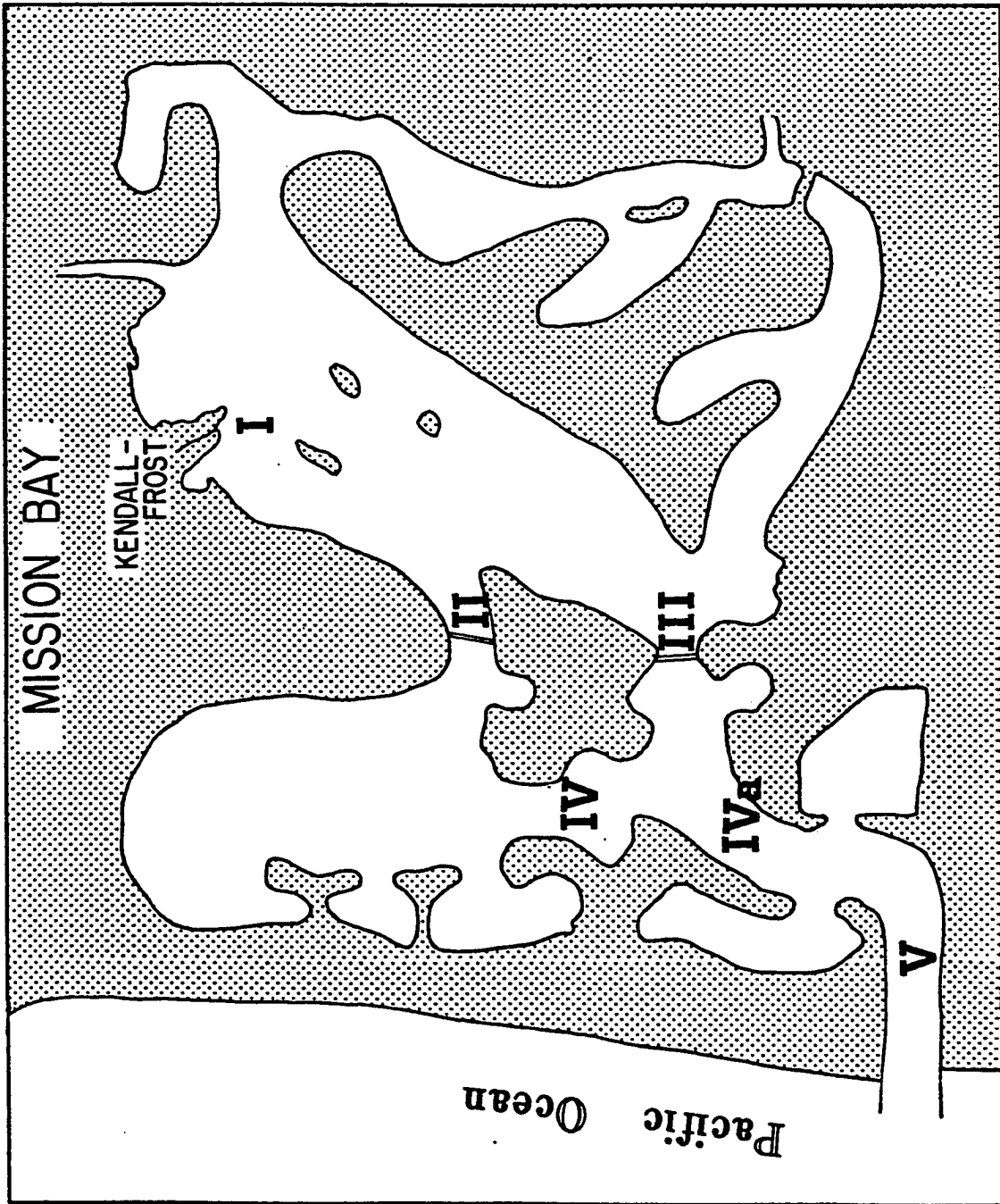
Plankton samples were collected at 5 stations in Mission Bay (Figure 13) using two 5" diameter Clarke Bumpus devices with #20 (75  $\mu$ ) mesh nets. Tows were made concurrently 0.5 m below the surface (called surface samples) and 1.5 - 2.0 m below the surface (called midwater samples). Two replicate tows (surface and midwater) were made at each station. Water volumes filtered per sample ranged from 0.5 to 20 m<sup>3</sup>. Plankton samples were collected on November 5, 1979, March 16, 1980, May 12, 1980 and August 25, 1980.

#### Kendall-Frost Sampling

##### General procedure

Plankton samples were collected over the Kendall-Frost mudflat at mid flood or mid ebb tide from a small inflatable raft or by wading. Surface samples were collected in plastic 1-gallon jars (= 0.004227 m<sup>3</sup>). Empty jars were filled by hand  $\approx$  0.2 m below the water surface. Near bottom samples, < 0.5 m above the sediment-water interface, were collected with a modified Van Dorn water sampler. A Van Dorn bottle was mounted horizontally on a long handle and stoppers were released with a line running to the top of the handle. This apparatus when held from the raft permitted collection of near-bottom water without disturbing the sediment surface. The water was allowed to flow through it for  $\approx$  60 sec. before closing the sampler. Water collected in this manner was then processed in 1-gallon units.

Figure 13: Plankton stations in Mission Bay sampled with Clarke-Bumpus nets.



All plankton samples collected in jars or with the modified Van Dorn sampler were sieved immediately in the field through a 63  $\mu$  mesh screen and then preserved in 5% formaldehyde and seawater. Plankton samples collected with the Clarke Bumpus nets were also preserved in 5% formaldehyde.

Prior to sorting, all samples were rinsed through a 63  $\mu$  mesh screen with fresh water. Single gallon (0.004227 m<sup>3</sup>) samples from the mudflat were sorted completely. Net tow samples were subsampled. These plankton samples were rinsed and placed in 250 ml graduate cylinders. Four 10 ml replicates were subsampled with a plunger from the well-mixed 250 ml slurry to give a sample of 1/25 of the original. When necessary to permit ease of sorting, each of these 10 ml samples was again subsampled in the same manner to yield four replicates representing 1/625 of the original sample.

#### Spatial analysis

The plankton in waters overlying Sites A and C (Figure 11) were sampled monthly (or more often) from March 1981 through December 1981. Four 1 gallon samples were collected in  $\approx$  0.5 m of water at  $\approx$  + 2.0 ft tide level during maximum ebb or flood tides.

#### Temporal analyses

##### Annual and seasonal variation

Plankton samples collected over the Kendall-Frost mudflat on scattered dates between March 1980 and August 1980 and monthly during 1981 were used to assess annual and seasonal fluctuations in meroplankton abundances.



### Tidal and diurnal variation

The waters overlying the Kendall-Frost mudflat were sampled intensively to investigate effects of tidal phase and light-dark cycles on the behavior and distribution of the meroplankton, particularly polychaete larvae.

The sampling was conducted during 4 tide series: April 14, 1980, 0800 - 2000; May 10, 1980, 0700 - 1900; July 15-16, 1981, 2100 - 0900; and July 27-28, 1981, 1930 - 0730. The 1980 sampling periods encompassed mainly daylight hours, the 1981 sampling periods spanned primarily dark (night time) hours.

On each date surface samples were collected from a plastic raft every 90 minutes through a complete tidal cycle. Four one-gallon replicates were taken and processed in the field and sorted as described earlier. On May 10, 1980 water samples for salinity analysis were collected in citrate bottles concurrently with the plankton sampling. In most cases 3 of 4 replicates were counted.

### Analysis of plankton sampling methods

#### Gallon jar vs. Van Dorn collections

The efficiency of the gallon jar collections was examined. When the jars are opened subsurface, exiting air creates excessive turbulence which might entrain particles or otherwise alter faunal densities in the water samples. Van Dorn samples do not pose this problem as the water has a chance to equilibrate before the sampler is closed. The two methods were compared using plankton data from samples collected on June 10, 1981. Four replicate samples were taken using each method. Mean

values for each species or taxon were compared using t tests; variances were compared with F tests (Table 4).

Both methods appear to sample invertebrate larvae with equal efficiency. However, more harpacticoid copepods and nematodes were collected by the Van Dorn sampler. This may be due to active avoidance of gallon jars or to slight but significant differences in proximity of the sample water to the mud surface. Though the differences between mean values of harpacticoid copepods and nematodes sampled with the 2 methods were not statistically significant, variances did differ significantly from one another ( $p < .002$ ). Absolute values of polychaete and other larvae may be determined from gallon jar samples, while absolute values of harpacticoid copepods and nematodes should not be. However, it is still possible to compare relative abundances of these latter taxa at different stations or different times. For example, though gallon jars undersample nematodes, there were significantly fewer nematodes in Site A than Site C gallon jar samples ( $t_3 = 5.249$ ,  $p = .004$ ) on June 10, 1981.

#### Small-scale patchiness

Horizontal patterns. On June 26, 1980, I collected plankton samples along a horizontal transect over the western mudflat in order to assess the magnitude of small-scale patchiness among major components of the plankton. Gallon jar sampling was generally done at one site (within a radius of several meters). The transect sampling examined the error introduced by a lack of spatial replicates.

Plankton at 4 surface stations, approximately 75 meters apart, was sampled along a transect perpendicular to the shoreline from  $z = -2.0$

Table 4  
Analysis of Plankton Collectors

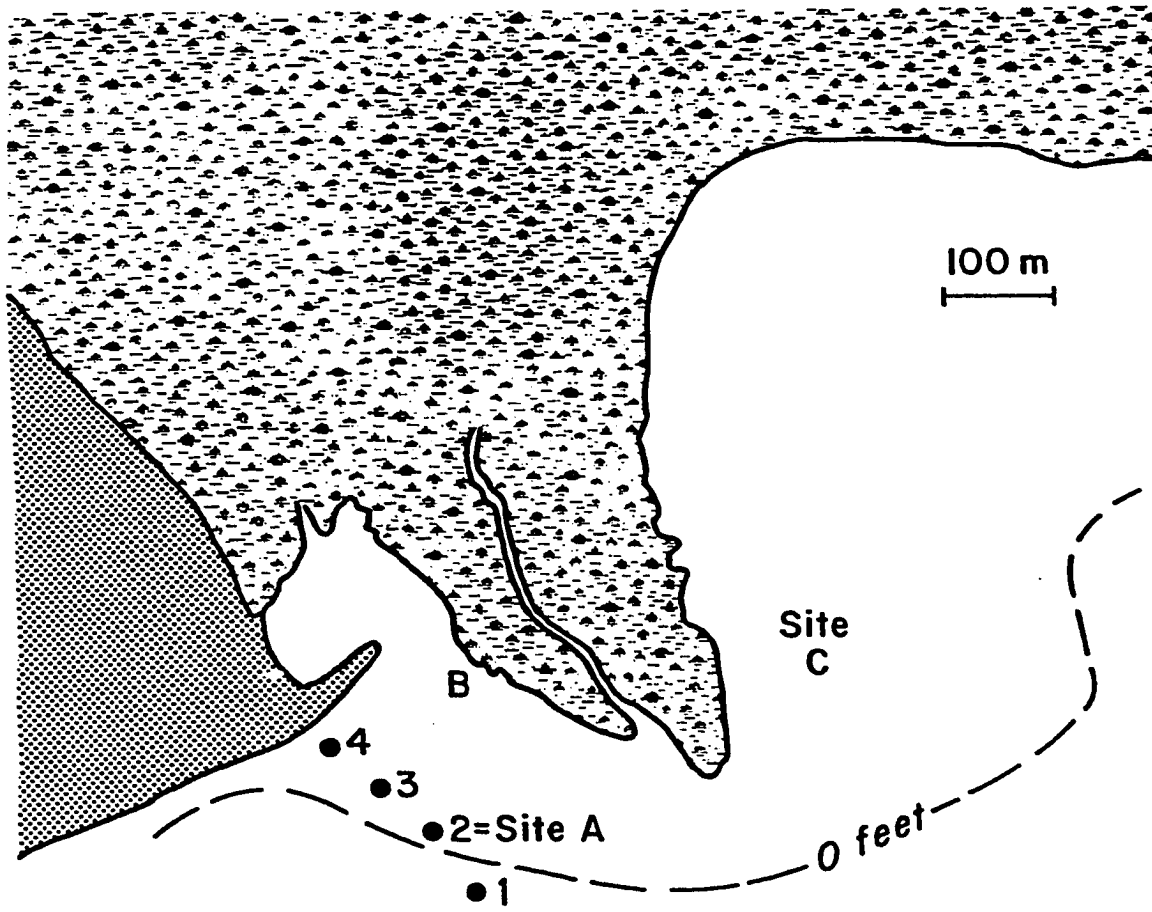
	mean (#/.004227 m <sup>3</sup> )		t test		F test	$\frac{s_1^2}{s_2^2}$	P
	Gallon Jars	Van Dorn Sampler	t	P			
Total Polychaete Larvae	201.0	179.5	0.541	.61	F <sub>3,3</sub>		
<u>Pseudopolydora paucibranchiata</u>	84.0	74.8	0.525	.62	1.57		>.50
<u>Polydora ligni</u>	8.8	7.5	0.289	.78	3.21		>.20
<u>Rhynchospio arenicola</u>	14.5	10.8	1.473	.19	7.86		>.00
Other spionid polychaetes	9.0	10.5	-0.320	.76	1.69		>.50
Bivalve Larvae	2.5	0.5	0.894	.406	19.0		<.02
Phoronid Larvae	0.5	0.5	0	1.00	3.0		>.20
<u>Oikopleura spp.</u>	0.25	0.5	-0.655	.54	1.32		p>.20
Harpacticoid Copepods	1.8	23.5	-1.729	.14	2499.00		p<<.002
Nematodes	3.3	10.5	-1.885	.11	25.23		p<.02

ft to +4 ft above Mean Low Low Water (Figure 14). Sampling Site A occurs as the second station along this transect. Four one-gallon replicate samples were collected at each station during high tide, 0930 - 1000. Table 5 gives mean values ( $\pm 2$  S.D.) and the results of one way ANOVA to compare stations, for each species or taxonomic grouping. For most of these species variance between stations was no greater than variance among replicates within a station. The exceptions to this were Pseudopolydora larvae and harpacticoid copepods. Pseudopolydora larval densities were almost identical at stations 1, 2 and 3 but significantly lower at the shoreward station 4. (ANOVA,  $p < .05$ ) Harpacticoid copepods were patchily distributed with highest abundances at stations 1 and 4. These data suggest that at the time of sampling most species did not exhibit any significant patchiness on the scale examined. Samples taken over the middle of the mudflat are likely to represent the range of densities of invertebrate larvae encountered over most of the mudflat.

Vertical patterns. Several samples were collected at station 1 (-2.0 ft) at 3 depths at 1100 on June 26, 1980 to determine whether surface sampling was an appropriate method to estimate densities of invertebrate larvae over the mudflat. Most of the larvae under study are photo-positive during much of their planktonic life and would be expected to reside in surface waters shortly after their release. Most of the invertebrate larvae were found in the surface samples and all the invertebrate taxa considered in this dissertation were most abundant in surface waters (Table 6).

Figure 14: Plankton sampling stations over the Kendall-Frost mudflat, Mission Bay, California, June 26, 1980.

# KENDALL-FROST MARSH RESERVE



MISSION BAY

Table 5

Plankton Abundance\* over the Kendall-Frost Mudflat:  
Horizontal Patterns  
(June 26, 1980)

	Station I (Bayward)	2	3	4 (Shoreward)	One Way Analysis of Variance between Stations p < .05
<u>P. paucibranchiata</u>	27.5 ± 13.1	29.5 ± 23.0	28.3 ± 13.7	11.3 ± 10.8	p < .05
<u>P. ligni</u>	4.75 ± 9.6	2.0 ± 4.7	.0 ± 0.0	1.0 ± 1.4	NS
<u>Rhynchospid arenicola</u>	9.0 ± 4.7	13.5 ± 21.8	3.75 ± 4.5	3.75 ± 1.4	NS
Bivalves	4.5 ± 7.0	2.75 ± 2.60	3.0 ± 4.70	0.0 ± 0.0	NS
Phoronid	1.75 ± 2.60	1.50 ± 2.24	0.5 ± 1.0	0.0 ± 0.0	NS
Unid Spionid	5.25 ± 4.33	8.5 ± 4.58	5.75 ± 5.89	5.5 ± 11.0	NS
Harpacticoid copepods	16.66 ± 8.22	9.25 ± 7.80	2.5 ± 4.58	17.75 ± 15.1	p < .05
Calanoid copepods	26.67 ± 25.52	9.0 ± 17.49	1.75 ± 2.96	7.75 ± 7.40	NS

\*#/gallon (.004m<sup>3</sup>),  $\bar{X} \pm 2$  S.D.

Table 6  
Vertical Distribution of Meroplankton over the  
Kendall-Frost Mudflat

	Mean #/gallon		
	Surface	Midwater	Near Bottom
meters below surface	(0.3)	(1.0)	(2.0)
<u>Pseudopolydora paucibranchiata</u>	14.0	6.0	1.5
<u>Polydora ligni</u>	1.5	1.0	0.0
<u>Rhynchospio arenicola</u>	2.5	1.0	0.0
Unid. Spionid	14.0	4.0	0.0
Bivalve Veligers	2.0	0.0	1.0
Actinotrocha	4.0	0.0	0.0



## Results

### Mission Bay Plankton Distributions

The taxa encountered during the quarterly survey of Mission Bay plankton (1979-1980) are listed in Table 7. Trends observed for specific taxa are discussed below.

#### Meroplankton

Bivalve veligers (Figure 15) were most abundant in August and November samples (over  $2,000/m^3$ ) at mid-bay stations. Densities were higher at mid depths than at the surface at all stations except the Ship Channel (V), where on 3 of 4 sampling dates, near surface densities were higher. Bivalves occur in the benthos throughout Mission Bay but are most common in the mid and back bay regions (Dexter, 1979).

Spionid polychaete larvae (Figure 15), like bivalves, were abundant during all sampling periods with maximum densities (over  $2000/m^3$ ) recorded in August 1980. At mid and back-bay stations, midwater tows caught more larvae than surface tows, with the exception of Station I (back bay) in May, when there were 10x more larvae at the surface than mid depths. Spionid larvae in the Ship Channel (Station V) were more abundant in surface tows than in midwater tows. In all instances spionid larvae decreased in abundance from back-bay Station I towards the ocean, though Station IVa exhibited high densities in August. Spionid polychaetes occur in the benthos throughout Mission Bay and attain highest densities in intertidal areas (unpublished data).

A close look at the larval distributions of Pseudopolydora paucibranchiata (Figure 15) reveals trends similar to the spionids as a group. More larvae were found in midwater than surface tows at all

Table 7

## Mission Bay Plankton

Meroplankton

Polychaete larvae

Pseudopolydora paucibranchiataPolydora ligni

Unid Spionids

Nereid larvae

Polynoid larvae

Bivalve larvae - veligers

Gastropod larvae

Cyphonautes

Ophioplutei

Actinotroch

Crab Zoea

Nauplii

Cyprids

Coelenterate medusae

Mullers larvae

Larval fish

Nematodes

Ostracods

Turbellaria

Holoplankton

Calanoid Copepods

Acartia tonsa

Harpacticoid Copepods

Cyclopoid Copepods

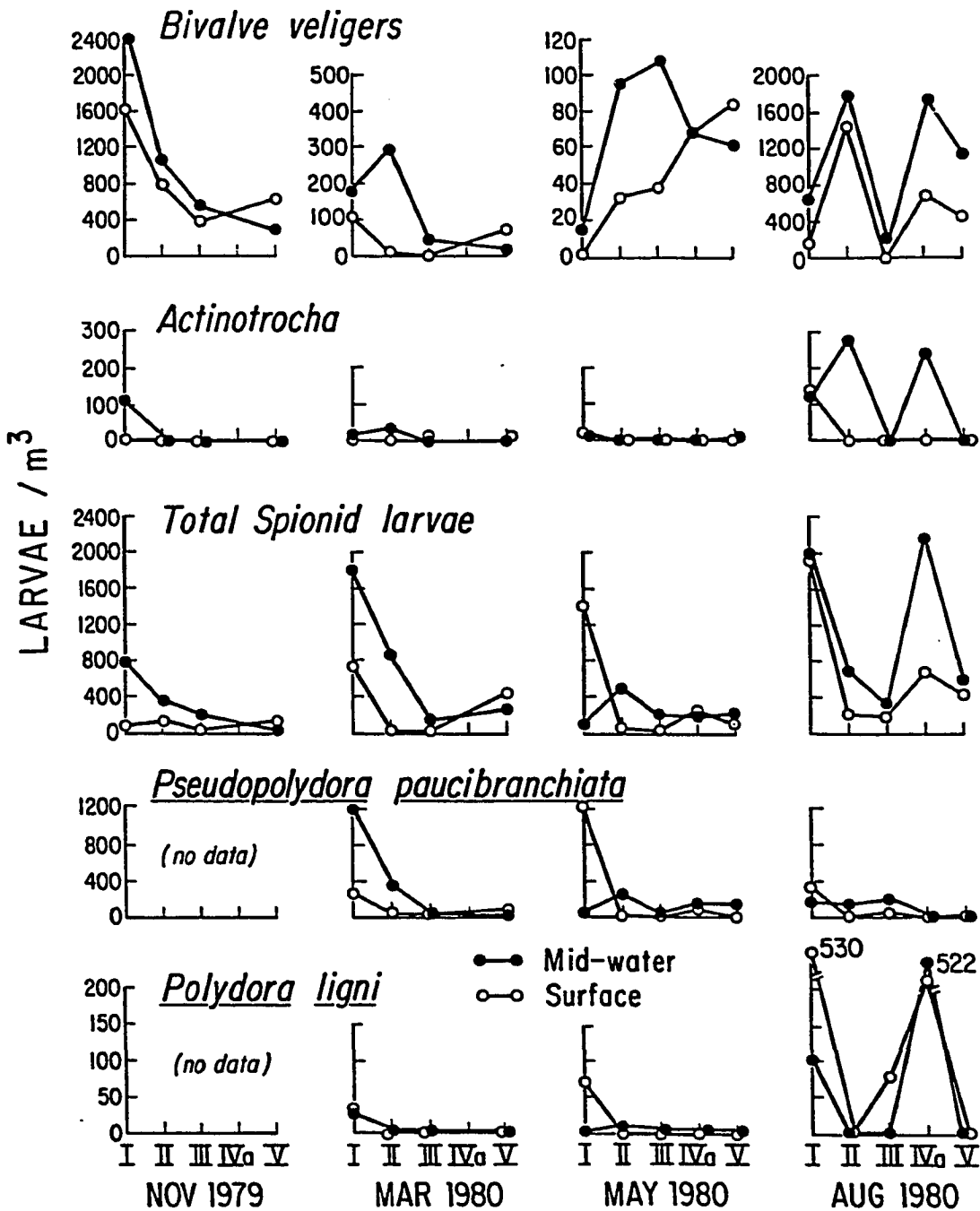
Oithona sp.Oikopleura sp.

Chaetognath

Cladocerans

Foraminifera

Figure 15: Mission Bay Meroplankton: a quarterly survey of  
Bivalve, Spionid, Pseudopolydora paucibranchiata,  
Polydora ligni and phoronid larval abundances,  
1979-1980.



stations except Station I, where in May and August more larvae were present at the surface. Station I is nearest the site of origin (Kendall-Frost Reserve) for many of the Pseudopolydora larvae, which swim to the surface as newly released 3-setiger forms. Densities were highest (over  $1200/m^3$ ) in the plankton in March and May—corresponding to a period of active Pseudopolydora reproduction and recruitment on the Kendall-Frost mudflat. Station I (where the adult population is centered) always exhibited the greatest abundance of Pseudopolydora larvae and densities declined toward the front bay.

Polydora ligni larvae (Figure 15), though never abundant, were most common in August. The majority of P. ligni larvae occurred at Station I during March and May, but in August a second source of larvae must have been present near Station IVa (Figure 13), perhaps in Bonita Cove (see Figure 2), a small shallow inlet opening into the main channel. No clear depth preference was observed in P. ligni larval distributions.

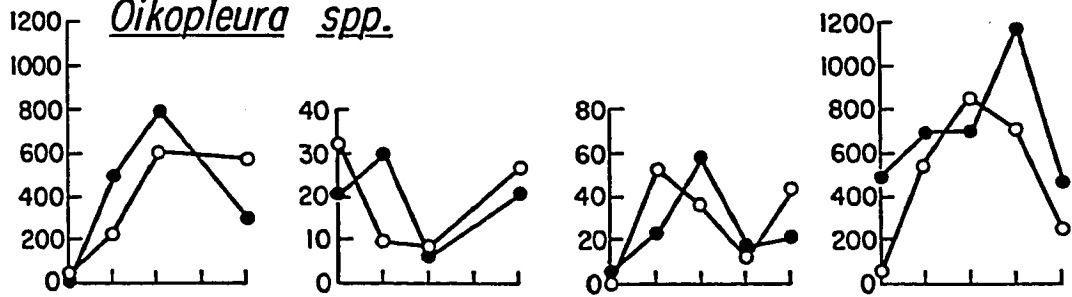
Phoronid larvae (actinotrocha), generally rare, were most abundant in August (Figure 15). Actinotroch larvae occurred primarily in midwater samples, except at Station I where surface and midwater densities did not differ.

#### Holoplankton

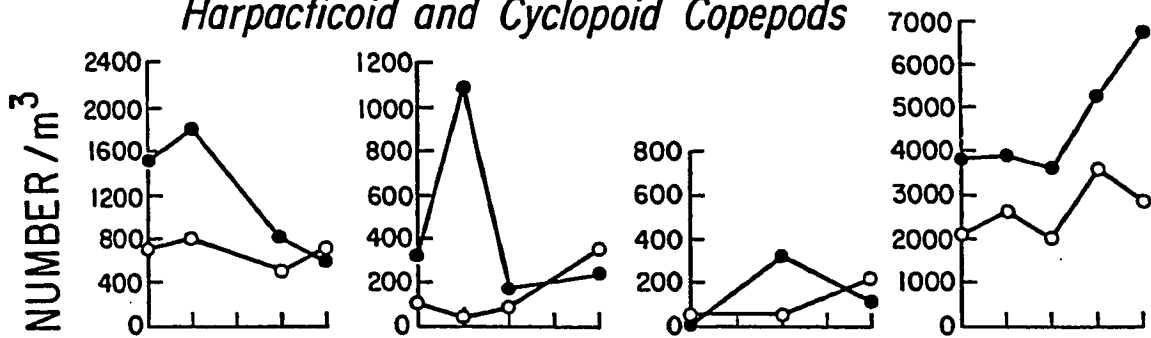
Oikopleura spp. densities were highest in August and November (over  $1,000/m^3$ ) (Figure 16). The mid bay stations (II, III and IVa) generally had the highest densities (except in March), and more Oikopleura were present in midwater than surface samples.

Figure 16: Mission Bay Holoplankton: a quarterly survey of Oikopleura spp., calanoid, harpacticoid, and cyclopod copepod abundances, 1979-1980.

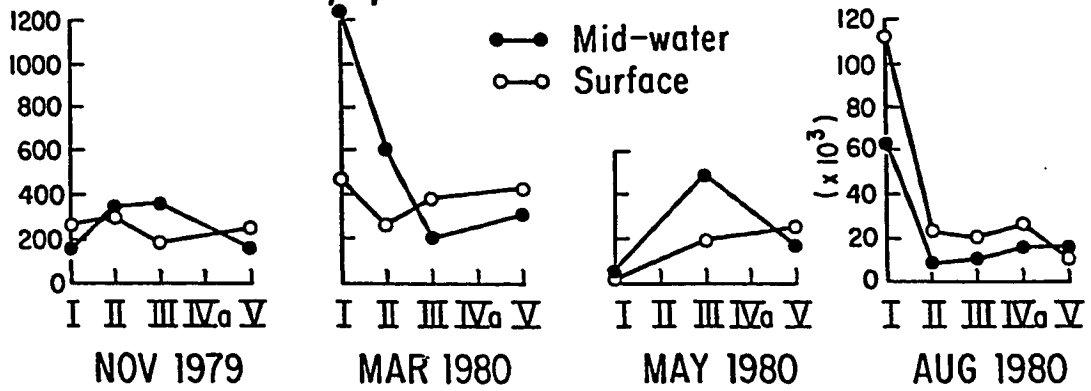
*Oikopleura spp.*



*Harpacticoid and Cyclopoid Copepods*



*Calanoid Copepods*



Harpacticoid and cyclopoid copepods (Figure 16) were most abundant in August samples. More copepods were present in mid than surface waters except in the Ship Channel where surface values were slightly higher in March, May and November. In these months peak densities occurred at mid-bay stations; in August densities increased towards the Ship Channel.

Calanoid copepods were 3 orders of magnitude more abundant in August than in other months (Figure 16). Acartia tonsa accounted for over 90% of the individuals. In August more calanoid copepods were present in surface than midwater samples, but in other months there were no clear trends. Highest densities were encountered at Station I in March and August, while in November and May the copepods were evenly distributed throughout the bay.

#### Kendall-Frost Plankton Distributions

Table 8 provides a list of species or taxa found in waters overlying the Kendall-Frost mudflat. Only a few of these are sufficiently abundant to discern spatial and temporal patterns in distribution. The following discussion will focus on the polychaete larvae which are released from adults on the mudflat, and will draw on patterns seen in other taxa to interpret the passive or active nature of the polychaete distributions.

#### Spatial patterns

##### Site A vs. Site C

Pseudopolydora paucibranchiata. Pseudopolydora larvae were more abundant (though not significantly) in the water at Site A than at Site



Table 8  
Kendall-Frost Plankton

The following taxa were collected from waters overlying the Kendall-Frost mudflat during 1980 and 1981.

<u>Oikopleura</u> sp.	Grass shrimp
Gastropod Veliger	Mysids
Muller's larvae	Ascidian tadpole
Bivalve veligers	Anthomedusae
<u>Musculus senhausii</u>	Sipunculan larva
Actinotroch larvae	Oligochaete
Polychaete larvae	Turbellaria
<u>Pseudopolydora paucibranchiata</u>	Nemertean
<u>Polydora ligni</u>	Tadpole larva
Unid spionid	Calanoid Copepods ( <u>Acartia tonsa</u> )
<u>Rhynchospio arenicola</u>	Harpacticoid Copepods
Nereidae	Cyclopoid Copepods
<u>Capitella capitata</u>	Brachyuran Zoea
Polynoidae	Nauplii
<u>Owenia</u> sp.	<u>Post-Larval Stages</u>
<u>Eteone</u> sp.	Polychaetes
<u>Armandia bioculata</u>	<u>Odontosyllis phosphorea</u> (adult and juvenile)
Chaetognaths	<u>Exogone lourei</u> (adult)
Ostracods	<u>Streblospio benedicti</u> (juvenile)
Cladoceran	<u>Rhynchospio arenicola</u> (juvenile)
Cumacean	<u>Fabricia limnicola</u> in tube (1)
Gammarid Amphipods	Sabellid
Caprellid Amphipods	<u>Eteone</u> sp.
Isopods	<u>Capitella capitata</u>
Nematodes	<u>Polycipes</u> sp.
Fish eggs, fish larvae	Tubificid Oligochaete
<u>Atherinops affinis</u> (top smelt)	<u>Musculus senhausi</u>

C ( $t_8 = 1.579$ ,  $p = .15$ ) (Figure 17). This difference was most dramatic during the March and June abundance peaks and was probably due to a greater number of adults in the benthos releasing larvae at Site A (see Figure 39). There were no detectable differences between the numbers of competent (> 10 setiger) larvae at the two sites, though the 1981 numbers were very small. The abundances of Pseudopolydora larvae at the two sites are correlated with one another ( $r = .701$ ,  $p < .05$ ); peaks and troughs in abundance occurred at the same time.

Polydora ligni. There was no significant difference between larval abundances at Sites A and C ( $t_8 = .898$ ,  $p = .39$ ) though like Pseudopolydora, Site A exhibited higher peak densities (seen in May and July) (Figure 18). There was no significant correlation in abundance pattern between sites ( $r = .259$ ,  $p > .05$ ). Benthic abundances of Polydora ligni were somewhat higher at Site A than C in 1981 (Figure 40).

Rhynchospio arenicola. Larval abundances were well correlated at Sites A and C ( $r = .716$ ,  $p < .05$ ) but higher at Site A ( $t_8 = 2.259$ ,  $p = .05$ ) throughout the spring (Figure 19). Abundance peaks occurred in the plankton in January, early May and late June. 1981 benthic abundances were higher at Site A than C (Figure 41).

Though larvae of each species seemed somewhat more abundant in waters overlying Site A than Site C, the species' densities did not exhibit a temporal correlation with one another. Each species exhibited several abundance peaks concurrently at Sites A and C, during the 8 - 10 month period. However, the timing of most of these peaks did not overlap for different species.

Figure 17: Pseudopolydora paucibranchiata larval abundances in  
waters over the Kendall-Frost mudflat, 1980-1981  
( $\bar{X} \pm 2 \text{ S.D.}$ )

*Pseudopolydora paucibranchiata*

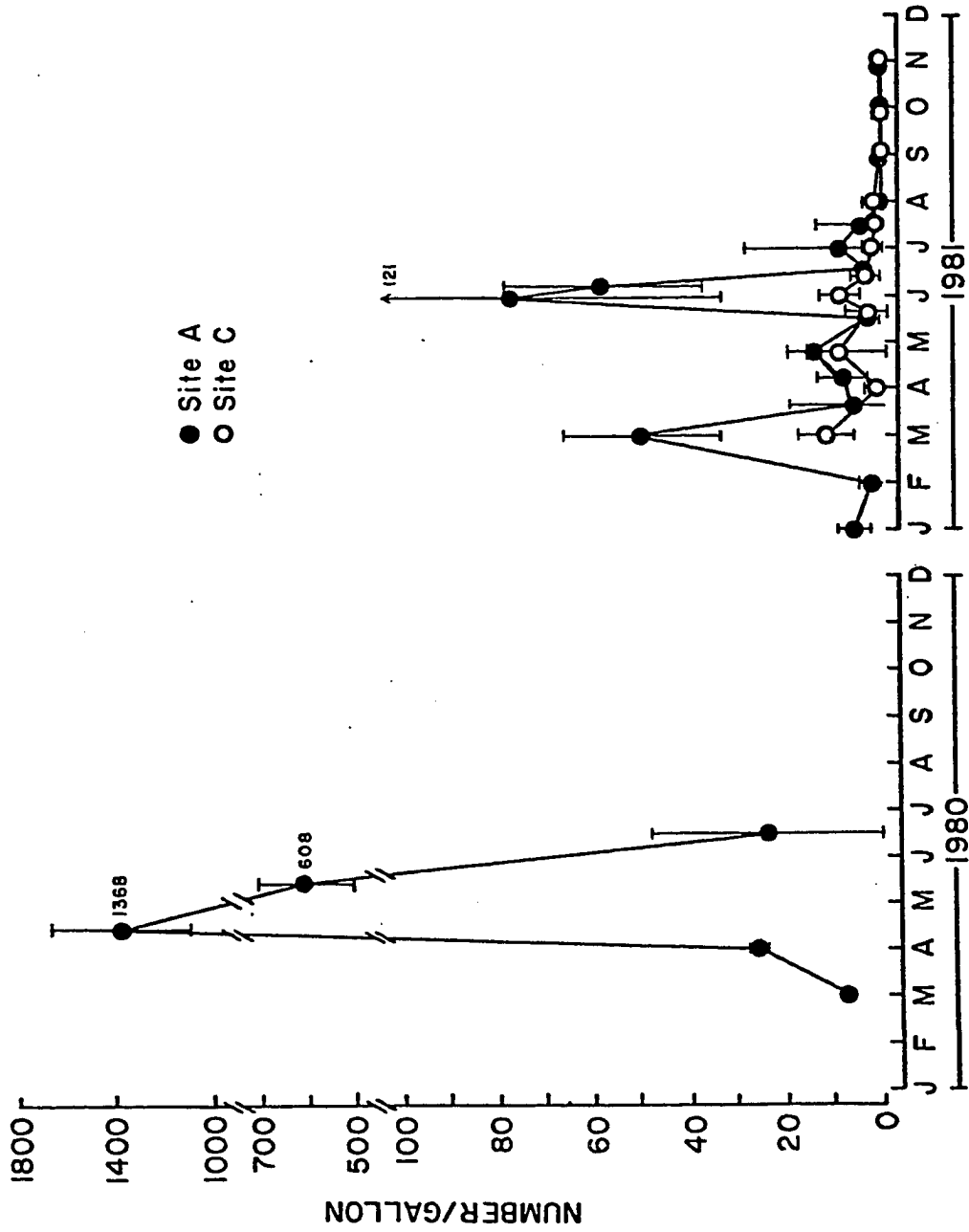


Figure 18: Polydora ligni larval abundances in waters over the Kendall-Frost mudflat, 1980-1981 ( $\bar{X} \pm 2$  S.D.).

*Polydora ligni*

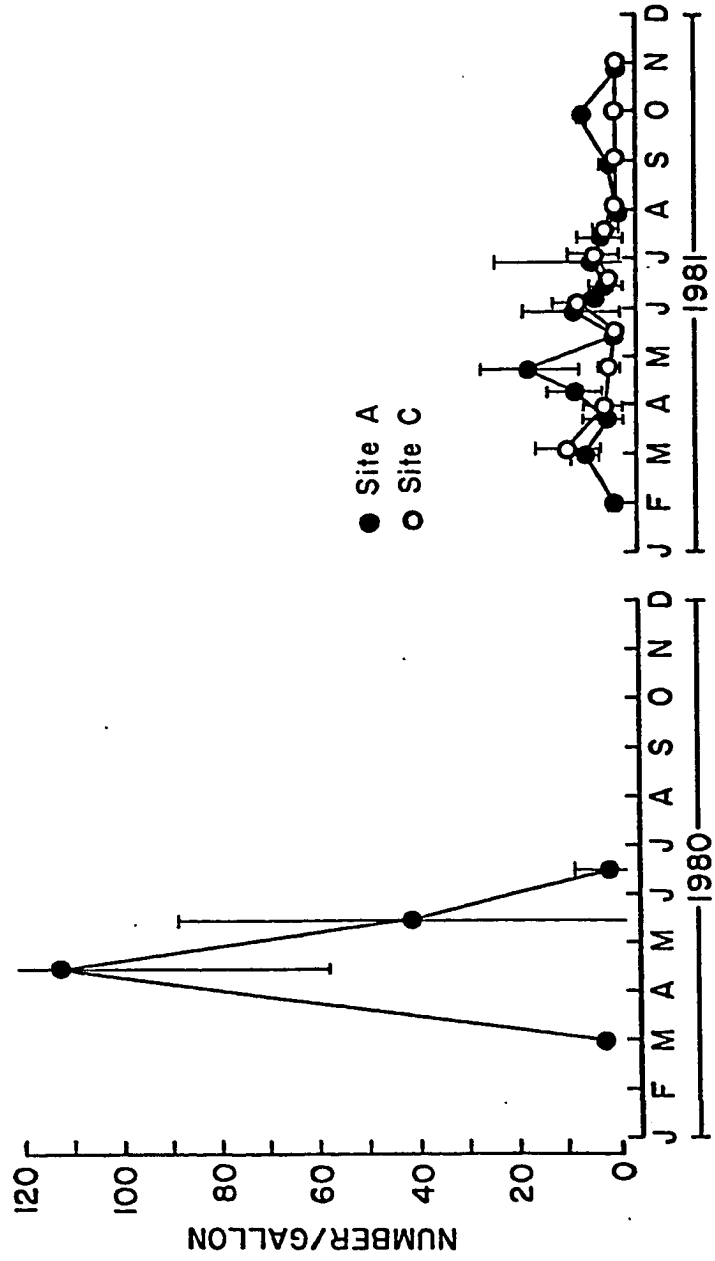
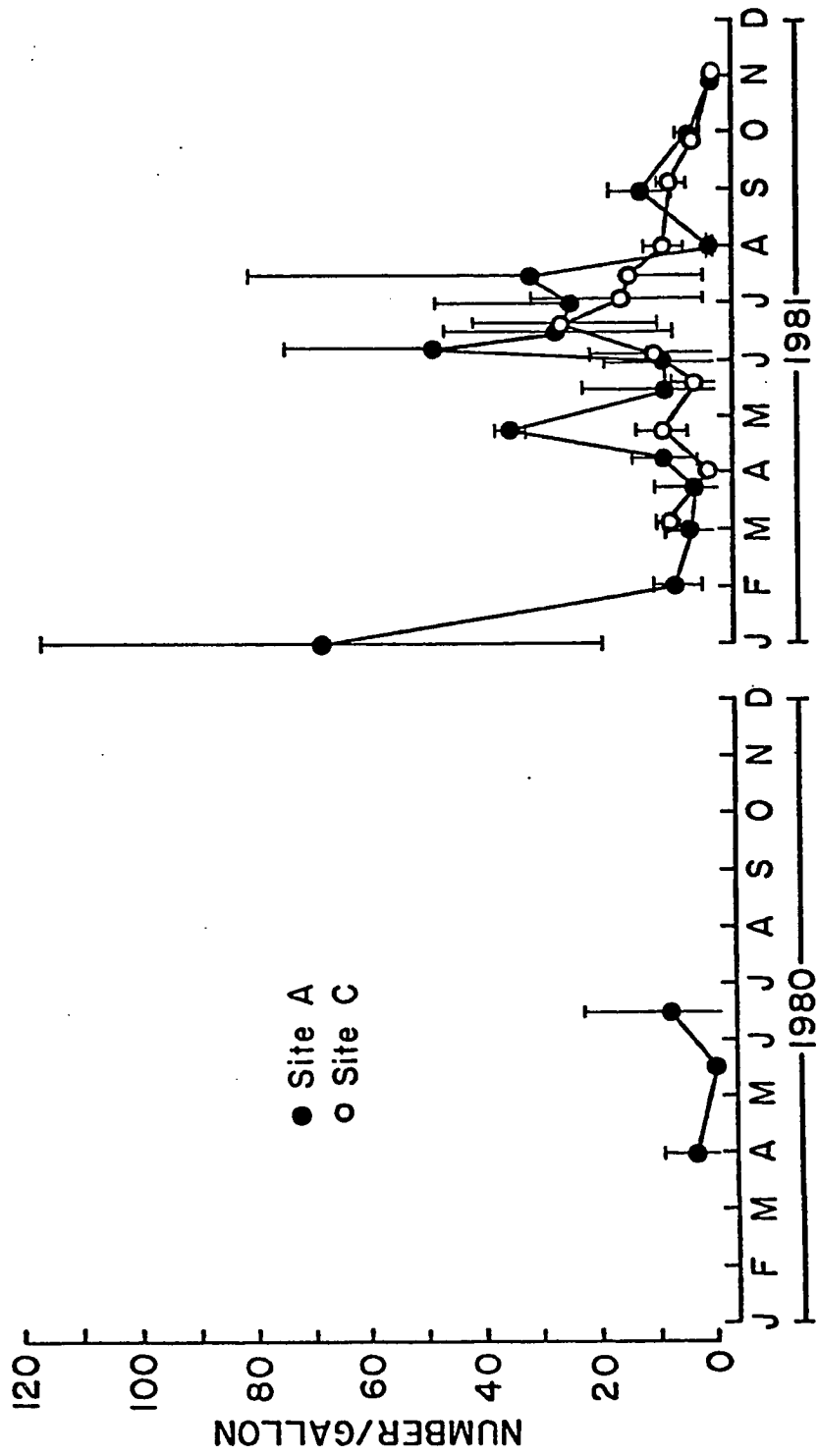


Figure 19: Rhynchospio arenicola larvae over the Kendall-Frost mudflat, 1980-1981 ( $\bar{X} \pm 2$  S.D.).

*Rhynchospio arenicola*





### Temporal patterns

Temporal variations in larval abundance in the plankton were observed during this study. Annual fluctuations in planktonic abundance are a well-documented phenomenon for some benthic species (Loosanoff, 1964; Coe, 1956) and are reflected in annual variation in recruitment and benthic abundances. Season variations are the best understood of temporal patterns and were observed for most of the species in this study. Lunar cycles seem to be important to some components of the plankton, particularly crustaceans. Finally, both tidal cycles and diurnal light-dark regimes had a major influence on plankton abundance patterns over the Kendall-Frost mudflat.

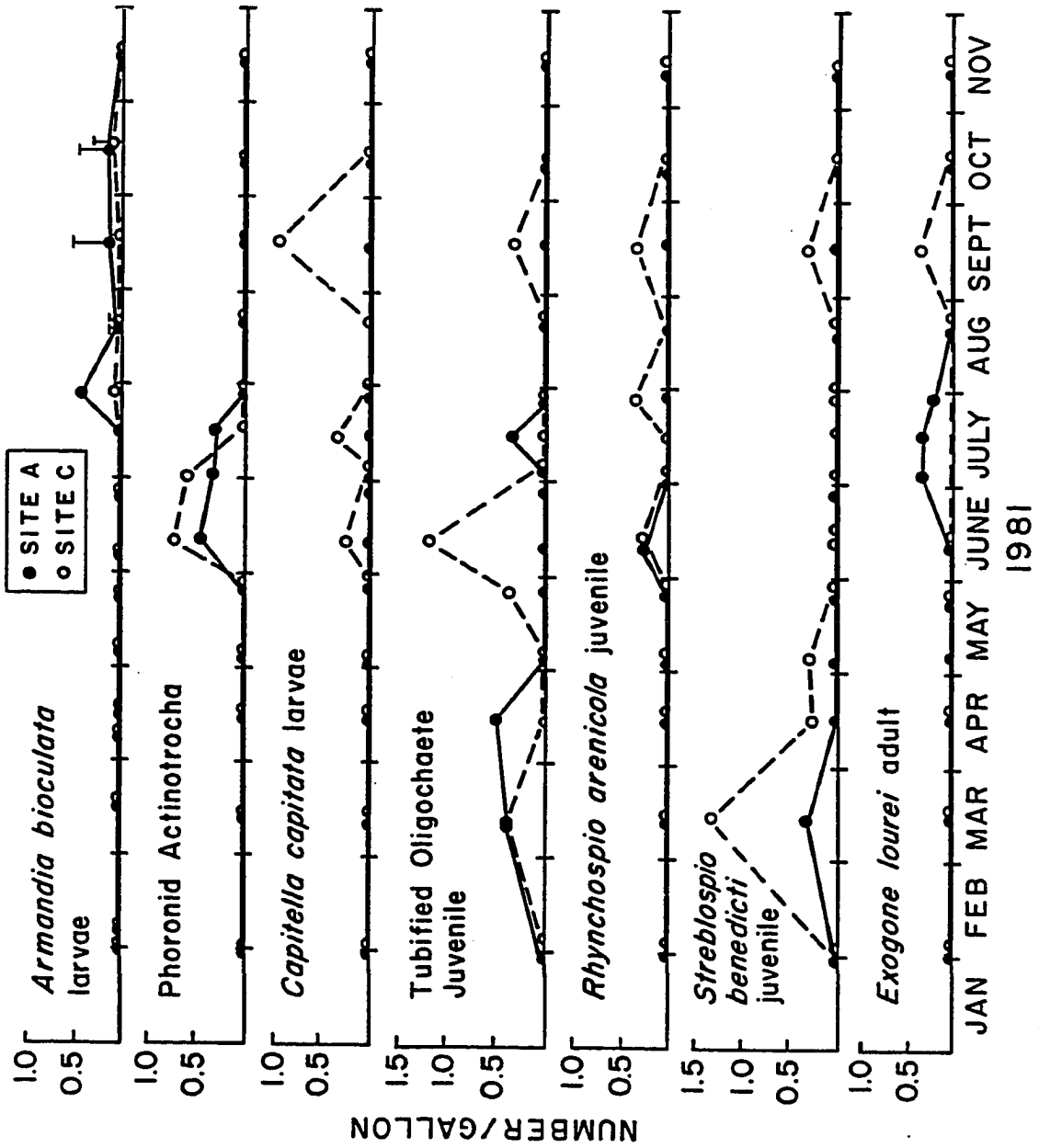
### Annual variation

A regular plankton sampling program for waters overlying the Kendall-Frost mudflat was begun in 1981. Prior to that time sampling took place on a few scattered dates between March and August of 1980. From counts of those samples it appears that both Pseudopolydora paucibranchiata and Polydora ligni obtained higher larval densities during April of 1980 than during any period in 1981. Pseudopolydora was 2 and Polydora was one order of magnitude more abundant in April 1980 than in April 1981 (Figures 17, 18).

### Seasonal variation

Several species represented in the plankton exhibited sharp seasonal peaks. Armandia bioculata for example was present only briefly each year in summer (Figure 20). Most of these larvae probably originated from eggs spawned by Armandia living subtidally in Mission Bay. Pseudopolydora larvae were present from January through August with one

Figure 20: Meroplankton in waters over the Kendall-Frost mudflat: Armandia bioculata, Capitella capitata, actinotrocha, oligochaete juveniles, Rhynchospio juveniles, Streblospio juveniles, Exogone adults.



or more peaks in spring (Figure 17). Polydora ligni exhibited a pattern similar to Pseudopolydora (Figure 18), while Rhynchospio larvae were abundant all year with peaks every month or two (Figure 19). Capitella larvae appeared during the latter half of the year, as did Exogone lourei adults and Rhynchospio juveniles (Figure 20). Phoronis sp. actinotrochs were present in summer (June and July), while Streblospio juveniles were most abundant in spring and fall. Oligochaetes were present sporadically throughout the year, (Figure 20).

#### Diel variation

1980 daytime sampling. The April 14 sampling program revealed a bimodal pattern of abundance for bivalve veligers and the 4 abundant species of polychaete larvae, (Pseudopolydora paucibranchiata, Polydora ligni, Rhynchospio arenicola and an unidentified spionid) with peak abundances 2 1/2 hours after the first high tide and 1 1/2 hours before the next high tide (Figure 21). Variances during these peak periods of abundance were also very high. The May 10 sampling presented a similar pattern for P. paucibranchiata and P. ligni during the ebb tide (Figure 22). Peak abundances occurred 1 1/2 hours after high tide; however, a clear second peak did not occur during ebb tide. The other two spionid species were rare or absent in most May 1980 samples.

This bimodal pattern was not seen in some of the more rare meroplankton (e.g., phoronids on April 14, 1980 and May 10, 1980) (Figure 23). Caprellids and gammarid amphipods (not counted in April 14, 1980 samples) exhibited peak abundance just before, during and after low tide on May 10, 1980 (Figure 23).

Figure 21: Larval abundances in waters over the Kendall-Frost mudflat, sampled during a complete tidal cycle. April 14, 1980; 0800 - 2000 ( $\bar{X} \pm 2$  S.D.).

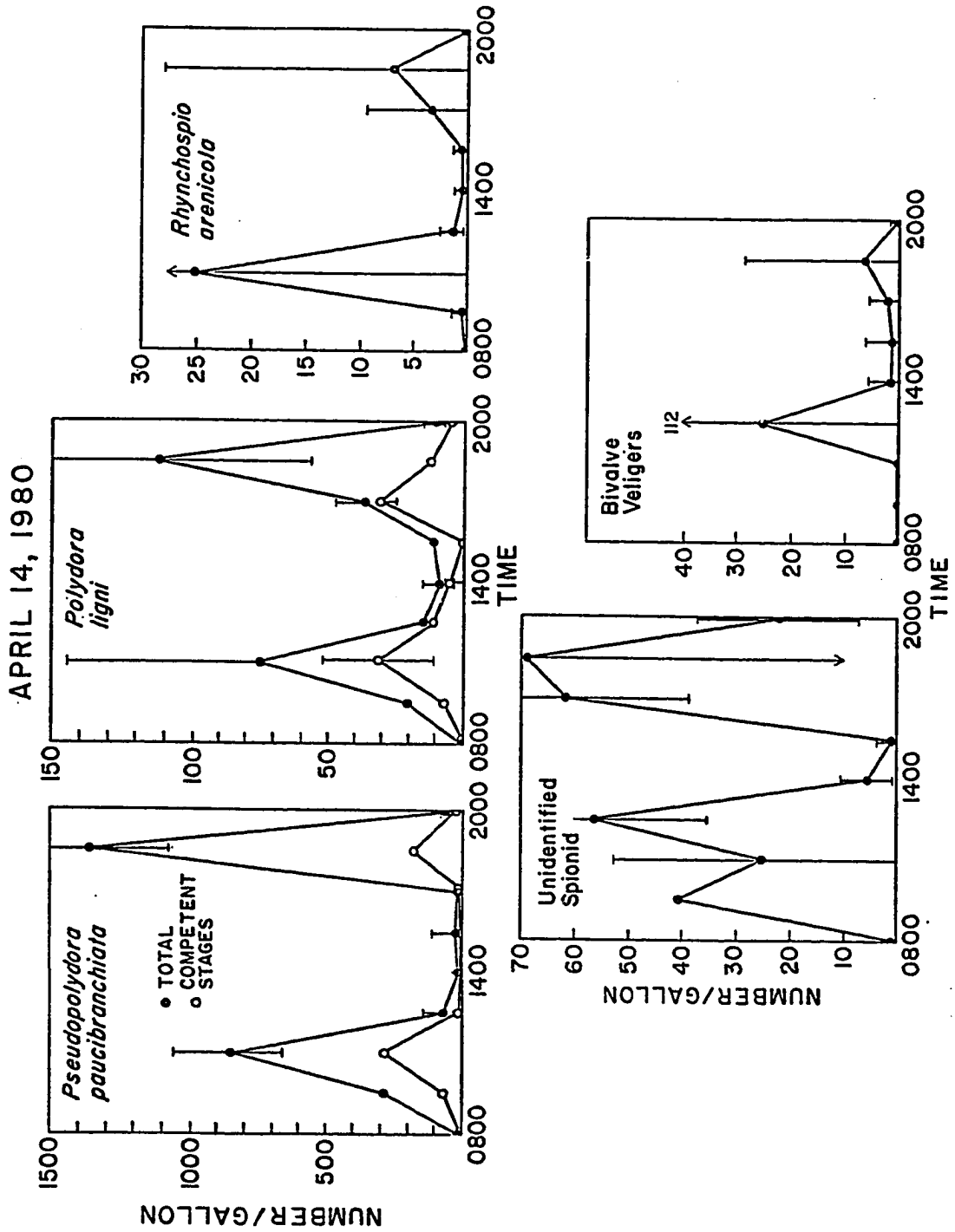


Figure 22: Polychaete larval abundances in waters over the Kendall-Frost mudflat sampled during a complete tidal cycle. May 10, 1980; 0700 - 1900 ( $\bar{X} \pm 2$  S.D.).

MAY 10, 1980

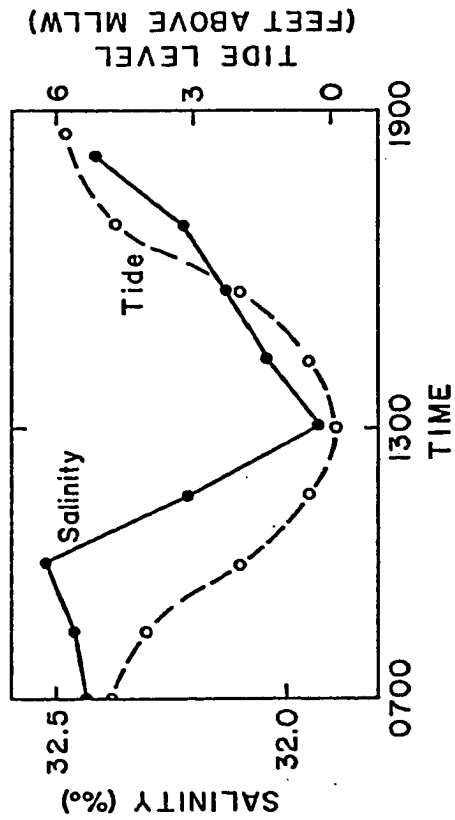
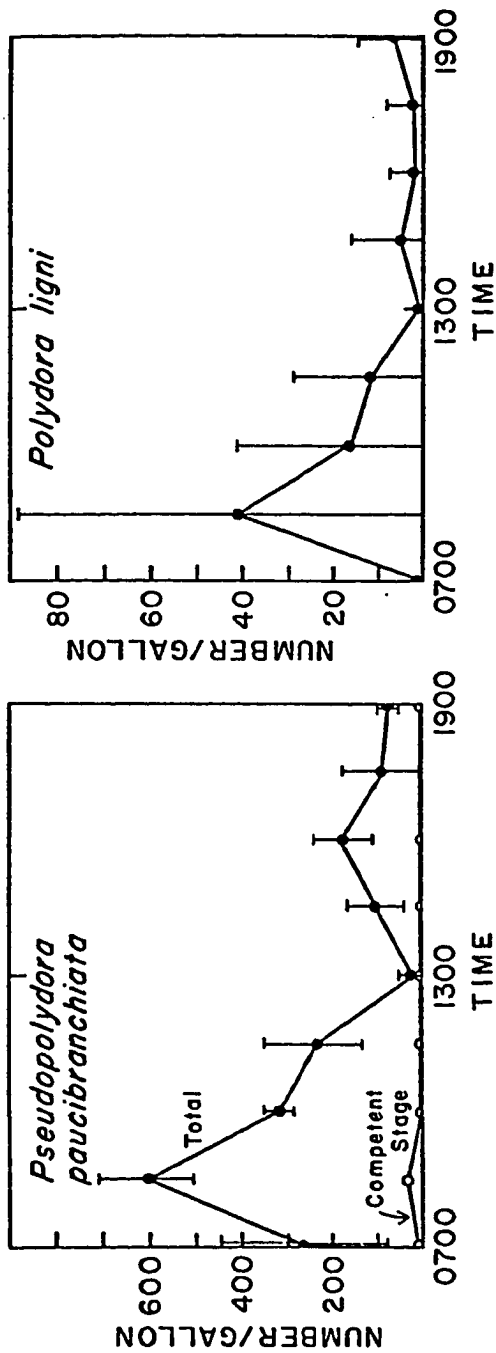
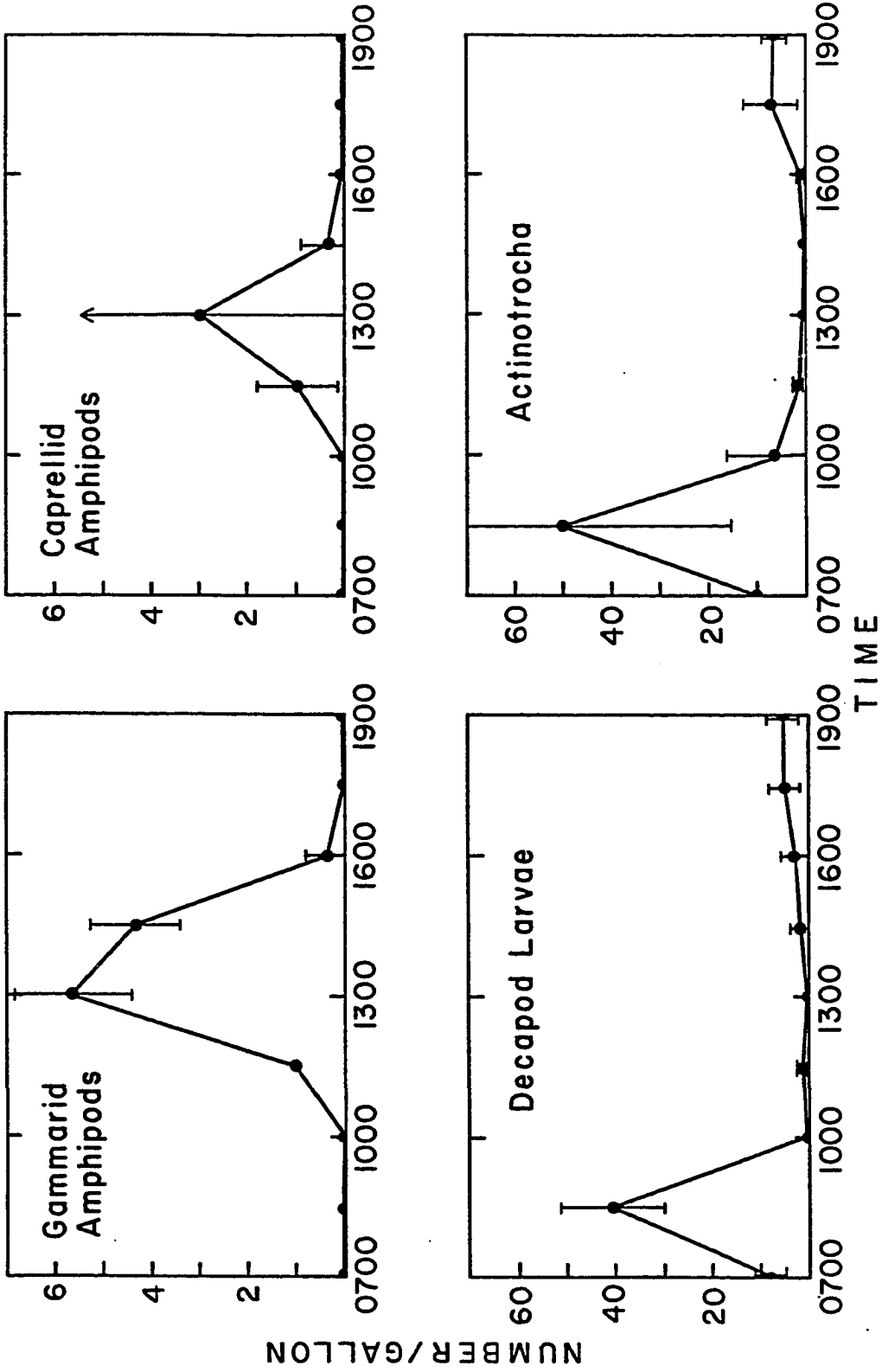




Figure 23: Plankton abundances in waters over the Kendall-Frost mudflat sampled during a complete tidal cycle: actinotrocha, decapod larvae, amphipods. May 10, 1980; ( $\bar{X} \pm 2$  S.D.).

MAY 10, 1980



Nocturnal sampling: 7/15-16 and 7/27-28, 1981

Tidal heights for both nocturnal sampling dates are presented in Figure 24.

a. Polychaetes. On both night-time sampling dates Rhynchospio arenicola was the numerically dominant larval polychaete. Total polychaete abundances on July 15 - 16 peaked at low tide due to a massive spike of Rhynchospio. On July 28 total polychaete abundances peaked at dusk high and dawn high tides, with very few present at low tide. Omission of the Rhynchospio collected in 0430 (low tide) samples on July 16 would cause the abundance patterns for total spionids on the two dates to be similar.

Pseudopolydora paucibranchiata larvae were approximately 1/3 as abundant on July 28 as on July 16, 1981, but tidal cycle dynamics were similar. Peaks occurred at high tide (dusk) with relatively low numbers during ebb, low, flood, and dawn high tides (Figure 25). On both sampling dates late development stages ( $\geq 10$  setigers) mimic the early development stages, suggesting that there is no spatial or behavioral separation between the two groups. Competent stages ( $\geq 10$  setigers) seem approximately one third as abundant as early stages ( $< 10$  setigers) during high and ebb tides, but are comparable in abundance during low and flood tides, when newly released larvae have been presumably washed off the mudflat. This suggests that larval release may occur during high or ebb tide.

Maximum abundances for Polydora ligni were observed during dusk at high tide and the ebb tide following it on July 16 and July 28, though larvae were more abundant on the first sampling date (Figure 26). The late stage larvae ( $\geq 12$  setigers) did not exhibit this pattern.

Figure 24: Tidal heights on the Kendall-Frost mudflat during nocturnal plankton sampling. July 15 - 16, July 27 - 28, 1981.

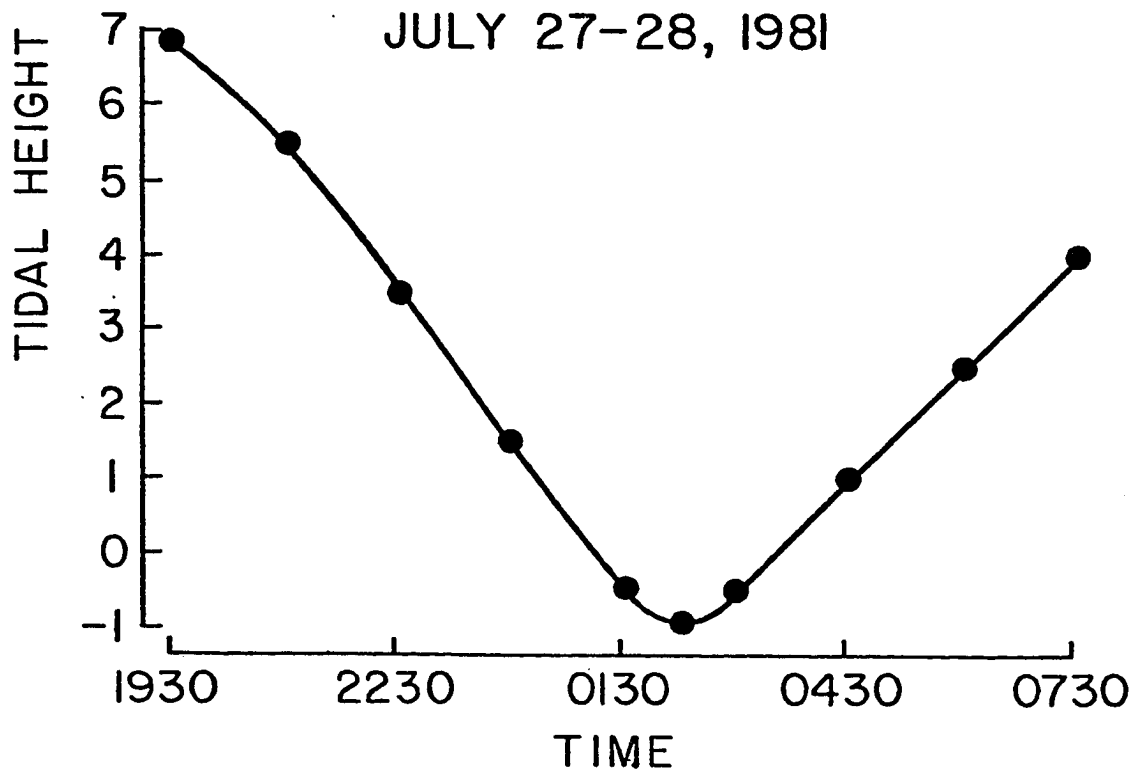
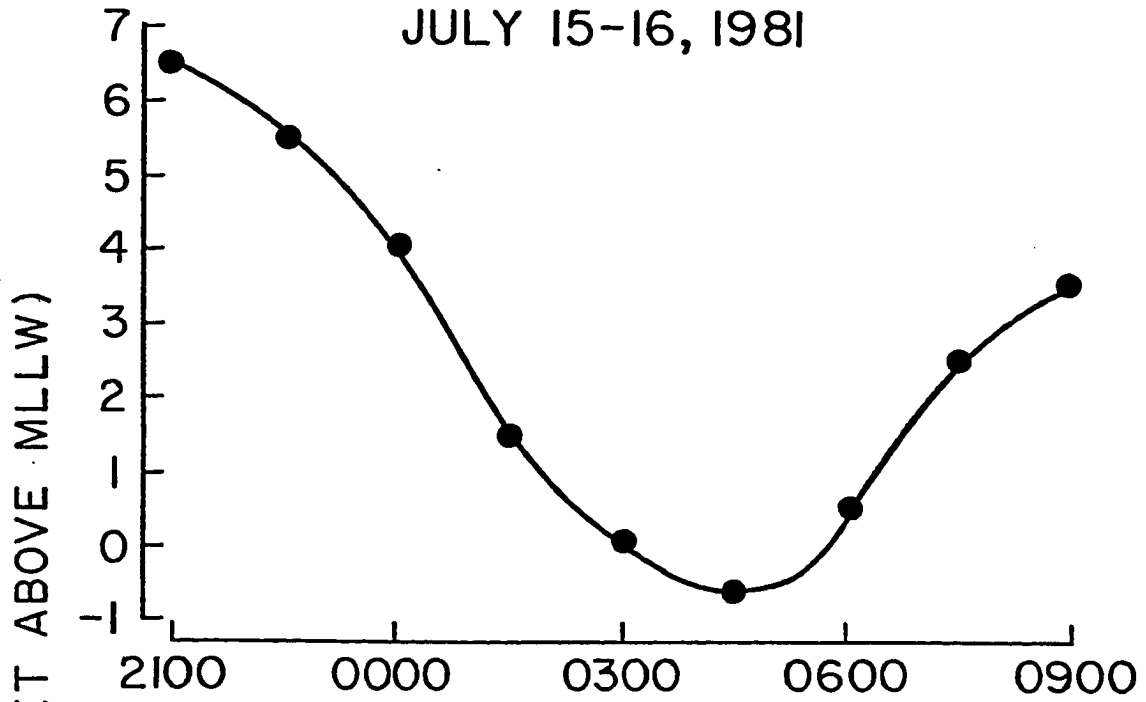


Figure 25: Pseudopolydora paucibranchiata larval abundances in the Kendall-Frost plankton: nocturnal sampling during a complete tidal cycle. July 15 - 16, 1981 (full moon) and July 27 - 28 (new moon), 1981. ( $\bar{X} \pm 1$  S.D.)

*Pseudopolydora paucibranchiata*

JULY 15-16, 1981

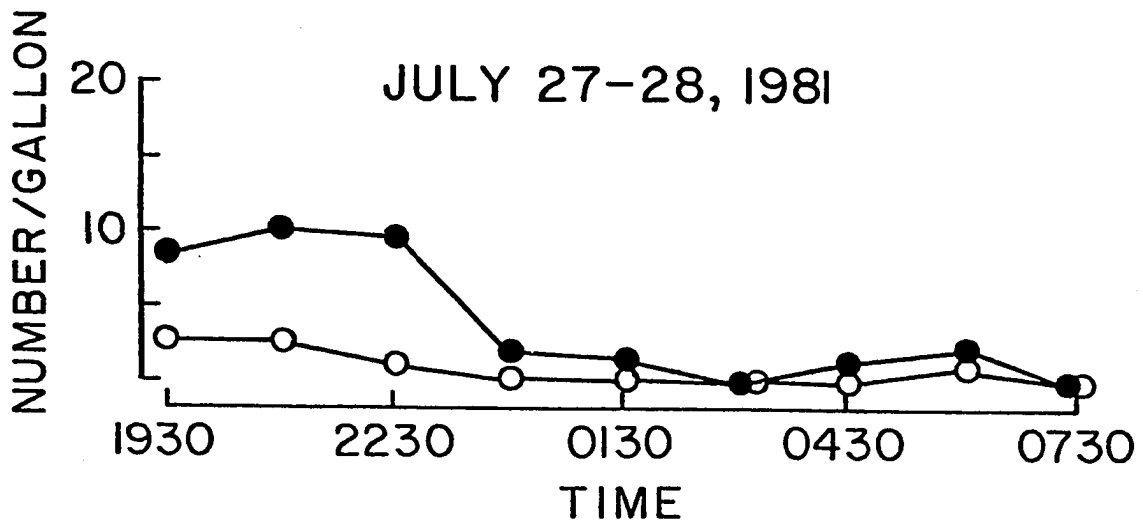
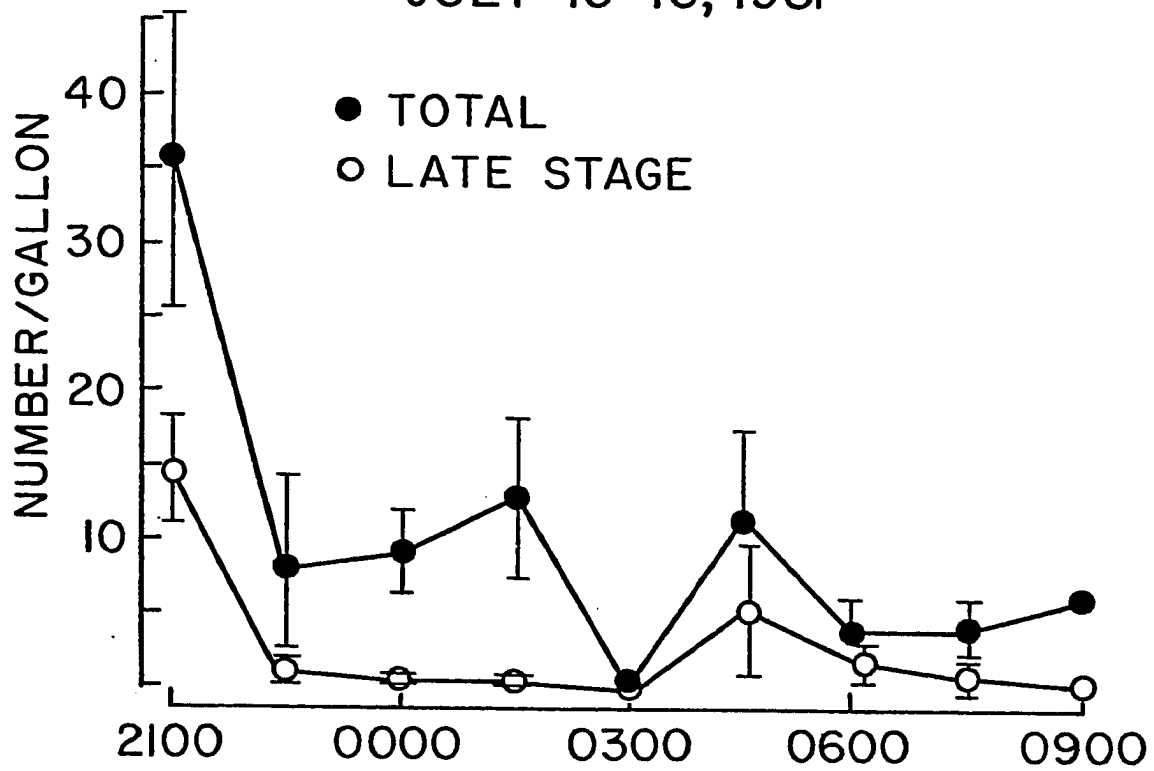
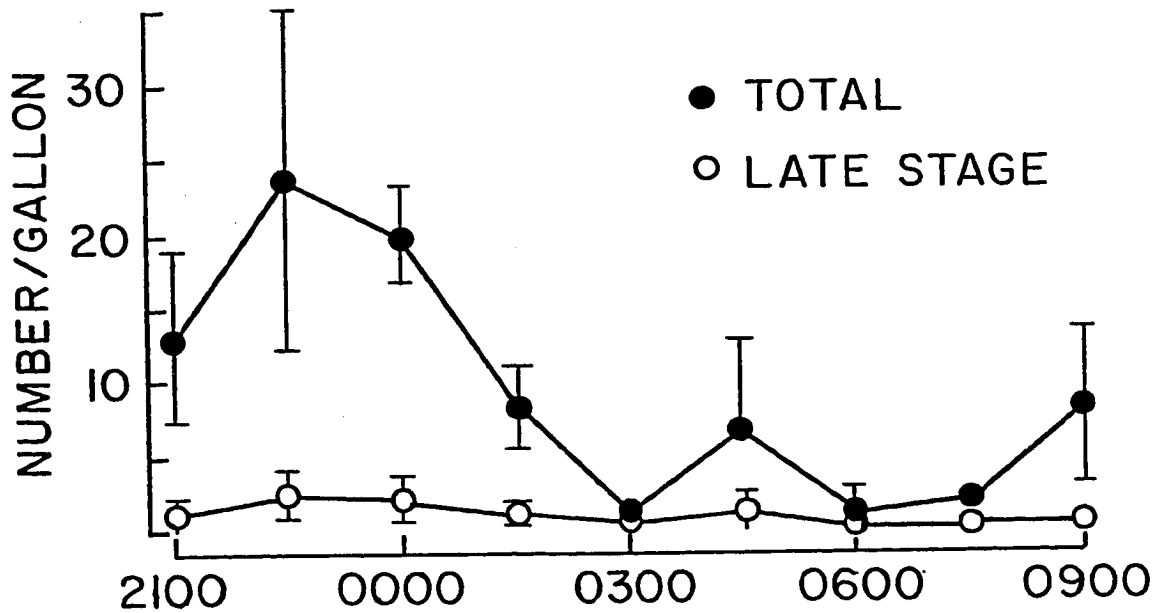


Figure 26: Polydora ligni larval abundances in the Kendall-Frost plankton: nocturnal sampling during a complete tidal cycle. July 15 - 16 (full moon) and July 27 - 28 (new moon), 1981. ( $\bar{X} \pm 1$  S.D.)

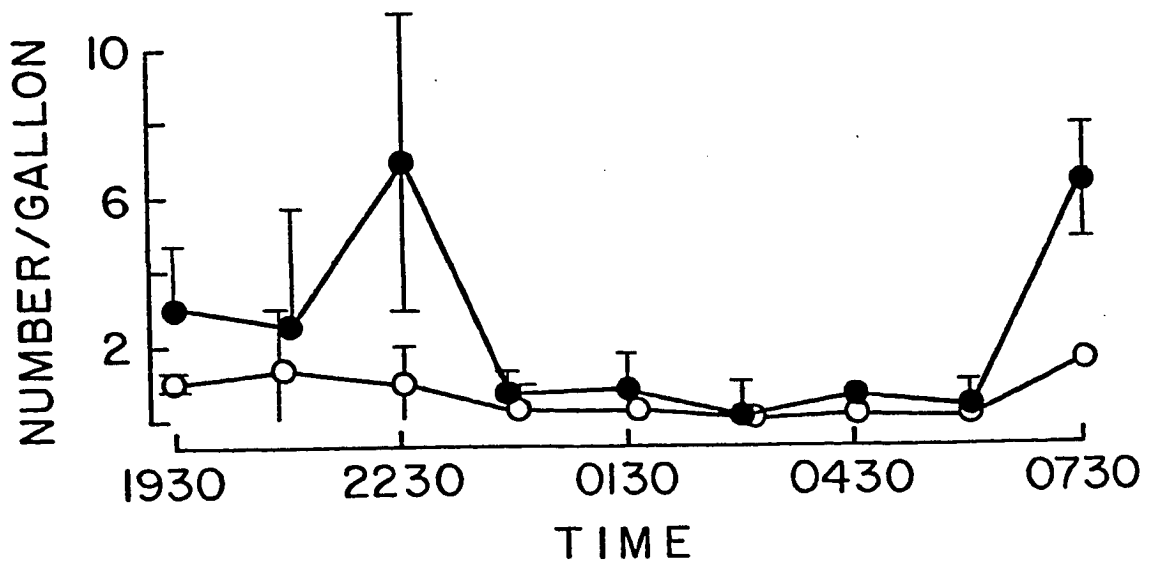


*Polydora ligni*

JULY 15-16, 1981



JULY 27-28, 1981



Their abundances remained fairly constant throughout the sampling period on both dates, suggesting that the competent larvae are not responding to tidal or day - night cycles. The abundance maxima observed for Polydora ligni may be due to larval release patterns.

With one exception, Rhynchospio arenicola abundance patterns were similar on both sampling dates. A sharp spike with a 5-fold density increase occurred at low tide on July 16 (full moon). No such spike was seen on July 28 (new moon) though maximum abundances were attained at high tide (dawn) (Figure 27). Late stage larvae ( $\geq 8$  setigers) did not exhibit the same fluctuations in abundance as seen in earlier developmental stages, though they also exhibited a low tide spike on July 16 (Figure 27). This pattern suggests that the maxima were not due to a sudden release of new larvae.

An unidentified species of Polydora (Figure 28) exhibited sharp abundance maxima at mid-ebb and flood tides on July 28, 1980, similar to those seen for the spionid polychaetes in 1980 daytime samples. These peaks were associated with periods when +3 to +4 feet of water covered the mudflat (at the sampling station) and may have been caused by a patch of larvae (originating elsewhere in the bay) moving by the sampling station as the tide ebbs then floods. The larvae did not belong to any of the abundant polychaete species on the mudflat.

Armandia bioculata larvae were abundant only on July 28, 1981. They peaked at dusk high tide with a smaller rise in abundance at maximum flood tide (Figure 28). This pattern resembles that of Pseudopolydora larvae on the same date. Armandia larvae probably originated elsewhere in Mission Bay; adult Armandia were not present, and juveniles were just beginning to appear on the mudflat.

Figure 27: Rhynchospio arenicola larval abundances in the Kendall-Frost plankton: nocturnal sampling during a complete tidal cycle. July 15 - 16 (full moon) and July 27 - 28 (new moon), 1981. ( $\bar{X} \pm 1$  S.D.)

*Rhynchospio arenicola*

JULY 15-16, 1981

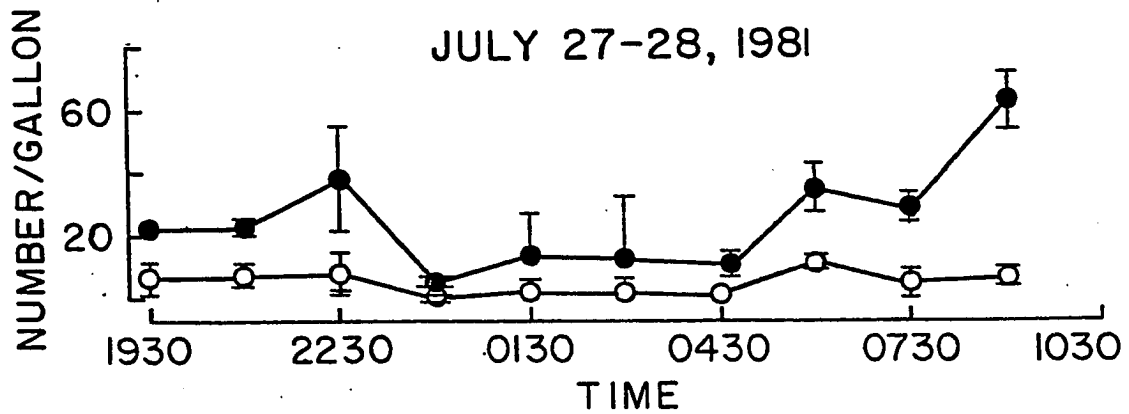
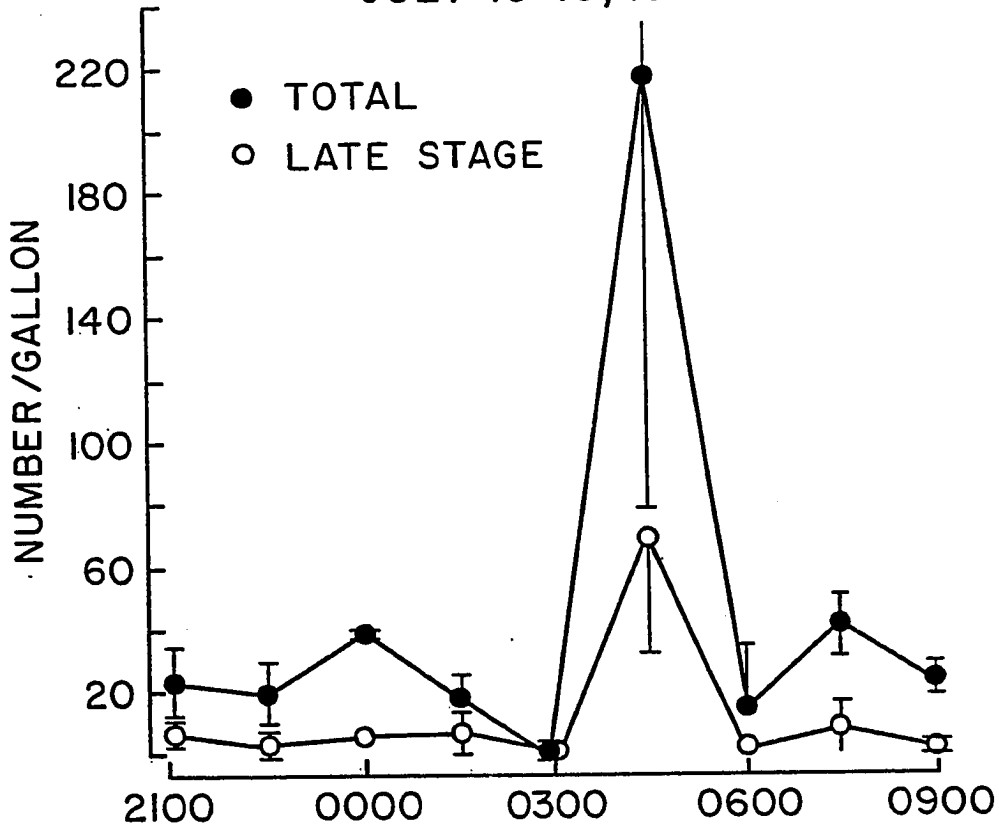
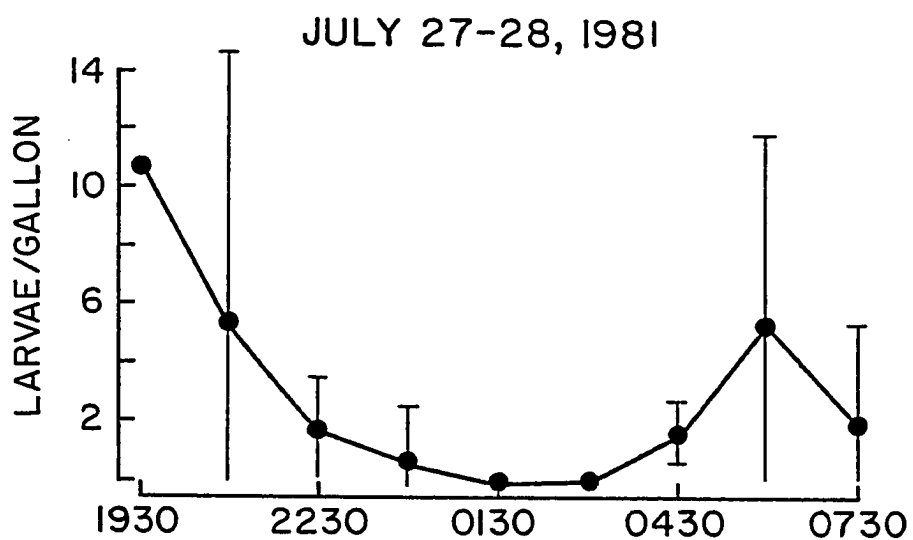
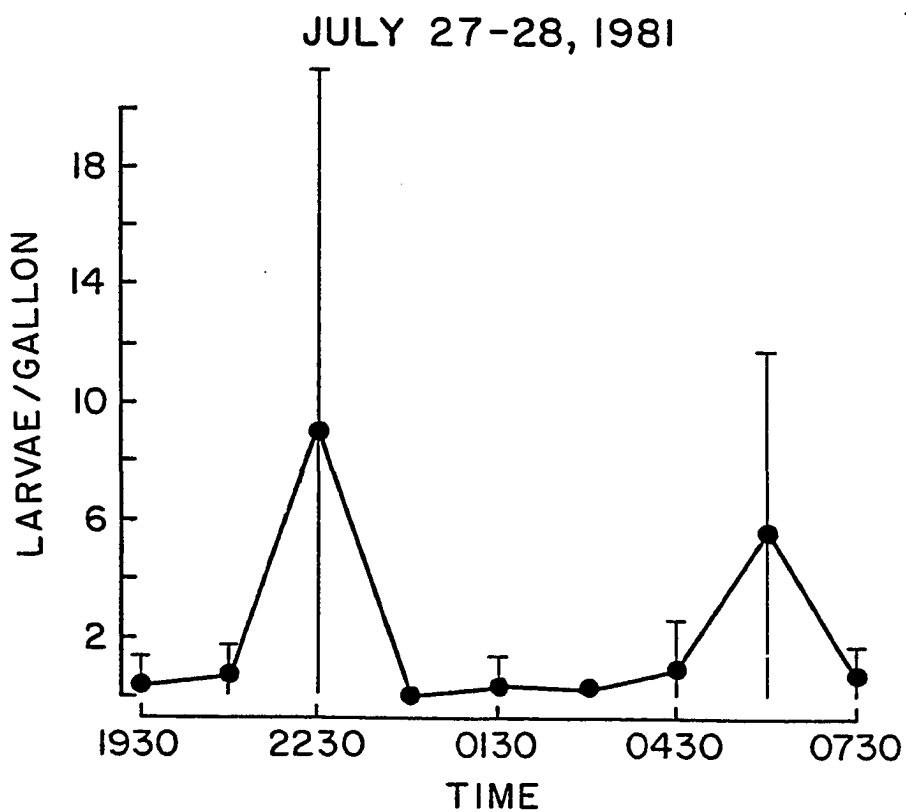


Figure 28: Armandia bioculata and Polydora sp. larval abundances in the Kendall-Frost plankton: nocturnal sampling during a complete tidal cycle. July 27 - 28, 1981. ( $\bar{X} \pm 1$  S.D.)

*Armandia bioculata**Polydora sp.*

Several polychaete species entered the water column at night as adults. Seven adult Exogone lourei were collected between 2100 (July 27) and 0130 (July 28); two of these were females carrying eggs. Only one Exogone was collected on July 16 (at 0130). The light from the full moon may have inhibited excursions from the benthos, though one adult Exogone was collected from waters overlying the mudflat during daylight hours (1500) on September 16, 1981.

Two Odontosyllis phosphorea adults were collected from the plankton at 0130 on July 28. This species is known to enter the water column at dusk on new and full moons and to release a phosphorescent mucous to attract males (Fraser, 1915; Gary Leischman, pers. obs.). Phosphorescent individuals were also observed on Zostera at low tide on July 28.

b. Crustaceans. Both gammarid and caprellid amphipods peak in abundance at or near low tide (Figure 29). This pattern is not associated with diurnal cycles since it was observed on both night sampling dates (July 16 and July 28, 1981), and the one light period (May 10, 1980) for which amphipods were counted.

Brachyuran crab zoea (Pachygrapsus sp. and Uca sp.) occurred only in night (dark) samples. On both the full moon (July 16) and just prior to the new moon (July 27) in July 1981, zoea appeared at the surface 1 1/2 hours after high tide (at the beginning of ebb tide) (Figure 30). A few zoea were present at the next sampling period 1 1/2 hours later and none were recorded for the remainder of the evening or early morning. Many more were present during the full moon than during the period 4 days prior to the new moon. P. DeCoursey (pers. comm.) has

Figure 29: Amphipods in the Kendall-Frost plankton: nocturnal tidal sampling. ( $\bar{X} \pm 1$  S.D.)



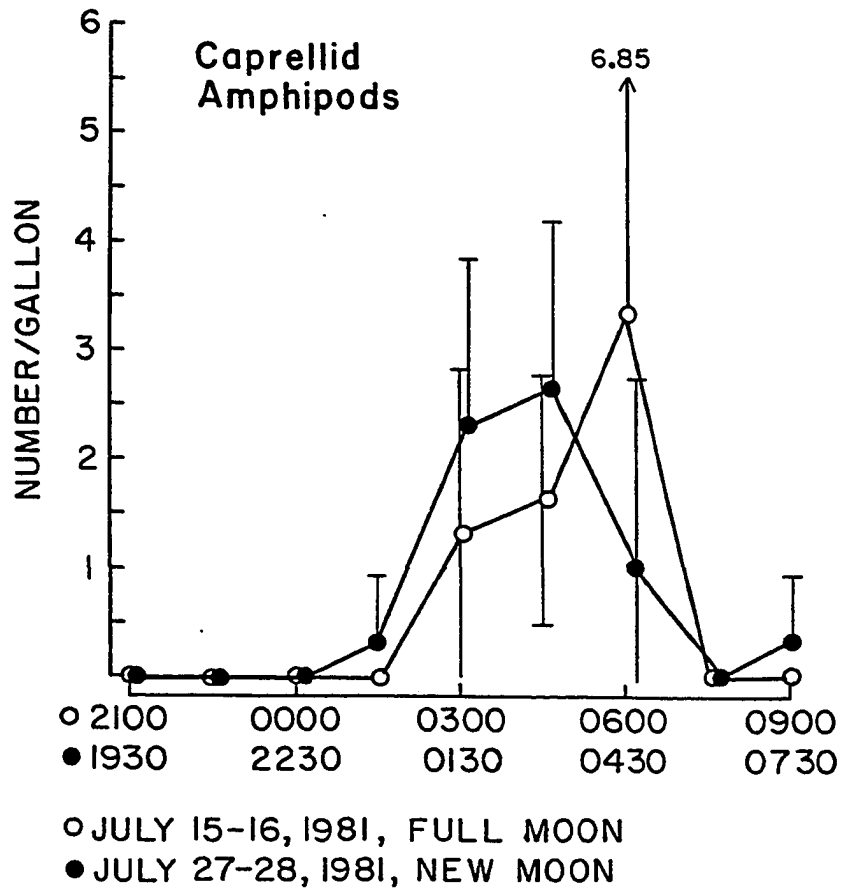
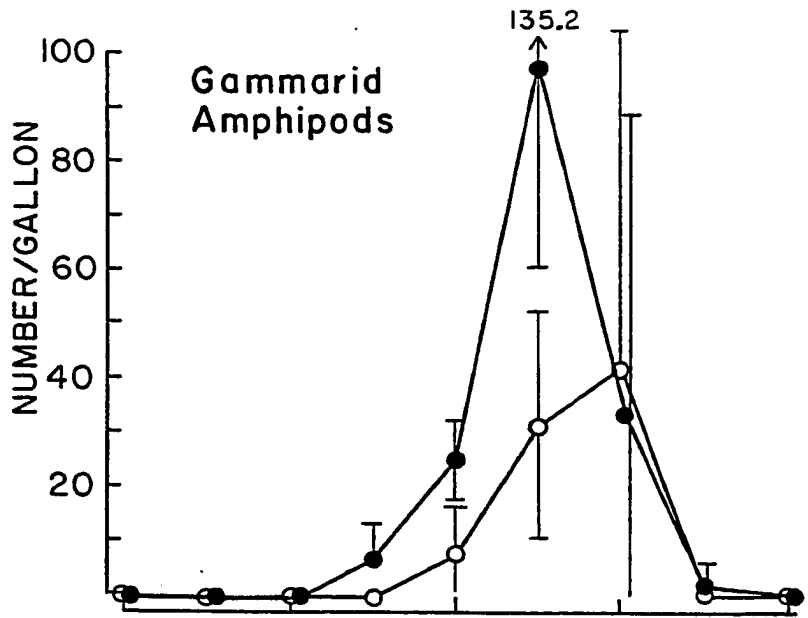
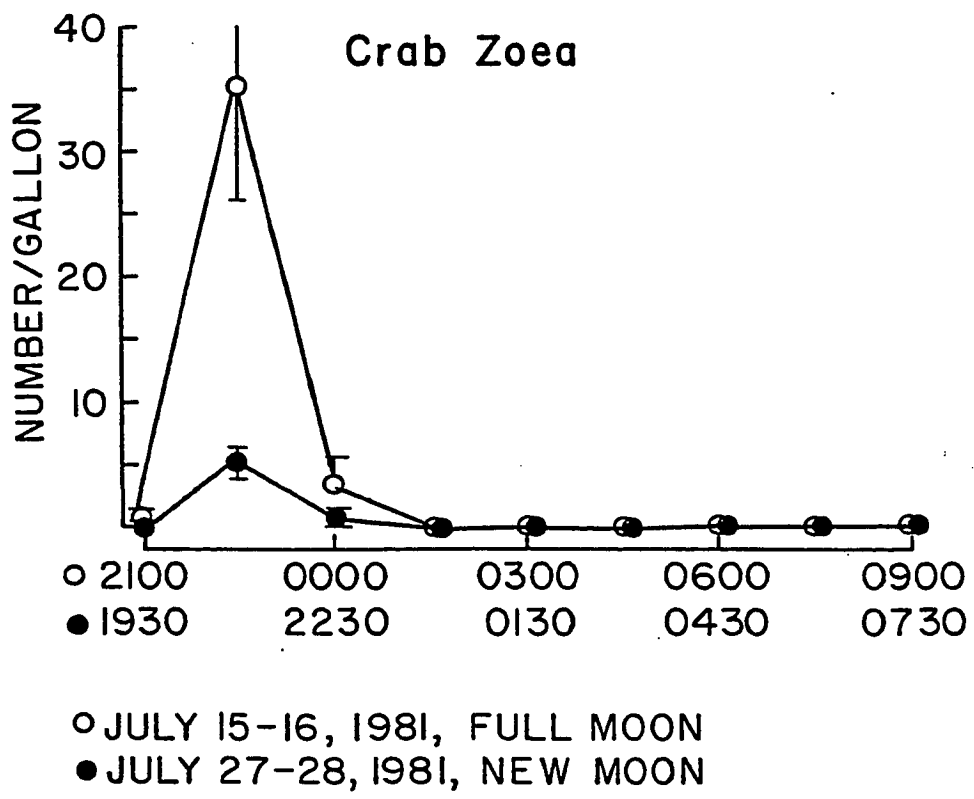
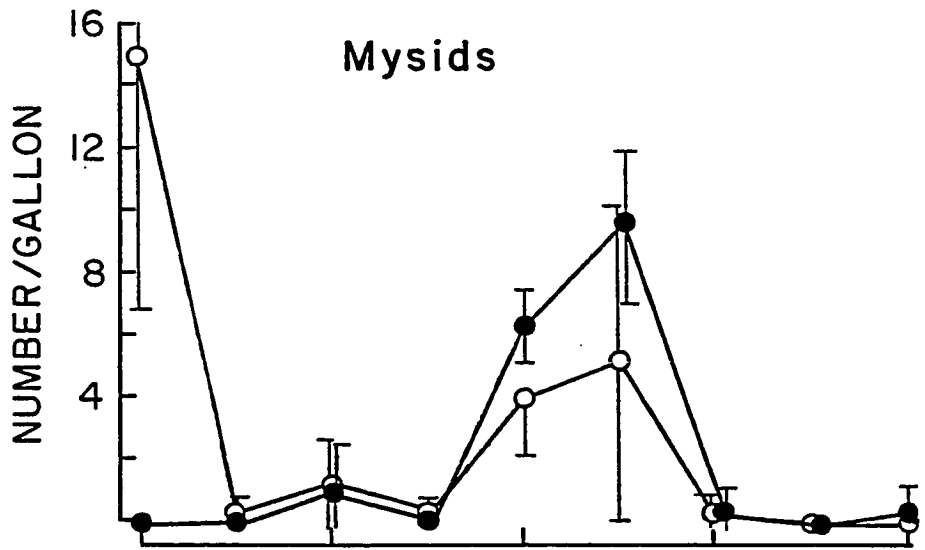


Figure 30: Crab zoea and mysid abundances in the Kendall-Frost plankton: nocturnal sampling during a complete tidal cycle. July 15 - 16 (full moon) and July 27 - 28 (new moon), 1981. ( $\bar{X} \pm 1$  S.D.)



observed a sharp hatching spike for Uca larvae during full and new moon night-time spring tides in South Carolina. Hatching always occurred on the ebbing tide and timing cues were associated with water movement. Her findings agree well with patterns observed on the Kendall-Frost mud-flat.

Mysids were also present only in the nighttime samples (Figure 30). On July 16 (full moon) they exhibited a large peak at high tide<sup>1</sup> (dark) and another smaller peak during low tide. Two weeks later they exhibited one large peak at low tide corresponding to the one observed previously and no high tide peak. The explanation for the low tide peaks may resemble that for amphipod abundance peaks at low tide.

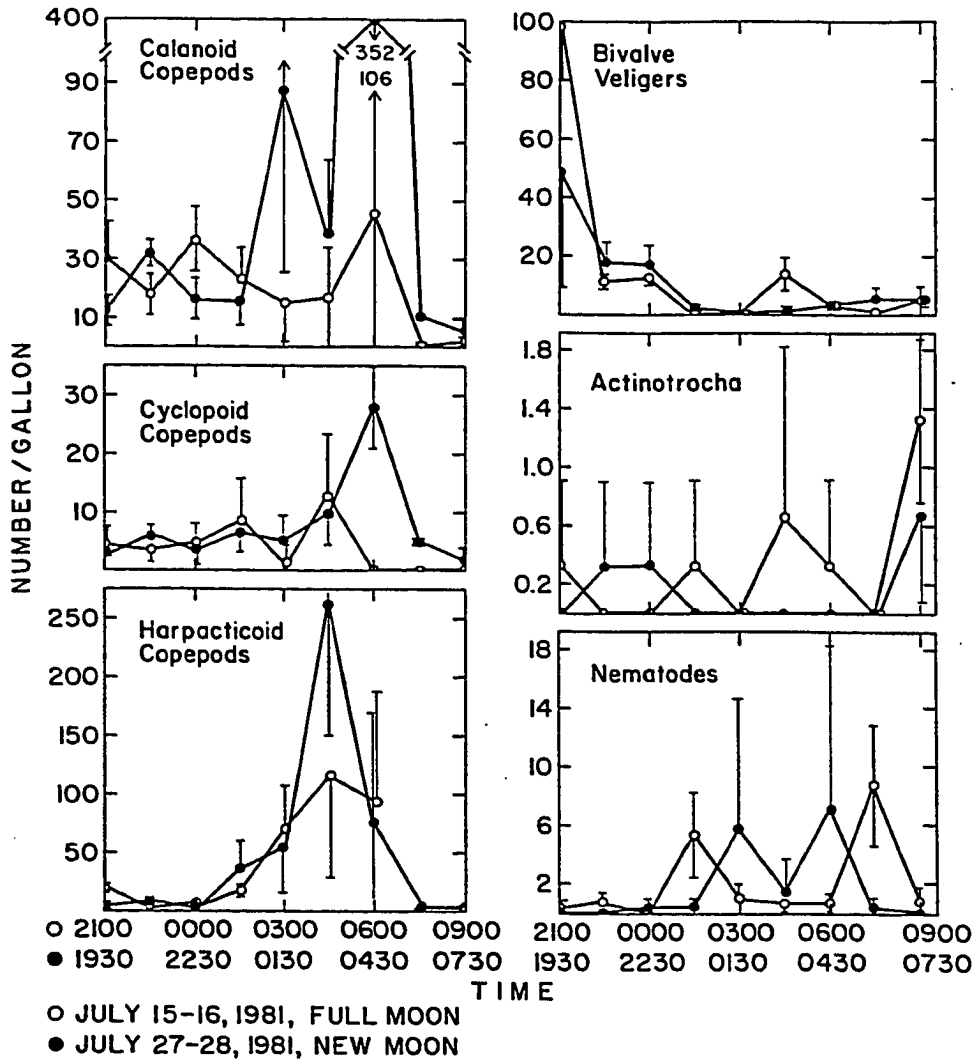
Harpacticoid copepods exhibited the only consistent pattern for both July sampling dates. Like the amphipods, they appeared during slack low tides and were not collected during high tides (Figure 31). Calanoid copepods (Figure 31), primarily Acartia tonsa, exhibited a sharp spike during mid flood tide on July 28. The maximum abundance also occurred during mid flood tide on July 16 but was not a distinct spike and copepods were only 1/8 as abundant. Abundances (other than the maximum values) were comparable on both July sampling periods. Cyclopoid copepods were much less abundant and the least consistent (Figure 31). On July 28 they exhibited a sharp peak during ebb tide but maximum abundances occurred during low tide on July 16.

Nematode abundances were very low on both nighttime sampling dates with 2 spikes, just before and after low tide (Figure 31). On both

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<sup>1</sup>It is now believed by the author that the high tide peak (only) was actually caused by the release of Callinassa californiensis larvae, and they were misidentified as mysid juveniles.

Figure 31: Nocturnal tidal sampling: Calanoid, Cyclopid and Harpacticoid copepods, Nematodes, Phoronid and Bivalve larvae. July 15 - 16 (full moon) and July 27 - 28 (new moon), 1981. ( $\bar{X} \pm 1$  S.D.)



nights (July 16 and July 28) the flood tide peak was slightly higher than the ebb peak. Specific water velocities may trigger nematode swimming response, causing them to enter the water column, or nematodes may be resuspended passively.

c. Other taxa. Bivalve larvae exhibited maxima at dusk high tide on both July 1981 sampling dates (Figure 31) though veligers were more abundant during the high tide on July 16 than on July 28. Numbers of veligers declined during ebb tide and remained low throughout the low and flood tides. Gastropod larvae exhibited no consistent patterns on July 16 but were most abundant during high and ebb tides on July 28 (new moon). Phoronid larvae were present but not common. The only pattern to emerge was the occurrence of maximum values on July 16 and July 28 in dawn samples near high tide (Figure 31).

### Summary and Discussion

#### Bay Wide Plankton Distributions

The 5 stations sampled in this study (Figure 13) were chosen to represent back, mid, and front bay (ocean exit) regions. It is clear from the plankton distributions at these stations that the forms sampled are primarily estuarine species, whose populations are centered in Mission Bay. Densities of most mero- and holoplanktonic taxa are highest at back (I) or mid-bay (II, III, IVa) stations. All of the taxa considered were most abundant in summer (August) with the exception of Pseudopolydora larvae, whose densities were highest in spring.

Most of the meroplankton, including bivalve, phoronid and polychaete larvae, were more abundant in midwater than near surface samples, except in the Ship Channel where the pattern reversed. This

reversal may occur because larvae rise to remain in warmer waters, though the Ship Channel does not seem to be vertically stratified (Figure 7).

The holoplankton do not exhibit such distinct trends. Harpacticoid copepods, known to migrate up and down from the sediments, were usually found deeper in the water column (except in the Ship Channel) but calanoid copepods and Oikopleura spp. did not demonstrate a consistent vertical distribution pattern. Like the meroplankton, holoplankton abundances were often greater in Ship Channel surface waters than at mid depth.

All plankton sampling was conducted during ebb spring tides. Back bay samples were collected just after high tide, and Ship Channel samples just before low tide, to view maximum movements and oscillations of estuarine plankton. It appears that none of the major components of the plankton are restricted to one portion of the bay. Water exchange with the ocean during extreme tides is such that some larvae originating in the back bay may be carried to the front bay. Though vertical plankton distribution patterns remained fairly consistent from one season to another, the horizontal distributions of holoplankton throughout the bay did not. Invertebrate larvae were generally more abundant at back bay Stations I and II but even this pattern did not hold at all times.

#### Kendall-Frost Plankton

##### Plankton composition

The waters overlying the Kendall-Frost mudflat contain representatives of many of the benthic species inhabiting the mudflat sediments (Table 8). Those polychaete species with feeding larvae, such as



Pseudopolydora paucibranchiata, Polydora ligni, Rhynchospio arenicola and Armandia bioculata, are present seasonally, often in great abundance. Several polychaete species possess nonfeeding larvae with facultative planktonic stages of short duration. Of these species Streblospio benedicti larvae were never, and Capitella capitata (Mission Bay variety) larvae were rarely collected in plankton samples over the mudflat. These findings suggest that when larvae of these species do enter the water, they remain close to the mud surface and are planktonic only a short time.

Post-larval stages of many of the mudflat infauna are common in the plankton (Table 8). Juvenile and adult specimens of the polychaetes Streblospio benedicti, Rhynchospio arenicola, Exogone lourei, Odontosyllis phosphorea, and tubificid oligochaetes, have appeared repeatedly in gallon jar water samples collected during ebb and flood tides. Single juvenile specimens of the polychaetes Eteone dilatata, Capitella capitata, Fabricia limnicola, and an unidentified sabellid (probably Chone sp.), as well as a juvenile mussel, Musculus senhausii and a juvenile gooseneck barnacle (Polycipes sp.) were also collected in plankton samples. Many of these "single specimens" may have been lifted into the water column by tidal resuspension. Nematodes, harpacticoid copepods, ostracods and peracarid crustaceans—gammarid and caprellid amphipods and cumaceans—occur in the waters over the eel grass beds at lower tide levels. Most of the post-larval forms commonly present in the plankton also appear in sediment trays placed on top of the mud surface (see Chapter IV). They colonize as juveniles or adults via the water column.

### Spatial patterns

Small-scale sampling conducted over the mudflat in June 1980 (Table 5) demonstrated moderate variability among replicates from a single sampling site. However, little additional variation was observed in samples from 4 stations, approximately 75 m apart along a north-south (bay to shore) transect (Figure 14). Station 4, sampled in approximately 1 foot of water (nearest the shore), did yield significantly fewer Pseudopolydora larvae than the other stations.

Vertical sampling (Table 6) conducted in June 1980 at Station 2 confirmed that most of the species of interest congregate in surface waters over the mudflat. Surface sampling is therefore an appropriate method of detecting larval availability in the plankton.

A comparison of meroplankton composition at Sites A and C demonstrated that the water column is not a uniformly well-mixed "soup" of plankton. Planktotrophic larvae of P. paucibranchiata, P. ligni and R. arenicola were consistently present at both sites but significantly more abundant at Site A. This may have been due to larval release patterns, as benthic abundances of these species are higher at Site A. Competent (ready to settle) larval stages may also choose to remain near the preferred adult habitat. Some post-larval stages also exhibited site differences in abundance, though numbers were too small to be statistically significant. Capitella capitata larvae, Rhynchospio arenicola juveniles and Streblospio benedicti juveniles were consistently more abundant at Site C than Site A (Figure 20).

### Temporal patterns

The Kendall-Frost plankton was studied during part of 1980 (March-August) and all of 1981. During this period order of magnitude changes were observed in Pseudopolydora paucibranchiata and Polydora ligni larval availability. The large sets of spionid larvae in spring 1980 may have been related to the raw sewage spill in Mission Bay which occurred during February and March of that year.

Most of the infaunal species on the mudflat exhibit seasonal reproductive activity reflected by increased larval availability in the plankton. P. paucibranchiata, P. ligni and R. arenicola were most abundant in spring and summer. Armandia bioculata appeared each year in late summer. Even S. benedicti, which reproduces all year, exhibited seasonal peaks in brooding activity and larval availability.

Intensive sampling during night and day tidal cycles revealed dramatic variation in plankton abundances over 12 hour periods. A variety of factors may have influenced meroplankton abundances during the sampling periods. Light and dark cycles, in particular the dusk and dawn transitions, are known to induce animal migrations (Hamner, 1981; Greening and Livingston, 1982). Stage in the tidal cycles defined both the height above the mud surface at which sampling took place, and the source, direction, and speed of water moving by the sampling station. Each of these factors affects the species composition and abundances in the plankton. Lunar cycles may also influence plankton patterns (Aldredge and King, 1980). Three of the 4 sampling periods (April 14, 1980, May 10, 1980 and July 27, 1981) occurred on or near the new moon, the other (July 16, 1981) was on the full moon.

Daytime sampling on April 14, 1980 revealed a distinct bimodal abundance pattern for most taxa. Larvae of the polychaetes P. pauci-branchiata, P. ligni, R. arenicola, and an unidentified spionid, as well as bivalve veligers, exhibited maximum densities and variances at mid ebb (1100) and late flood (1830) tides with distinct minima at slack high and low tides. A large mass or patch of larvae oscillating with the tides in the back of Mission Bay could produce a pattern of this nature. Larvae pass by the sampling station as the tide ebbs and again as the tide floods. The phoronids, always rare, did not exhibit this pattern.

Daytime samples taken on May 10, 1980 revealed early ebb tide peaks in abundance for several larval polychaetes, phoronid larvae and decapod larvae, but the flood peaks seen in the previous month were muted or absent. Salinity samples collected at the plankton station every 1 1/2 hours on May 10 revealed a fluctuation in salinity (0.5 o/oo) implying an oscillating water mass in the back bay (Figure 22). Salinity was highest (32.5 o/oo) during morning and evening high tides when the ocean and front bay influence was greatest. Salinity dropped during low tides.

The night-time samples collected in July 1981 bore little resemblance to the daytime samples collected in April and May the previous year. Nocturnal meroplankton abundances exhibited several distinct patterns. The most dramatic of these was the appearance of epibenthic crustaceans in the plankton just before low tide, a peak in abundance during low tide and a drop in numbers as the tide floods. This was seen on the full (July 16) and new (July 28) moon for gammarid and caprellid amphipods, harpacticoid copepods and mysids (Figures 29, 30, 31). There

are several possible explanations for the apparent low tide maxima. If these crustaceans migrate continually from the benthos, but swim only several feet off the bottom, they would not appear in the surface samples until the tide dropped to a low level. Alternatively, migrations may occur only near or at low tide. This would permit organisms to be carried back over the mudflat by subsequent tidal (flood) motion and to avoid transport towards the ocean, away from appropriate habitat. A third alternative combines the previous two. Migrations occurring only during slack tides (high and low) but limited in vertical extent would also produce the observed patterns of abundance.

Pseudopolydora larvae and Callianassa larvae exhibited sharp abundance peaks on the full moon at dusk high tides (July 16). Bivalve veligers exhibited these patterns during both full and new moon sampling periods. Lunar cycles may have affected larval release patterns and swimming behavior in the polychaetes and Callianassa. Rhynchospio exhibited a tremendous low tide maximum during the full moon but not the new moon. However, the fact that both early and late stage larvae exhibited similar fluctuations in Pseudopolydora and Rhynchospio suggests that they were not simply larval release phenomena. In contrast, release of crab zoea is known to be associated with lunar cycles and triggered at ebb tide (DeCoursey, 1980). On both new and full moon, Pachygrapsus and Uca zoea appeared in the water column just after dusk high tide.

Larval abundances of the major polychaete species P. paucibranchiata, P. ligni, and R. arenicola were lower on July 28 (new moon) than on July 16 (full moon). This may have been due to a normal seasonal decline in availability associated with the onset of summer. Alternatively, a rhythmic swimming response to lunar cycles or a behavioral

response to light levels associated with full and new moon could have generated the observed variation. These differences in nocturnal abundances between sampling dates were not seen in calanoid, cyclopoid or harpacticoid copepods or in the amphipods, phoronids, bivalves or mysids. Copepods were slightly more abundant during the latter (new moon) sampling date.

Marked differences were seen between the 1980 daytime samples and the 1981 nighttime samples. The distinctive bimodal distribution so apparent in April 1980 was not observed in 1981. This may have been due to annual (or seasonal) differences in larval availability. Perhaps larval density must be high to observe patch oscillation in the back bay. Phototactic swimming behavior, occurring only during daylight, could have been absent in the 1981 nocturnal sampling program. Swimming behavior will influence larval availability in surface waters and therefore the observed plankton distributions during a diel cycle.

The plankton investigations conducted over the Kendall-Frost mudflat investigated temporal and spatial patterns of meroplankton only superficially. Both stochastic and cyclic phenomena clearly influence small-scale plankton abundances, and thus dispersal patterns. An attempt to sort out effects of annual and seasonal variation, lunar cycles, light and dark transitions, tidal height and water motion, would require an extensive sampling program spanning many years, seasons and phases of the moon.

#### Implications for Dispersal

The bay-wide and Kendall-Frost sampling programs provide evidence for dispersal abilities of the Kendall-Frost polychaetes. For

most of the 7 species considered in this work, populations are limited to or concentrated on the Kendall-Frost mudflat. The presence of their larvae in the water column in other parts of Mission Bay, particularly in the Ship Channel, which exits to the ocean, indicates potential for long distance dispersal.

All the polychaete species, with the exception of Fabricia limnicola, were collected repeatedly in waters overlying the Kendall-Frost mudflat. P. paucibranchiata and P. ligni were present solely as larvae. R. arenicola larvae and juveniles occurred in the mudflat plankton. S. benedicti and C. capitata possess facultative planktonic larval stages but were rarely collected as larvae in the plankton. However, S. benedicti juveniles were present in the water column on numerous sampling dates. E. lourei which lacks a planktonic larval stage, develops specialized swimming setae and enters the plankton as an adult, sometimes while brooding young. Post-larval stages of S. benedicti, R. arenicola and E. lourei were collected only in waters overlying the Kendall-Frost mudflat and not in other parts of Mission Bay.

Only P. paucibranchiata, P. ligni and possibly R. arenicola are capable of long distance larval movement. Larvae of these three species were collected from the plankton in the front regions of Mission Bay and in the Ship Channel. However, polychaete larval densities were generally much lower in the front than in the back bay waters. Circulation studies (Chapter II) suggest that water movement in the back of Mission Bay near the Kendall Frost mudflat is sluggish. For drift tubes released near the mudflat, the probability of exiting the bay to the ocean was approximately 3%. This corresponds well to the pattern of dilution seen in spring for Pseudopolydora larvae distributed throughout Mission Bay

(Table 9). There were approximately 30 times fewer Pseudopolydora larvae in the Ship Channel than at Station I, adjacent to the mudflat where larvae are released.

These data suggest that only those polychaete species in the Kendall-Frost assemblage with planktotrophic larvae are capable of long distance dispersal. However, only a small fraction of the larvae released by these species ever leaves Mission Bay. Dispersal for most individuals of all 7 polychaete species appears to be restricted to the back portion of Mission Bay, and probably occurs mainly over the Kendall-Frost mudflat itself.



Table 9  
 Abundance of Pseudopolydora paucibranchiata  
 larvae in Mission Bay

	March 1980 #/m <sup>3</sup> *	May 1980 #/m <sup>3</sup> *
Kendall-Frost Mudflat Surface	1,656	6,400 - 143,800
I. Back Bay		
Surface	345	1,082
Midwater	1,458	125
II. North Bridge		
Surface	160	16
Midwater	320	280
III. South Bridge		
Surface	0.7	4
Midwater	0.8	22
IV. W. Vacation Isle		
Surface	--	104
Midwater	--	135
V. Ship Channel		
Surface	93	17
Midwater	54	62

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\* Average of two replicate net tows.

## CHAPTER IV

### POLYCHAETE LIFE HISTORY AND COLONIZATION PATTERNS

#### Introduction

In contrast to the previous chapter, which addresses events in the water column, this chapter focuses on processes occurring in the sediment or near the sediment - water interface. This chapter presents much of the evidence for my interpretation of polychaete dispersal patterns. In this chapter, I describe: (a) the larval development patterns of each species; (b) benthic abundance patterns of each species at three sites on the mudflat; and (c) the results of settlement and colonization experiments. This latter section includes studies of polychaete recruitment into midwater jars (placed around Mission Bay) and settling cartons (placed on the Kendall-Frost mudflat), field and laboratory experiments which tested for larval settlement preferences (substrate type and biotic factors), and defaunation experiments which examined colonization rates and mechanisms in response to several levels of disturbance. Sampling techniques and experimental methods are presented first, followed by results of the various investigations.

#### Methods and Materials

##### Laboratory Studies of Larval Development

Basic life history traits were investigated by examining polychaetes collected in the field and raised in the laboratory. Features such as reproductive seasonality, egg size, brood size, stage at release and stage at settlement were determined from gravid or brooding specimens and new recruits collected in benthic samples (both

preserved and live) between 1978 and 1981 on the Kendall-Frost mudflat. Size measurements were made with ocular micrometers on Spencer compound and Wild dissecting microscopes.

The duration of the planktonic larval phase was studied for Pseudopolydora, Streblospio, Polydora, Rhynchospio, and Capitella larvae released in the laboratory by adults collected on the Kendall-Frost mudflat. Larvae were raised individually in disposable glass culture tubes (13 x 100 mm) at room temperature and fed Monochrysis leuteri, Playtmomas sp., Dunalliella sp. and Chlamydomonas sp. (cultures obtained from J. Jordan, SIO Food Chain Group). Larvae were observed every other day for swimming activity, phototaxis and signs of settlement.

Detailed investigations of variability in planktonic period and effects of substrate availability on this variability were conducted for one planktotrophic species (Pseudopolydora) and one lecithotrophic species (Streblospio). One hundred and five Pseudopolydora larvae, released at the 3 setiger stage, were raised in a windowless room with 9 hrs of light per day (Experiment I). Approximately 0.5 cm of fine sediment from site A was added to the bottom of 50 of the tubes at the beginning of the study (March 28, 1980). A replicate experiment was run under a natural light regime (near windows) beginning April 7, 1980, using 50 Pseudopolydora larvae, half with sediments added to their tubes (Experiment II).

Newly released Streblospio larvae (9 setigers) settle within minutes of release in the presence of natural substrate. This was observed for all individuals of several broods. Sixty-seven newly released Streblospio were raised individually in vials without sediments, and monitored in the same manner as the Pseudopolydora larvae.

Exogone females brooding young were collected from the Kendall Frost mudflat and raised in plastic vials in standing seawater to monitor release and behavior of new larvae. Adults were fed dried, powdered Enteromorpha sp. Newly released Fabricia juveniles were observed in sediments collected from the field and sieved live through a 500  $\mu$  screen.

#### Larval Settlement Preferences

Observations of larval recruitment into settling trays on the mudflat suggested that larvae exhibit considerable choice in settlement substrates. Larval recruitment into sediment trays at sites A and C often exhibited marked differences; some species were far more abundant at one site or the other. A series of laboratory and field experiments were designed to examine larval settlement preferences for different types of sediments (azoic, natural Site A and natural Site C sediments) and different biotic conditions (adults, or tubes present or absent).

#### Laboratory studies

Both laboratory reared and field caught larvae were used in the laboratory settlement experiments. Pseudopolydora paucibranchiata and Polydora ligni larvae (3 setigers) were released in the laboratory from adults collected in intact cores taken from the mudflat in February through April, 1980. Larvae were raised in 15 dram plastic vials and fed Chlamydomonas sp., Monochrysis leuteri and Dunalliella sp. Larvae were also collected from waters overlying the mudflat during these same months by hand towing a 75  $\mu$  net for short periods.

A variety of sediment treatments was offered to test settlement preferences. Azoic sediments were generated by sun-drying the surface sediments collected from Sites A and C. Sites A and C natural treatments

were generated by wet sieving the top half centimeter of sediment from each site through a 177  $\mu$  screen. This removed macroinfauna, larvae, and much of the meiofauna but left protozoa and bacteria. "Adult" treatments were generated by adding several P. paucibranchiata adults in their tubes to Site A sediments.

Laboratory studies of Pseudopolydora settlement were conducted in fingerbowls (10 cm diameter) containing standing seawater. Sediments were placed in plastic vial caps (11 cm<sup>2</sup> x 0.3 cm depth) at the bottom of the fingerbowls. Each bowl contained 4 caps, 2 replicates of each of two treatments. Experiments were run from 2 to 7 days. Recruitment was recorded visually, using a dissecting microscope. Pseudopolydora and Polydora recruits construct tubes and are visible on the sediment surface within a few hours of settling. Settlement was highly variable. In some experiments many larvae settled, in others few did.

### Field Studies

#### Substrate studies

Field experiments to test for substrate preferences were conducted using 9 x 9 x 9 cm cartons placed in cages on the mudflat at Sites A and C for 4 days. This was done initially from March 22 - 26, 1979 at Sites A and C. At each of the 2 sites one 1/2 " wire mesh cage (30 x 40 x 12 cm) contained 2 replicates each of Site A and Site C natural sediments for a total of 8 cartons in the experiment. Cartons were filled with sun dried sediments to 2 - 3 cm depth. At the conclusion of the experiment sediments from each carton were sieved through a 250  $\mu$  screen and samples were preserved in 10% formalin and seawater.

The experiment was repeated again from April 4- 8, 1979, but only a few samples were sorted.

Biotic factors: Pseudopolydora settlement

The effect of Fabricia presence on Pseudopolydora recruitment was studied in spring, 1981. Plastic cartons (9 x 9 x 9 cm) containing azoic, "natural," or Fabricia tube mat treatments were placed on the mudflat for two week periods. Azoic cartons contained sediments collected from Site A and sun dried. Natural treatments contained undisturbed sediment cores with few or no Fabricia (few Fabricia were present on the mudflat in spring 1981) but with adult Pseudopolydora present at densities averaging 8 individuals/.001 m<sup>2</sup>. Fabricia tube mat treatments consisted of intact cores (9 x 9 x 9 cm) containing Fabricia at densities ranging from 22 - 153 individuals/.001 m<sup>2</sup>. These cores were collected on February 7, 1981 from the high intertidal in the east arm of Bahia de San Quintin, Baja California. The Fabricia cores were maintained in the laboratory under running seawater at Scripps until use in field experiments. Pseudopolydora was not present in the Fabricia cores from San Quintin (pers. observation) so any settlement of Pseudopolydora into Fabricia treatments was easily detected.

Six cartons (two of each treatment) were arranged in checkerboard fashion in each of two cages (1/2 " galvanized wire mesh, 30 x 40 x 12 cm) secured to the mudflat surface at Site A (+0.5 ft tide level). After 2 weeks on the mudflat, cartons were returned to the laboratory for immediate visual counts of Pseudopolydora settling into a circle of area 0.001 m<sup>2</sup> in the center of each carton. The experiment was carried out over 5 two week periods in March, April and May, 1981.

A Kruskal Wallance one-way ANOVA was used to test for differences between Pseudopolydora settlement in the three treatments. Replicate treatments for each sampling period were pooled and treatments were ranked among all the five experiments.

The effects of high density adult Pseudopolydora on Pseudopolydora larval recruitment were tested in the field at Site A in April 1980. Plastic cartons (9 x 9 x 9 cm) filled with 7 cm of sediment were placed in cages on the mudflat. Adult Pseudopolydora were present in 6 of 12 treatments at densities of 15 - 39 adults/.001 m<sup>2</sup>. After 2 weeks' exposure on the mudflat cartons were returned to the laboratory. Counts of the adult and recruit abundance were made visually with the aid of a dissecting microscope (60x magnification) for 0.001 m<sup>2</sup> areas marked in the center of each carton.

#### Benthic Sampling

Benthic samples for macrofaunal counts were collected from the mudflat using a PVC core 0.00108 m<sup>2</sup> (area) x 7 cm (depth). Initially, each sample consisted of three cores combined in a single container for preservation. When it became clear that a single core yielded many infauna, single 0.001 m<sup>2</sup> cores were counted as individual samples in order to save time sorting. Benthic samples were collected monthly from Sites A, B and C on the mudflat (Figure 11). Benthic abundances were monitored from 1/78 to 7/81 at Station A, from 3/80 to 7/81 at Station B, and from 7/78 to 7/81 at Station C. Four replicate cores were haphazardly placed within a 10 m radius of one fixed spot at each station. Comparable sampling methods were used to take control samples in benthic defaunation experiments.

All benthic samples (collected after August 1979) were preserved in 10% formalin and seawater for 3 or more days then sieved through a 500  $\mu$  mesh screen. Processed samples were sorted at 120x magnification with a Wild dissecting microscope. Prior to September 1979, benthic cores were screened in the field through a 500  $\mu$  screen and then preserved. Unfortunately, these methods resulted in loss of many of the soft-bodied non-tube building forms which were able to squirm through the screen. Concurrent sampling with both methods--sieving before and after preservation--revealed this loss to be greatest ( $\approx$  50%) for Streblospio benedicti, Exogone lourei and oligochaete species. Species which build permanent tubes or live in hard shells will not pass through a 500  $\mu$  screen during sieving.

#### Colonization Studies: Field Recruitment

##### Mid-water settling jars

The availability of competent (ready-to-settle) polychaetes was studied by placing settling jars in different regions of Mission Bay. Wide mouth gallon jars containing several centimeters of dried sediments (from the Kendall-Frost mudflat) were attached to PVC pipes and suspended from buoys at Stations I, II, III and V (Figure 4). Jars were suspended in the water column to sample near-surface, midwater and near-bottom depths. Jar openings were covered with coarse (1 cm<sup>2</sup>) nylon mesh to keep out large animals and were left in place for 2 weeks in July 1978 and June 1979. Deployment and recovery was done on Scuba. Sediments recovered from inside the jars were sieved through a 250  $\mu$  mesh screen, and preserved in 10% formalin and seawater. Samples were sorted for presence or absence of polychaete colonists only.



### Settling trays on the mudflat

Recruitment of macrofauna on the Kendall-Frost mudflat was monitored monthly by placing sediment-filled plastic cartons (9 x 9 x 9 cm) on the sediment surface for two week periods. Plastic cartons were enclosed in 1/2 " galvanized wire mesh cages (30 x 40 x 12 cm) and secured to the mud surface, in order to exclude large predators (fish, shorebirds, rays). Each cage held up to 6 cartons. Cartons were filled to 2 cm from the top with azoic sediments which had been collected from the mudflat and air dried. The mud surface in these cartons stood  $\approx$  10 cm above the surface of the surrounding sediments. Two cages were placed one meter apart at both Sites A and C. A third cage was placed later at Station A, 1 meter and equidistant from the other two cages.

Following recovery from the mudflat, each carton was sampled using a 0.00108 m<sup>2</sup> PVC core. Samples were preserved in 10% formalin and seawater solution for 3 or more days then sieved through a 250  $\mu$  screen prior to sorting. Specimens from all samples were sorted in fresh water under 120x magnification with a Wild dissecting microscope.

The presence of the 1/2 " mesh cages alters hydrodynamics in and around the sediment-filled cartons. The cage and the stakes holding it in place cause small-scale turbulence around the structures as the tide floods and ebbs. Inside the cage water movement is less and sedimentation rates are likely to be somewhat higher than outside the cage. These factors are known to affect larval recruitment, for some species enhancing settlement, for others diminishing it (Virnstein, 1977; Dayton and Oliver, 1980). Most of the species under study are opportunistic (see Grassle and Grassle, 1974) and their settling larvae are attracted to high sedimentation regimes. Thus, the recruitment into the

artificial apparatus does not mimic absolute numbers settling on the mudflat itself. However, it does provide information about annual and seasonal fluctuations in larval availability.

Most of the year cages remain clear of fouling algae and invertebrates. For brief periods during spring and summer, they become fouled with Ulva or diatom mats. When cages became completely fouled, recruitment was diminished and the resulting samples were discarded.

### Defaunation experiments

#### Logistics

A series of defaunation experiments were conducted on the Kendall-Frost mudflat in 1979, 1980 and 1981 to examine the relationship between species' small-scale dispersal abilities and their response to several levels of disturbance. Colonization of defaunated plots was monitored to determine (a) the species composition of colonizing infauna and its predictability from year to year, (b) the rates of recovery for individual species and for the total macrofauna, and (c) the life history stages responsible for colonization. These experiments were carried out from May 27 through July 8 of each year at Site B (+2.0 ft above MLLW). In 1979 surface sediments were removed with a shovel to a depth of 5 cm from a single 40 x 100 cm plot. In 1980 and 1981, replicate plots of the same dimensions were defaunated in a similar manner. Defaunated patches ( $0.4 \text{ m}^2$ ) were designed to mimic pits created by rays and humans foraging on the mudflat. Removal of sediments resulted in removal of all macrofaunal organisms with the exception of a few deep-dwelling oligochates. Newly exposed sediments were initially anoxic but oxidized within a single tidal cycle. Sedimentation, normally high on

the mudflat, caused the plots to quickly resemble natural undisturbed sediment surfaces.

Sediment samples were taken from experimental plots at 0, 3, 8, 13, 21, and 40 days following defaunation. Samples were collected with a PVC core of 0.001 m<sup>2</sup> area and 7 cm depth. Three or 4 cores were collected from each defaunated plot on each sampling date and from surrounding "control" sediments at the start (day 0) and finish (day 40) of the experimental period. Benthic (undisturbed) samples were collected at this site once each month or two from March 1980 through August 1981 to monitor seasonal fluctuations in species composition.

Sediment cores were processed in the same manner as described for other benthic samples. All species were counted and gravid or brooding individuals were noted. The relative abundances of different life history stages were determined by generating size frequency histograms for experimental and control polychaetes. Size measurements of worms were made with an optical micrometer at 120x magnification. Fabricia and Exogone were measured for total length and Streblospio and Pseudopolydora, for the width of the 5th setiger. (Regression of width on length:  $r = .95$  for Pseudopolydora and  $r = .95$  for Streblospio.)

#### Statistical analyses

Paired t tests were used to assess differences between replicate defaunated plots. As there were no significant differences between replicates within each year, data for both plots were pooled in 1980 and 1981. Effects of years (1979, 1980 and 1981) and colonization period (3, 8, 13 and 40 days) were tested using a Two-Way Analysis of Variance. This was done separately for numbers of colonizing Pseudopolydora,

Streblospio, Exogone, and Fabricia. A One-Way Analysis of Variance was used to test for effects of years over all 4 species for each colonizing period (3, 8, 13, 21, and 40 days) and the two control sampling dates May 27 and July 8. Percent similarities were calculated using the formula:

$$2 \sum \text{minimum}(n_a \text{ or } n_b) / N_a + N_b$$

where  $n_a$  and  $n_b$  are the percentages of a particular species in samples A and B, and  $N_a$  and  $N_b$  are the total percent of macrofauna accounted for in samples A and B by all the species included in the analysis (Pseudopolydora, Streblospio, Exogone, Fabricia, Capitella, Rhynchospio and tubificid oligochaetes). Size frequency distributions of colonizing vs. control individuals were compared using a Kolmogorov-Smirnov test (Sokal and Rohlf, 1969). The frequency of brooding in colonizing vs. control worms was tested with a  $X^2$  Goodness of Fit test.

## Results

### Reproduction and Larval Development

This discussion presents the findings of field and laboratory studies of polychaete life histories. The life history traits described here are critical to an understanding of both long-distance and small-scale dispersal abilities.

#### Pseudopolydora paucibranchiata

Reproduction is highly seasonal in the Mission Bay Pseudopolydora population. Females lay eggs of  $\approx 80 \mu$  diameter (Blake and Woodwick (1975) report  $96 \mu$ ) inside their tubes where they are brooded to a 3 setiger stage. Eggs are laid in capsules with 15 - 35 eggs/capsule.

(Blake and Woodwick (1975) report 35 - 50 eggs/capsule.) One hundred to 250 larvae are brooded at one time, all in an identical stage of development. Larvae are  $\approx 200 \mu$  in length, photopositive and begin feeding immediately at the time of release. Larvae (Figure 32A) feed on phytoplankton and other similar sized organic particles. Embryos are brooded in the adult tube for approximately 2 days (Blake and Woodwick, 1975) and larvae develop in the plankton for 7 - 15 days when food supply is abundant and sediment is present. However, settlement may be delayed up to 45 days in the absence of suitable substrate (Figure 33). Larvae are competent to settle at 13 setigers, when they are  $\approx 500 \mu$  in length. Maturity is attained approximately 1 1/2 months after settlement.

The Mission Bay population appears to experience at least 2 overlapping generations per year. Those few individuals surviving through the winter become reproductive in January or February (Figure 34). Their offspring settle and reproduce in spring, resulting in a large recruitment peak in late spring (Figure 46). Some of these individuals may reproduce but many die off in the late summer. Adults probably live less than one year.

Pseudopolydora paucibranchiata larvae are common in the Mission Bay plankton from March through July, and in spring 1980 they were the most abundant organism in waters overlying the Kendall-Frost mudflat (Figure 17). Blake and Woodwick (1975) report pelagic larvae of this species present in Tomales Bay (northern California) each month except for January and February with highest numbers encountered from July through October. Populations of this species appear to exhibit different seasonality at each location. P. paucibranchiata was extremely

Figure 32: Polychaete larval stages

- A. Pseudopolydora paucibranchiata, 4 setiger larva, 300  $\mu$ .
- B. Polydora ligni, 4 setiger larva, 300  $\mu$ .
- C. Rhynchospio arenicola, 6 setiger larva, 350  $\mu$ .
- D. Streblospio benedicti, 9 setiger larva immediately after release from the parent, 550  $\mu$ .
- E. Exogone lourei, 6 setiger larva immediately after release from the parent, 500  $\mu$ .
- F. Fabricia limnicola, 11 setiger larva immediately after release from the parental tube, 1000  $\mu$ .

0

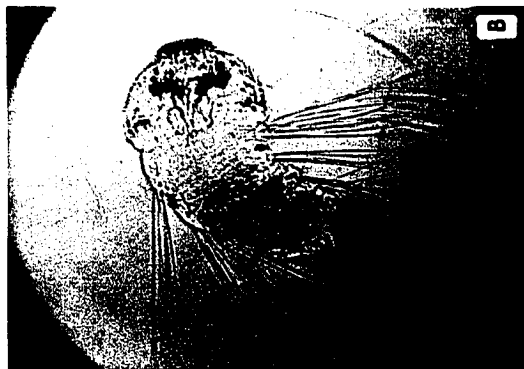
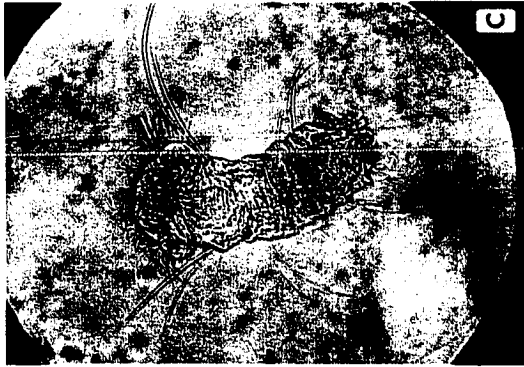
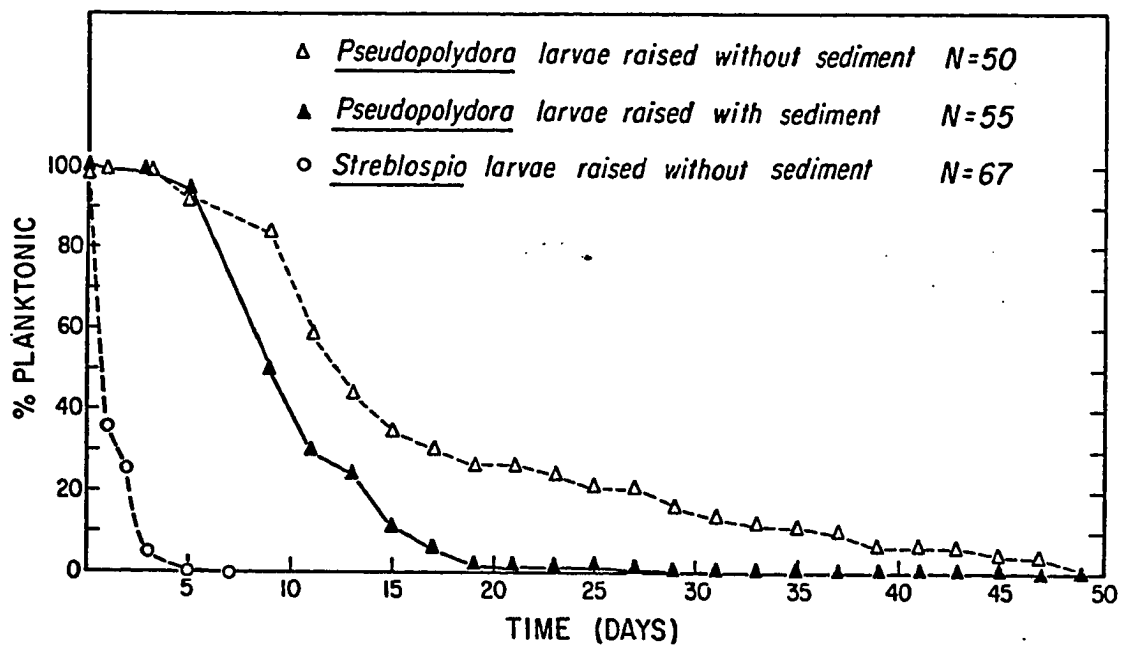


Figure 33: Laboratory rearing experiments, room temperature,  
April, May 1980.  
Experiment I - 9 hrs light per day  
Experiment II - normal day-night cycle



I



II

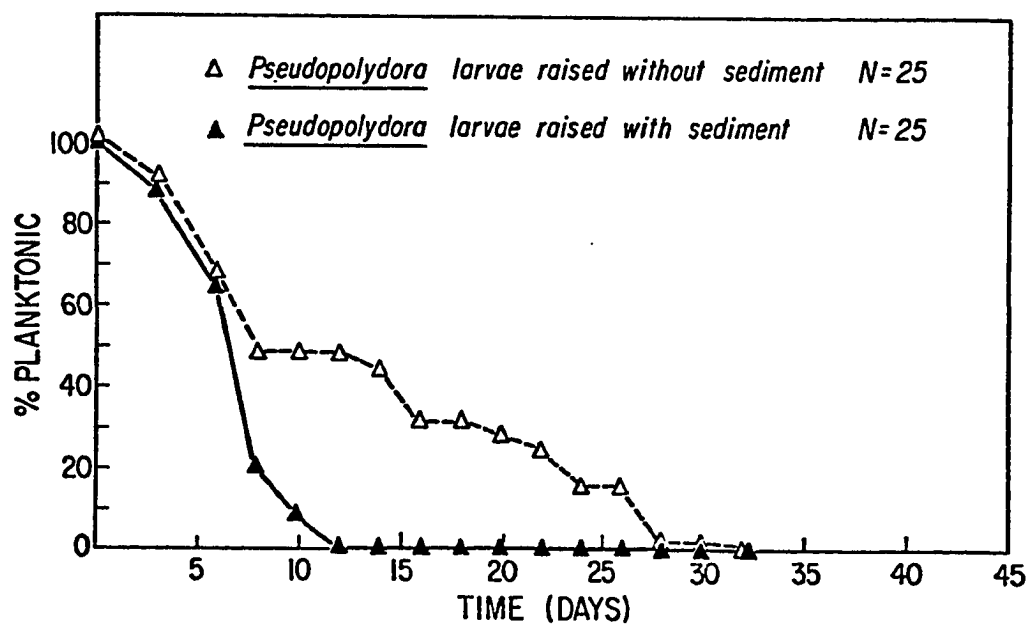
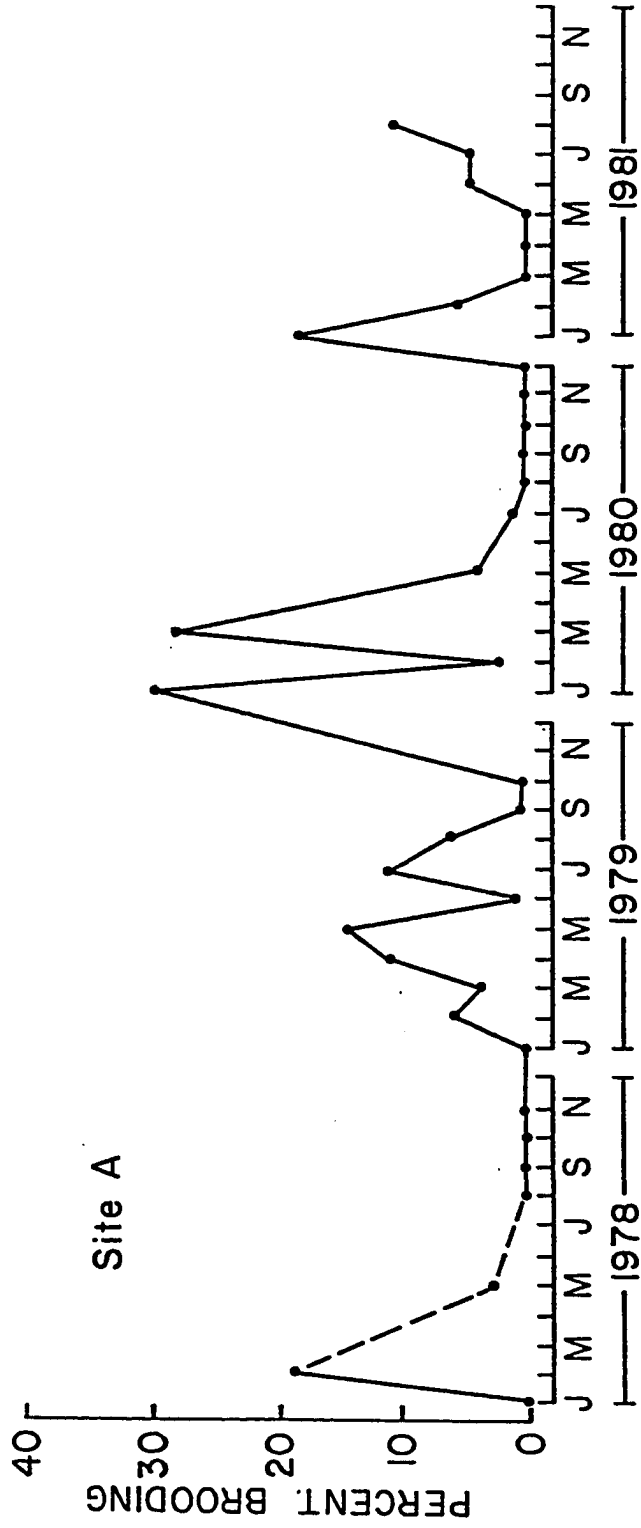


Figure 34: Pseudopolydora paucibranchiata brooding activity on the Kendall-Frost mudflat; Site A, 1978 - 1981.

*Pseudopolydora paucibranchiata*



abundant intertidally at Catalina Harbor on Catalina Island in October 1981 (pers. observation), while the Mission Bay population had already experienced its annual fall decline.

#### Polydora ligni

Polydora ligni is reproductive all year with peaks in larval availability occurring during the spring (Figure 18). Females deposit 70  $\mu$  eggs inside their tubes (Blake, 1969) in capsules of 50 or more eggs. Some of the eggs may serve as nurse eggs. Embryos are brooded to a 3 setiger stage (280  $\mu$ ) and released as photopositive, feeding larvae (Figure 32B). Two hundred or more larvae develop in each brood and two or more broods may be produced in a single season (Blake, 1969). In the presence of sediment, larvae spend approximately 14 days in the plankton before settlement. In the absence of substrate, larvae may extend planktonic development up to 48 days, indicating a competent period of up to four weeks. Settlement occurs at 12 - 17 setigers (1,000 - 1,300  $\mu$  length). Growth is rapid and maturity may be attained within three weeks of settlement (pers. observation). Generation time is approximately 4 - 5 weeks, and many generations may overlap each year.

#### Rhynchospio arenicola

Rhynchospio also broods its young. Embryos develop to the 3 setiger stage (175  $\mu$ ) inside dorsal brood pouches and are released as a photopositive feeding larvae (Figure 32C). Females carry 18 - 30 young per brood, all in synchronous development. A single female can produce at least two (probably more) broods in her lifetime. Larvae generally spend 7 - 14 days feeding in the plankton (in the absence of substrate) and settle at an 11 setiger stage (420 - 500  $\mu$ ). The competent period

may extend pelagic life up to one additional week. Generation time is not known but may be on the order of several months or more.

Reproduction occurs all year in this species. Larvae are present in waters overlying the mudflat in every month, but highest abundances (for 1981) occurred in January and in summer months (May - July) (Figure 19).

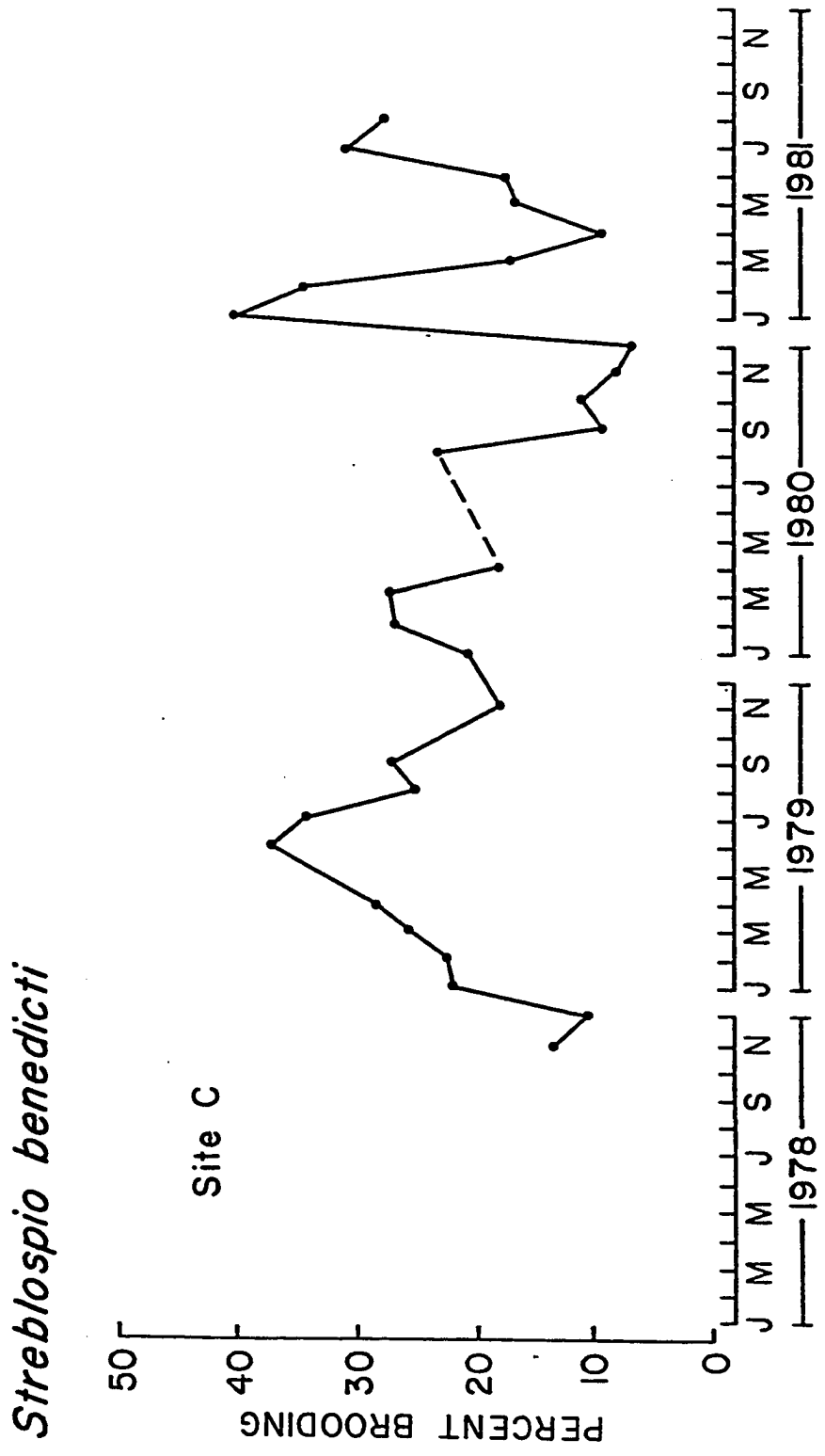
### Streblospio benedicti

Reproduction occurs year-round in the Mission Bay Streblospio population (Figure 35), but peak recruitment occurs in late spring and early summer (Figure 49). Eggs ( $53 \mu$  -  $75 \mu$  uncleaved, Dean 1965) develop to the trochophore stage in setigers 11 - 20 of the female and larvae are brooded on dorso-lateral pouches on setigers 21 - 28. Twenty eight to 36 larvae are brooded at one time, usually 2, occasionally 1, in each coelomic pouch. Early larvae develop in more anterior pouches while late larvae are brooded in posterior pouches. Streblospio benedicti is a semicontinuous spawner. Three or more sets of larvae may be brooded in succession.

Larval release occurs at the 9 setiger stage unless the female is disturbed, in which case 7 - 8 setiger larvae may be released. Nine setiger larvae are  $550 \mu$  in length and are capable of immediate settlement and metamorphosis (Figure 32D). They do not possess elongate swimming setae as shown in Dean (1965). In the presence of a strong unidirectional light, newly released larvae exhibit photopositive swimming behavior, but return to the sediment within minutes.

Larval development within brood pouches requires 4 - 7 days (Dean, 1965). Newly released larvae do not feed in the plankton and

Figure 35: Streblospio benedicti brooding activity on the  
Kendall-Frost mudflat; Site C, 1978 - 1981.



those released in the presence of suitable substrate settle within minutes of release. In the absence of sediment, larvae may swim for up to 3 days (Figure 33) before settlement and metamorphosis. However, Streblospio larvae were virtually never collected in the plankton over the Kendall-Frost mudflat or in Mission Bay. This contrasts sharply with reports of abundant Streblospio larvae in the plankton in Atlantic Coast estuaries (Dean, 1965; Campbell, 1957).

Maturity is attained in 1 - 3 months and the Mission Bay population probably experiences several overlapping generations per year. The life span of individuals is not known but I speculate that it could be one year.

#### Exogone lourei

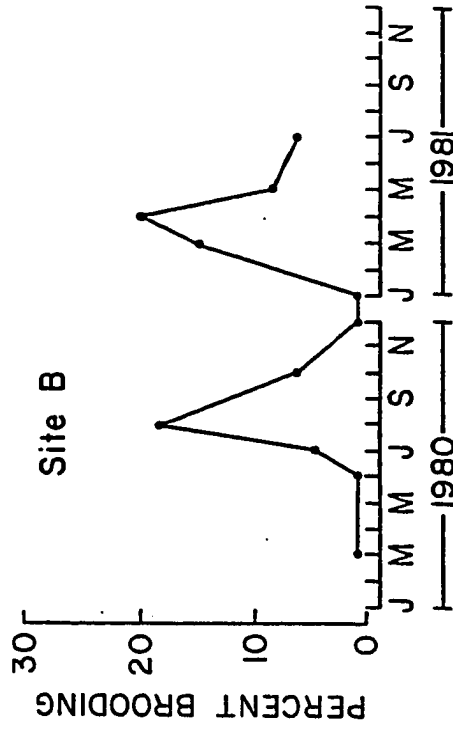
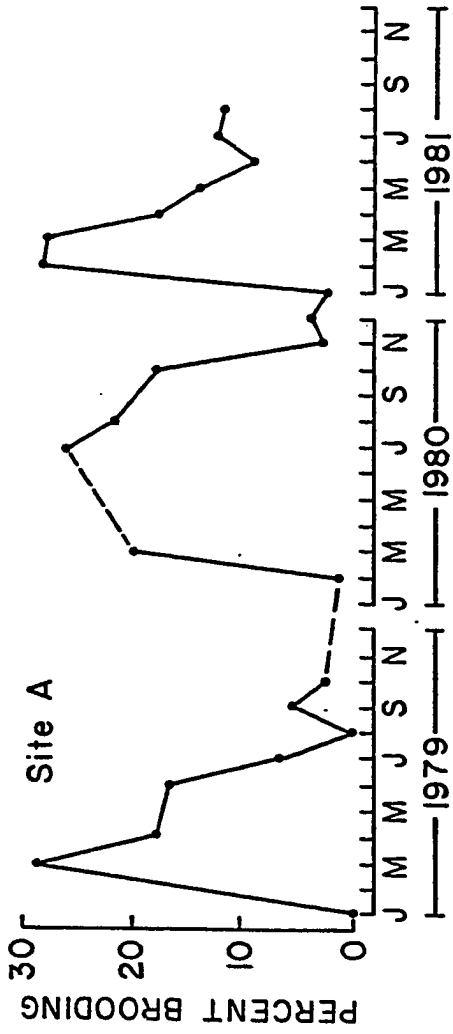
Exogone lourei reproduces all year. Brooding females have been observed in every month (Figure 36). However, most reproduction occurs in spring and from late summer to early fall. Reproductive activity slows from November through January. Females brood ova (100 - 110  $\mu$ ) attached ventrally between segments 11 and 25. Larvae develop on the female to a 6 setiger stage, during which time the larvae exhibit regular wriggling motion. The larvae do not appear to derive nutrition from the parent; substantial yolk supplies are present during development. On several occasions larvae were observed to survive attached to a dead female for several days at which time they successfully separated themselves. Laboratory observations suggest that females produce only one brood and then die.

At the time of release larvae have 6 setigers, are 400 - 500  $\mu$  in length (Figure 32E), and are capable of feeding on their own, though



Figure 36: Exogone lourei brooding activity Site A, 1979 - 1981;  
Site B, 1980 - 1981.

*Exogone lourei*



excess yolk often remains. Newly released larvae are benthic and do not swim, even when disturbed. Twelve to 30 larvae may be brooded at one time. Brood size is highly variable and may be a function of adult size, season and/or food supply (Table 10). All larvae in each brood develop synchronously. Development time is not known. Life span is probably less than one year.

Both male and female Exogone have been observed to develop swimming setae. Exogone adults, some carrying ova, have been captured occasionally in the water column over the mudflat, particularly in night samples. This species may swim up into the water for fertilization and then return to the sediment. Swimming setae have been observed on Exogone lourei from Elkhorn Slough, Monterey (C. Jong, pers. comm.). Swimming behavior associated with reproduction is common in syllids but has not been previously documented for Exogone.

#### Fabricia limnicola

All members of the subfamily Fabriciinae are reported to have direct development (Schroeder and Hermans, 1975). Gravid Fabricia and females brooding larvae have been observed in all months of the year except October and December. However, reproductive activity is greatest during summer months (Figure 37). Brooding activity is very often difficult to detect because larvae inside tubes are few in number and often resemble the sand grains in the tube walls. Females internally brood embryos two at a time to a length of 300  $\mu$ . They then deposit the unsegmented cell masses (in pairs) inside their tube where they develop to 11 - 12 setiger juveniles (Figure 32F). As many as 4 pairs of larvae may be brooded in a single tube at one time, each pair at a slightly

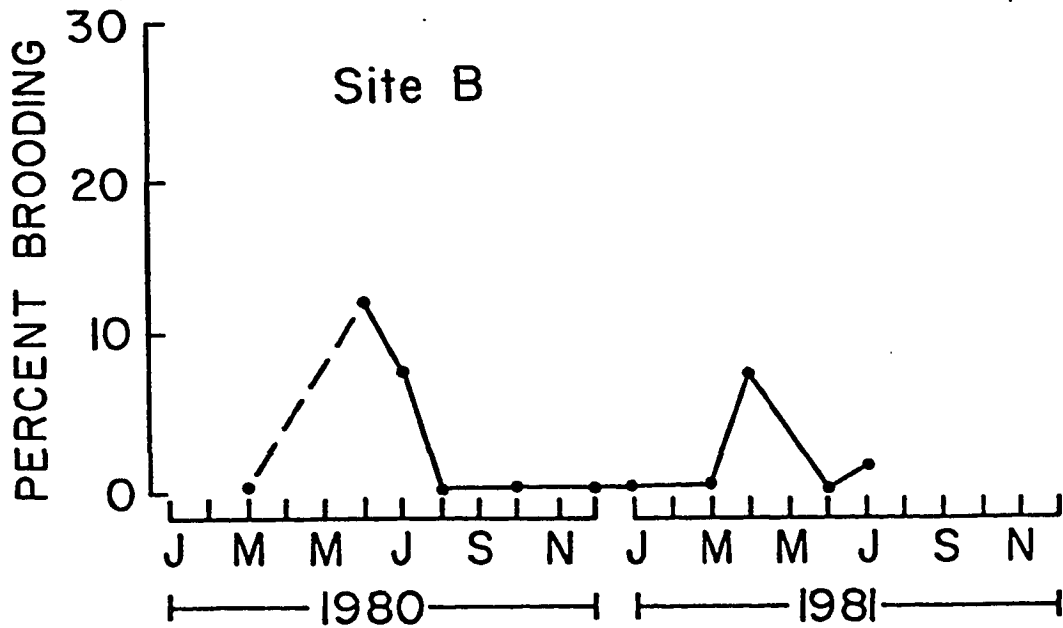
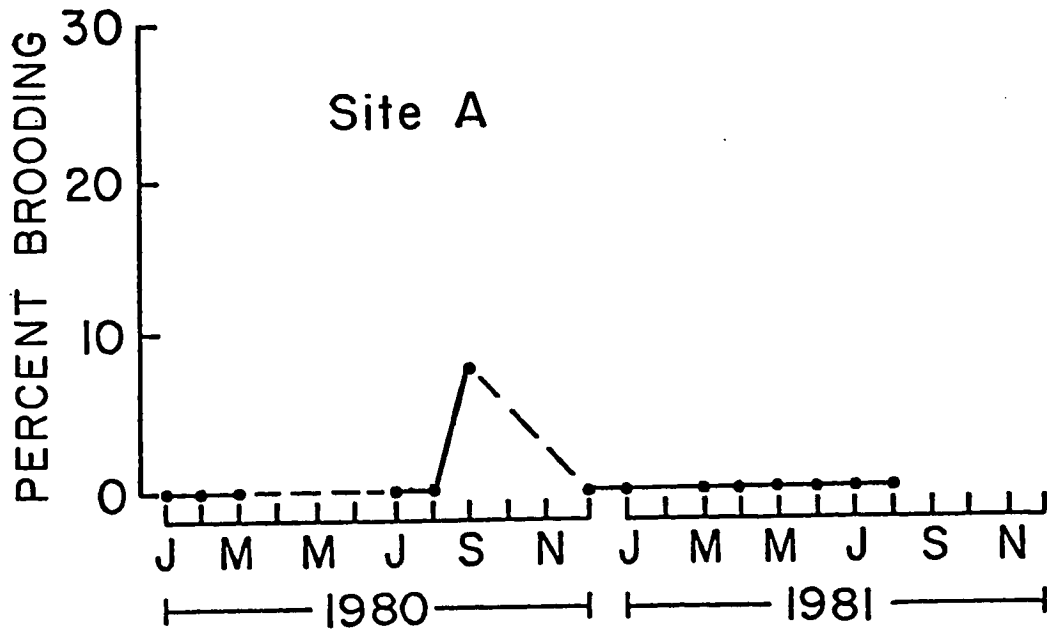
Table 10

Exogone lourei Brood Size

Date	n	#/Brood ( $\bar{x} \pm 2 \text{ S.D.}$ )
Summer 1978	29	16.3 $\pm$ 6.9
March 1979	9	20.3 $\pm$ 9.8
July - August 1980	17	17.6 $\pm$ 9.0
February 1981	17	23.1 $\pm$ 7.8

Figure 37: Fabricia limnicola brooding activity on the  
Kendall-Frost mudflat; Sites A, B and C, 1980 - 1981.

## *Fabricia limnicola*



different stage of development. At the time of emergence from the parental tube, juveniles are 900  $\mu$  to 1,000  $\mu$  in length and have a fully formed gut and tentacular crown. Newly released juveniles do not swim or enter the water column. They immediately construct tubes and take up an adult mode of existence. Fecundity is not known for this species but it appears that females are continuous breeders and produce pairs of larvae steadily for an extended period. No more than 8 larvae have been found in a single tube at one time, but one female might produce many more than that in her lifetime (probably  $\leq$  1 year).

Capitella capitata (Mission Bay variety)

Capitella capitata broods its young to a competent stage inside tubes constructed specifically for this purpose. Eggs (220  $\mu$  diameter) are deposited in a layer 1 egg thick inside the tube. Embryos develop within the tube to an 11 setiger stage in about 10 days at room temperature. Females aerate the tube during this period with forward and backward crawling motion. They do not appear to feed while brooding. Brood size is variable, ranging from 15 to 55 eggs/brood and larvae develop synchronously. Larvae have 11 setigers and are 440  $\mu$  in length at the time of their release. They may settle immediately or spend 1 to 2 hours in the plankton, but do not feed during this period.

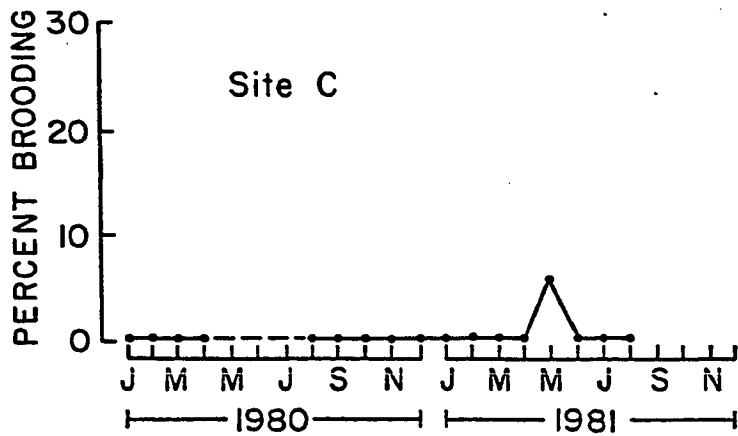
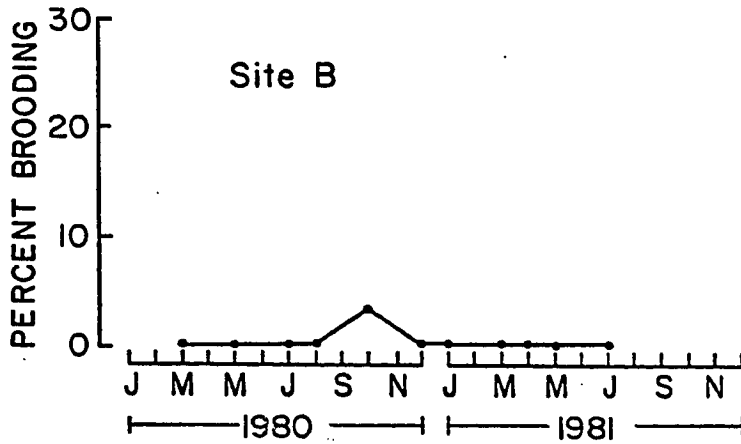
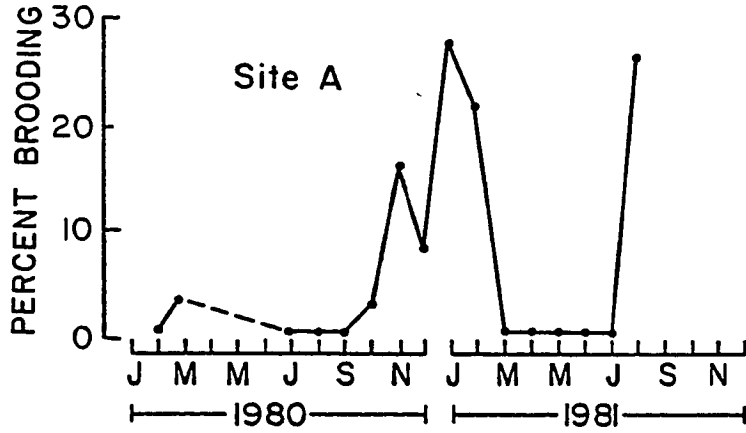
Generation time and the number of broods produced per lifetime are not known. Reproduction occurs all year but primarily in fall and winter. Brooding females have been recorded from October through February (Figure 38) and may comprise up to 28% of the total population.

It is possible that this species has an alternate life history with planktotrophic larvae. One individual, morphologically similar to

Figure 38: Capitella capitata brooding activity on the  
Kendall-Frost mudflat; Sites A, B and C, 1980 - 1981.



*Capitella capitata*  
(Mission Bay Variety)



the species discussed here, was found brooding 230+ small embryos. However, studies by Grassle and Grassle (1976) suggest that an alternate life history is indicative of the existence of a separate species.

#### Generalizations

Many life history traits are shared by the polychaetes described here, the dominant species on the Kendall-Frost mudflat. Adult size is always small,  $\leq 25$  mm, and size at recruitment is relatively large, between 500  $\mu$  and 1000  $\mu$ . Generation times are less than one year and for many species, on the order of 2 or 3 months. Young are brooded in all species, either within pouches on the adult (Rhynchospio, Streblospio), externally attached to adult (Exogone) or inside the adult tube (Pseudopolydora, Polydora, Fabricia, Capitella). Brood sizes are small, generally  $<200$  but often  $<50$ , and in most species females can produce several broods per lifetime.

Pelagic larval stages are reduced or flexible. Exogone and Fabricia lack planktonic larvae and Streblospio and Capitella larvae exhibit a brief facultative swimming period. Pseudopolydora, Polydora and Rhynchospio have a 1 - 2 week obligate planktonic development period, which may be extended in the absence of substrate suitable for settlement. These latter 3 species have planktotrophic development (in which the larvae feed); the first 4 possess lecithotrophic or direct development (nonfeeding larvae). Reproduction occurs through much of the year in most species, however brooding activity and larval availability exhibit strong seasonality.

The life history traits characteristic of the Kendall-Frost polychaete assemblage undoubtedly place constraints on dispersal. Brood

protection, small brood sizes and reduced pelagic larval periods will limit the frequency and spatial extent of dispersal events.

#### Larval Settlement

Substrate selection experiments were designed to help distinguish among effects of larval settlement preferences, adult-larval interactions and spatial patterns of larval availability in the interpretation of recruitment and colonization data. An attempt was made to (a) define species' preferences for sediments from different study sites, (b) determine larval attraction to or inhibition by adult conspecifics during settlement, and (c) examine effects of Fabricia tube mats on settlement. Each of these factors affects species-specific recruitment patterns and ultimately benthic distributions on the mud-flat.

Most of the experiments were conducted with Pseudopolydora paucibranchiata larvae. These larvae were the most abundant group in the Kendall-Frost plankton in 1980, when many of these studies were conducted. Pseudopolydora exhibited notable spatial and temporal variability in field studies of larval availability and recruitment. Much of the spatial heterogeneity observed in the benthos is found to be a result of settlement behavior.

#### Sediment preference experiments

Pseudopolydora recruitment in the laboratory was variable and often low in numbers. However, some trends were apparent. Pseudopolydora recruits consistently preferred site A and Site C natural sediments over azoic sediments (Table 11). In 4 of 6 experimental runs Site A sediments (somewhat sandier) received more recruits than Site C

Table 11

Laboratory Experiments: Pseudopolydora Settlement  
 (# settling/vial cap)

11a

<u>Larval Source</u>	<u>Duration</u>	<u>Sediment Type</u>		
		<u>Azoic</u>	<u>Site A</u>	<u>Site C</u>
Field	7	9	25	26
Field	7	0	35	26
Lab	7	0	3	0
Field	6	*	6	1
Field	5	*	2	3
Field	5	*	7	1

\*not tested

11b

<u>Larval Source</u>	<u>Duration</u>	<u>Adult Effects</u>	
		<u>Site A</u>	<u>Site A + P. paucibranchiata Adults</u>
Field	7	3	4
Field	7	5	9
Field	7	3	1
Field	7	0	3
Field	7	2	0
Field	6	1	0
Field	4	16	45
Field	3	7	7
Field	2	4	7
Field	2	2	2

sediments (somewhat muddier). In the two runs where the reverse was true, Site C counts were greater by only one individual.

In the field experiments (Table 12), settlement patterns were difficult to discern. Pseudopolydora and Exogone recruitment was higher at Site A than Site C, but within Site A there seemed to be little evidence for preference of one sediment type over another. In the March 1979 experiment (Table 12) Streblospio settled more heavily into muddier Site C sediments, independent of location. This trend was not observed in the April experiment.

Pseudopolydora recruitment: attraction to conspecifics

Laboratory experiments suggest slight attraction of P. paucibranchiata to conspecific adults (Table 11b). In many instances where recruitment was low, treatments with and without adults experienced equal or nearly equal settlement. In 5 of 10 runs recruitment was greatest in the presence of adults, in 2 runs recruitment was equal and in 3 recruitment was greatest in Site A sediments without adults (but only by 1 or 2 individuals).

Field experiments also suggest P. paucibranchiata were attracted to conspecifics at low density, when azoic sediments or a dense Fabricia mat were the alternative treatments (Table 13). However, high densities of Pseudopolydora adults were shown to inhibit recruitment in the field when the larval set was very high. (For a discussion of these results, see Chapter VI.)

Table 12  
 Field Studies of Sediment Preference:  
 Site A vs Site C  
 3/22/79 - 3/26/79

Field Site	A		C	
	A	C	A	C
Sediment Treatment				
<u>Species *</u>				
<u>P. paucibranchiata</u>	4 , 8	3 , 0	0 , 0	1 , 1
<u>P. ligni</u>	5 , 4	3 , 1	10 , 2	9 , 4
<u>S. benedicti</u>	0 , 0	4 , 23	8 , 10	27 , 21
<u>R. arenicola</u>	2 , 3	2 , 4	1 , 4	14 , 6
<u>E. lourei</u>	14 , 14	23 , 10	8 , 7	7 , 6
<u>C. capitata</u>	2 , 3	4 , 14	1 , 0	4 , 0

4/4/79 - 4/8/79

Field Site	A		C	
	A	C	A	C
Sediment Treatment				
<u>Species*</u>				
<u>P. paucibranchiata</u>	42	43	20	7
<u>P. ligni</u>	59	42	10	8
<u>S. benedicti</u>	1	0	45	39
<u>R. arenicola</u>	39	19	5	11
<u>E. lourei</u>	10	10	13	16
<u>C. capitata</u>	2	1	2	4

\* number settling into 9 x 9 cm cartons

Pseudopolydora recruitment: azoic vs. natural  
vs. Fabricia mat treatments

Pseudopolydora larval availability and the resulting recruitment in spring 1981 was much lower than in the previous year. Settlement into the experimental cartons was also much lower than in similar experiments (minus the Fabricia treatments) conducted in 1980. Despite the low numbers (Table 13), the trends were clear. Azoic treatments consistently received the lowest settlement, Fabricia treatments received intermediate numbers and natural treatments with adult Pseudopolydora present, received the most Pseudopolydora recruitment ( $X^2_2 = 8.0$ ,  $p < .025$ , Kendall Concordance). Fabricia tubes may inhibit but do not completely prevent Pseudopolydora settlement. In several of the settlement periods the natural and Fabricia treatments yielded similar numbers of newly settled Pseudopolydora (Table 13).

Benthic Abundance Patterns

Benthic abundances are shown for Pseudopolydora paucibranchiata, Polydora ligni, Rhynchospio arenicola, Streblospio benedicti, Exogone lourei, Fabricia limnicola and Capitella capitata at Sites A, B, and C in Figures 39 through 45. Although each species is present at each site, they show considerable variations in density over the Kendall-Frost mudflat.

Pseudopolydora abundances varied greatly over the Kendall-Frost mudflat (Figure 39). Densities were generally highest (up to  $60,000/m^2$ ) west of the main marsh arm at tide levels less than +1.0 ft (Site A), intermediate at higher tide levels (Site B) (but did attain  $64,000/m^2$  in

Table 13  
Pseudopolydora paucibranchiata Recruitment into 9x9x9xm Cartons  
 (#/.001m<sup>2</sup>, 4 replicates)

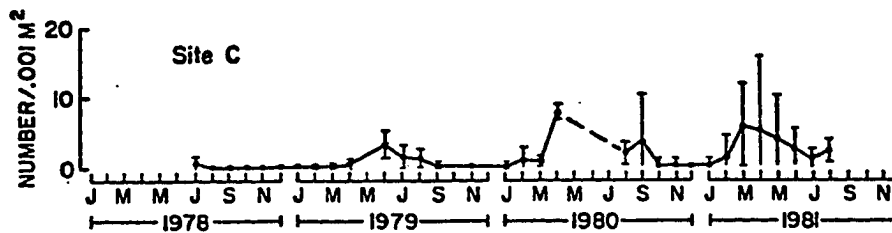
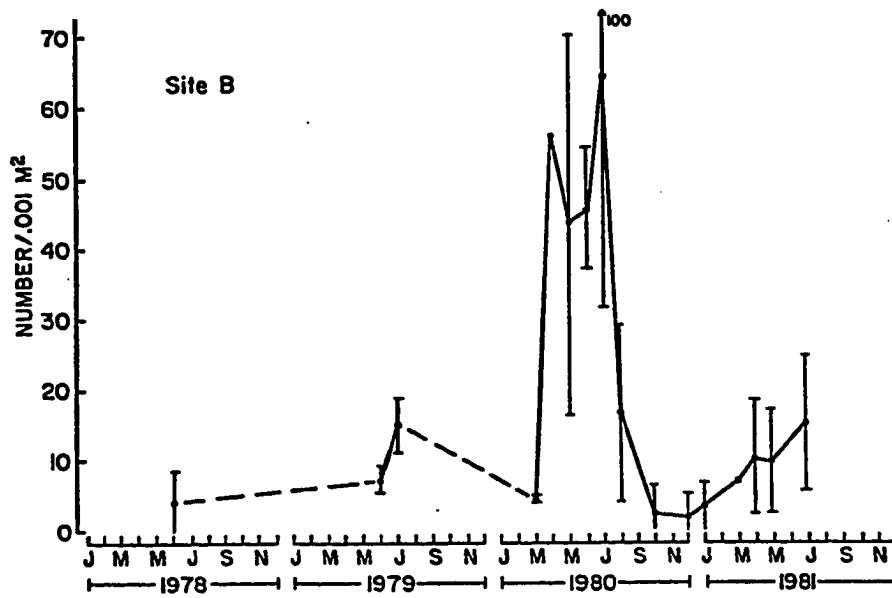
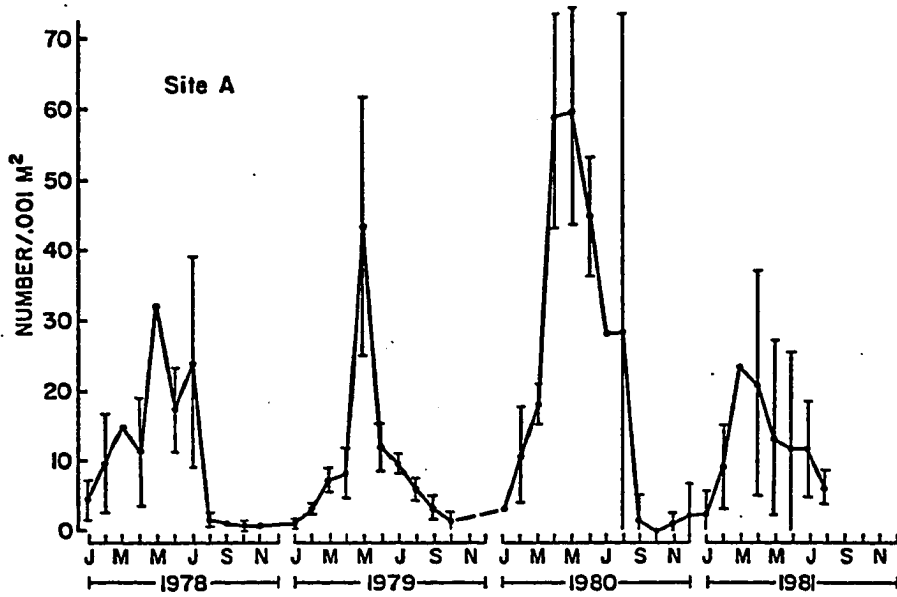
Treatment	AZOIC	NATURAL	FABRICIA TUBE MAT
Dates			
3/3/81-3/14/81	6,1,0,0	3,3,6,3	7,2,0,4
3/16/81-3/30/81	2,4,2,2	7,9,7,*	3,4,2,5
3/30/81-4/13/81	0,0,0,0	3,0,1,0	2,1,0,0,
4/13/81-4/27/81	0,0,1,1	1,0,2,2	0,0,2,1
4/27/81-5/11/81	0,0,0,2	2,2,4,4	0,0,1,0

\* carton damaged before counts were made



Figure 39: Pseudopolydora paucibranchiata benthic abundances  
on the Kendall-Frost mudflat; Sites A, B and C,  
1978 - 1981.

*Pseudopolydora paucibranchiata*



1980) and lowest (up to  $8,000/m^2$ ) at mid tide levels east of the marsh arm (Site C) in siltier sediments.

Benthic abundances were seasonal with maximum densities at Site A attained in May in 4 consecutive years (1978 - 1981). During fall and early winter the population died back to very low numbers. The dieoff may have been due in part to smothering by intertidal algae which cover the mudflat in August and September.

Pseudopolydora abundance cycles were annual at all 3 study sites but lagged 1 or 2 months behind at Sites B and C, as if these areas were settled only after the preferred sites (A) were occupied. This may actually occur as this species exhibits uniform spacing and territoriality at high densities. (See Chapter VI.)

Pseudopolydora females were found brooding larvae at Site A from February - May, 1978, February - August, 1979, January - July, 1980 and January - February, June - August in 1981 (Figure 34). Often there are several distinct peaks in the proportion of brooding individuals each year indicating possible maturation of several generations.

Polydora ligni densities on the Kendall-Frost mudflat were uniformly low (Figure 40). In late 1978 densities briefly reached  $14,000/m^2$  at the muddier mid intertidal site C but then remained low ( $< 4,000/m^2$ ) for the following 3 years. Densities at the sandier mid intertidal site (B) and the low intertidal site (A) remained consistently low ( $< 6,000/m^2$  and  $< 3,800/m^2$  respectively) throughout the 3 1/2 year study period.

Rhynchospio arenicola was most common in the low intertidal (Site A) where it attained densities up to  $22,700/m^2$  (Figure 41). It

Figure 40: Polydora ligni benthic abundances on the Kendall-Frost mudflat; Sites A, B and C, 1978 - 1981.

*Polydora ligni*

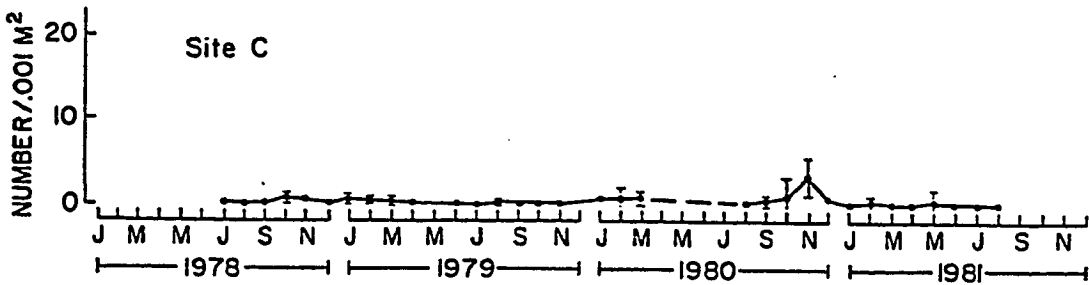
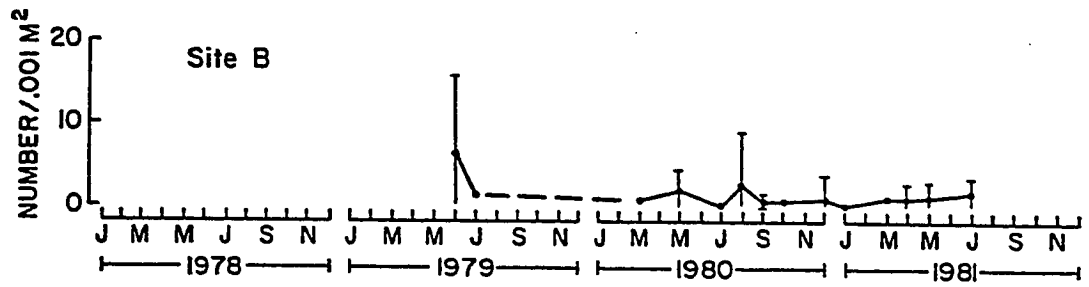
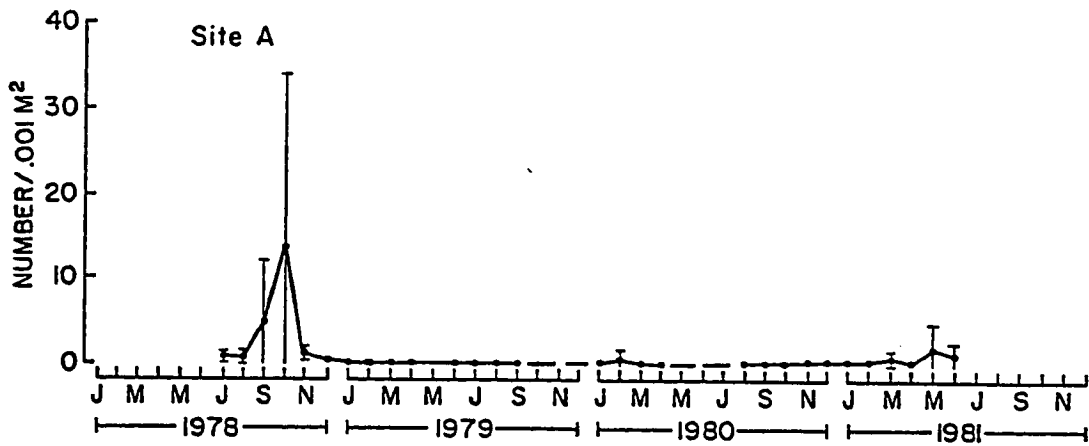
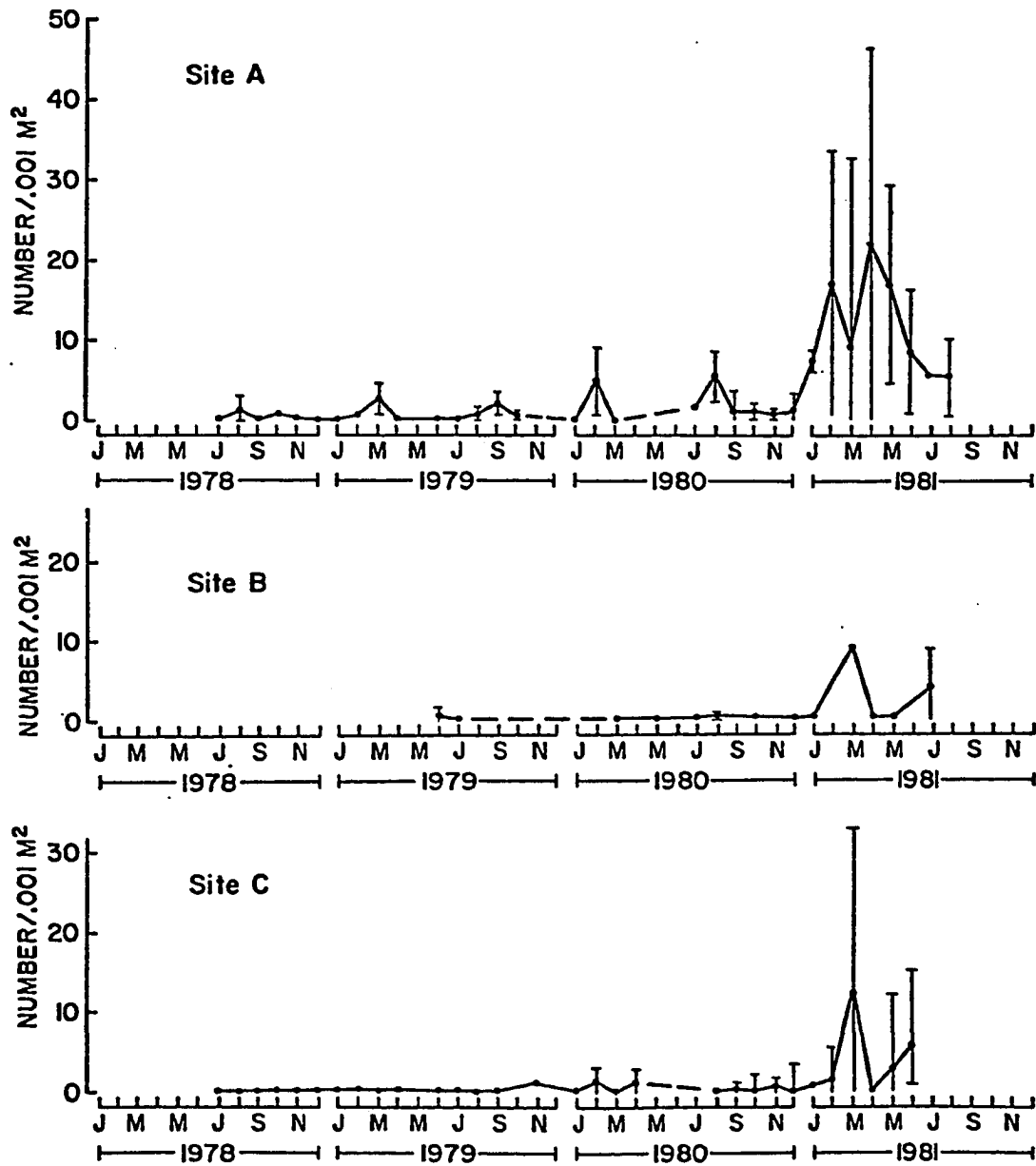


Figure 41: Rhynchospio arenicola benthic abundances on the  
Kendall-Frost mudflat; Sites A, B and C, 1978 - 1981.

## *Rhynchospio arenicola*



was less common at sandy (B) and muddy (C) mid intertidal sites where it reached densities of 8,000 and 12,500 individuals/m<sup>2</sup> (Figure 41).

Until 1981 Rhynchospio abundances remained low at all stations. During 1981, Rhynchospio densities increased 2-3 times in the low intertidal (Site A) over previous years, and density spikes were observed in March at both mid intertidal stations (B and C). No explanation can be given for the increase in Rhynchospio densities during 1981. It is possible that a decrease in Pseudopolydora larval densities and their recruitment success that year released resources in the plankton and/or on the bottom for use by Rhynchospio. This species exhibited two benthic abundance maxima per year in the low intertidal, one in February or March, the other in August or September (Figure 41). However, Rhynchospio larvae (Figure 19) exhibited many more fluctuations in the plankton during the year and only some of these resulted in enhanced recruitment into sediment trays or increased benthic abundances.

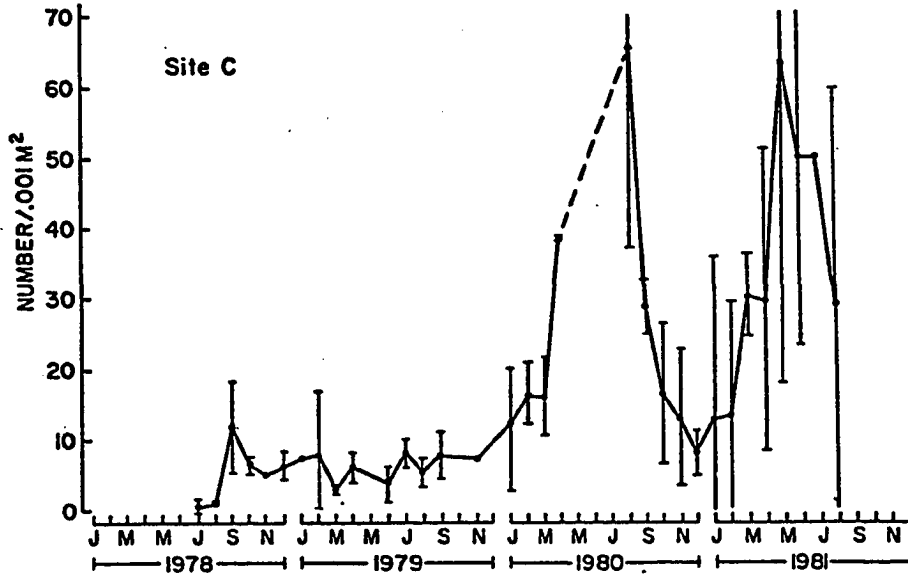
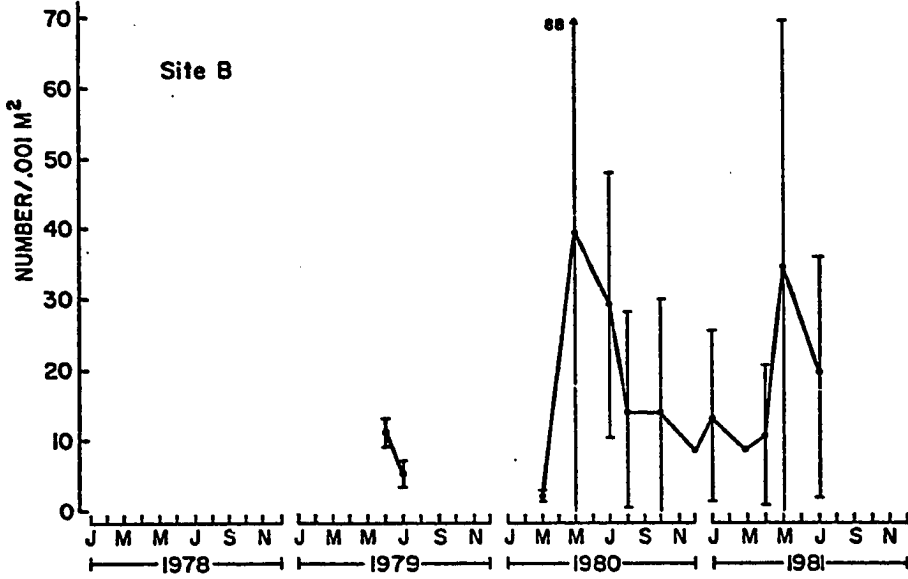
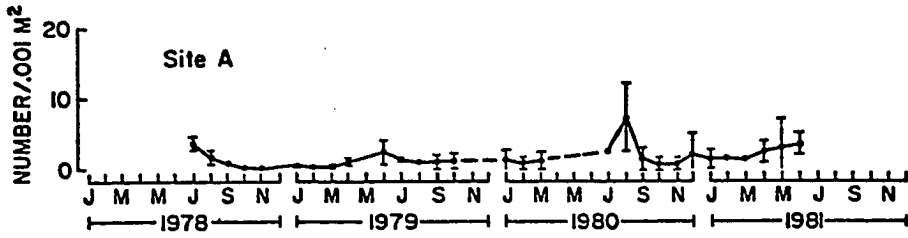
Streblospio benedicti abundances also varied greatly over the Kendall-Frost mudflat (Figure 42). Densities were highest (up to 68,000/m<sup>2</sup>) at Site C, east of the main arm of the marsh at mid tide levels. This site has the highest silt-clay content of the 3 sites studied (Figure 12). Densities were an order of magnitude lower (up to 3,500/m<sup>2</sup>) at Site A (0 to +1 ft tide levels), and intermediate (up to 39,000/m<sup>2</sup>) at Site B, the sandier +2 ft site west of the marsh arm.

Benthic abundances were highly seasonal with maximum densities occurring in June and July and minimum densities December - January at each site. Abundance patterns at all 3 study sites were internally consistent from year to year.



Figure 42: Streblospio benedicti benthic abundances on the  
Kendall-Frost mudflat; Sites A, B and C, 1978 - 1981.

*Streblospio benedicti*



Exogone lourei was consistently most abundant (up to 50,000/m<sup>2</sup>) at Station B (sandy mid intertidal west of the marsh arm) (Figure 43). It was also common at Site A, lower in the intertidal (up to 36,000/m<sup>2</sup>) and less common at the siltier mid intertidal Site C, east of the marsh arm (Figure 43). Exogone seems to prefer sandier sediments and P. Jumars (pers. comm.) found its abundance to be positively correlated with that of the sabellid Fabricia limnicola on the Kendall-Frost mud-flat. I have found Exogone to prefer sediments containing plant debris.

Exogone densities fluctuate during the year with no distinct seasonal patterns. However, colonization of sediment trays was greatest in fall (September - November) and in spring (March - May), corresponding to periods of highest benthic abundance.

Fabricia limnicola was most abundant in the high intertidal Site B (Figure 44) (with the greatest sand content) where it attained mean densities of up to 119,000/m<sup>2</sup>. Fabricia was much less common (up to 18,000/m<sup>2</sup>) in the low intertidal (Site A) and very rare (maximum density 500/m<sup>2</sup>) at the siltier mid intertidal Site C on the opposite side of the marsh (Figure 44).

Appropriate data do not exist to adequately determine the seasonality of Fabricia. Large annual fluctuations in density at Site B (where Fabricia is abundant) mask any seasonal cycle which may occur. However, at Site A where Fabricia occurred in low to moderate abundances, densities increased in late summer and early fall each year and dropped again in late winter or spring (Figure 44). Brooding activity was greatest in June and July (based on Site B individuals) (Figure 37) and the cycles seen lower in the intertidal may have resulted from summer population increase and expansion from Site B.

Figure 43: Exogone lourei benthic abundances on the Kendall-Frost mudflat; Sites A, B and C, 1978 - 1981.

# *Exogone lourei*

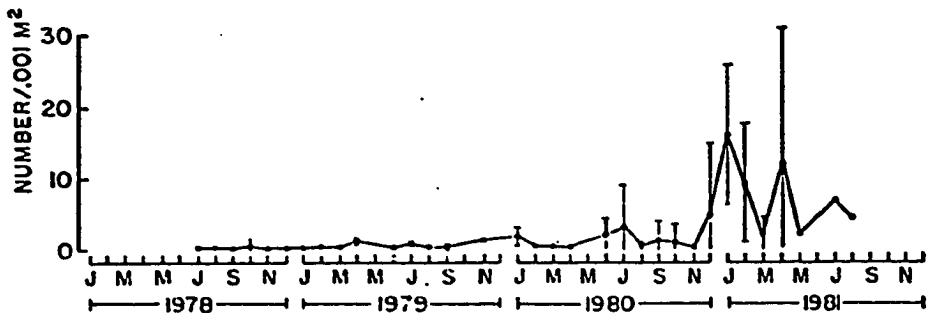
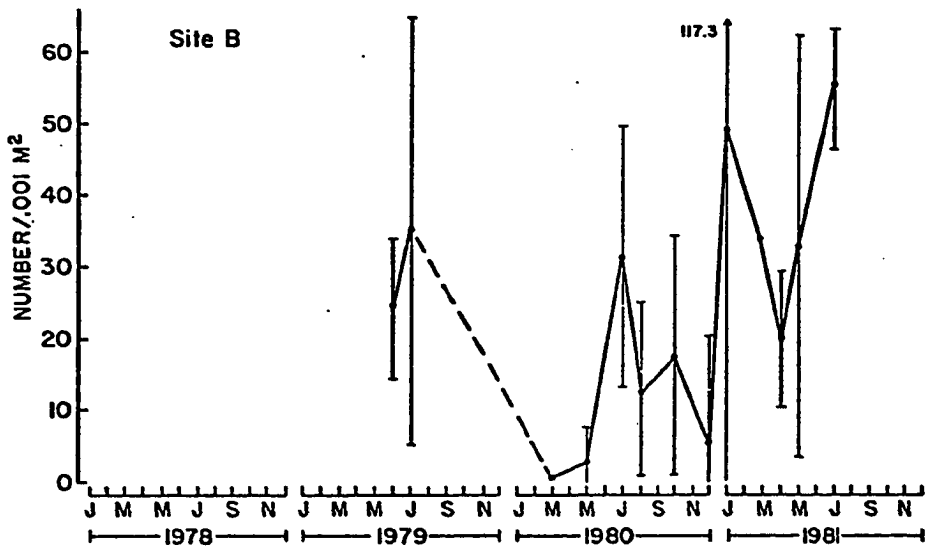
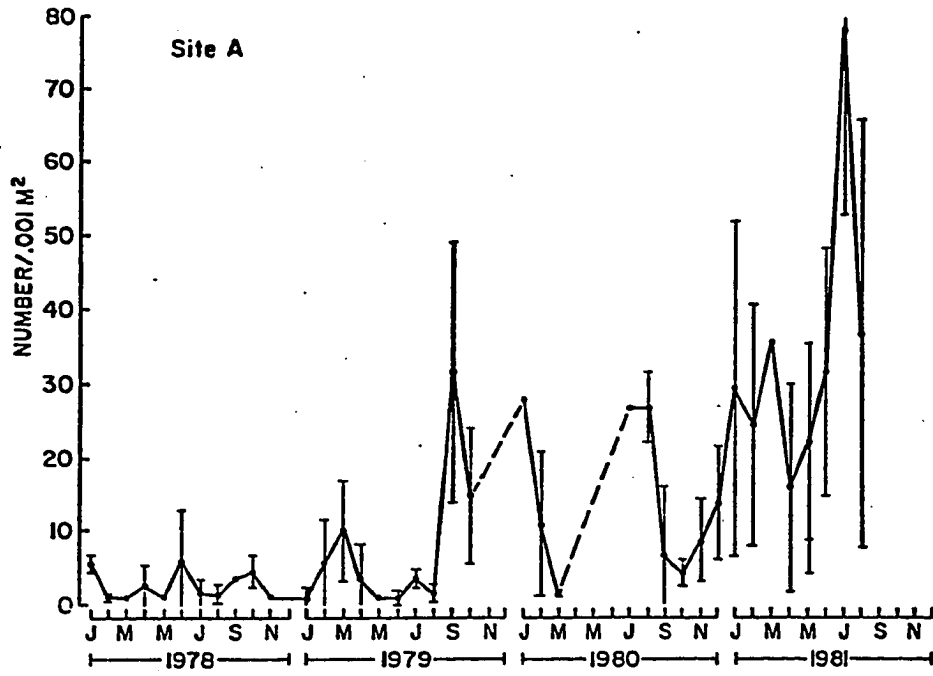
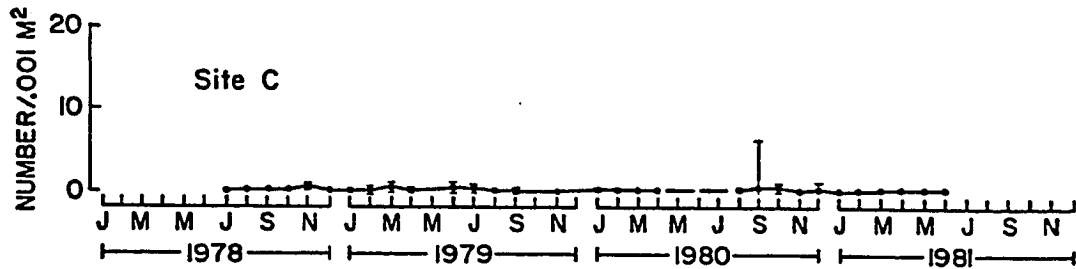
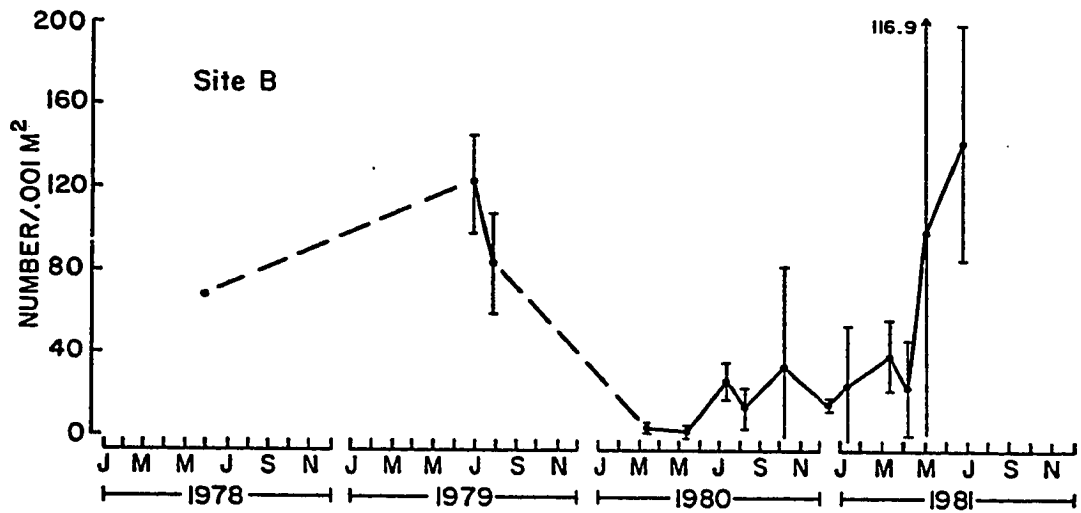
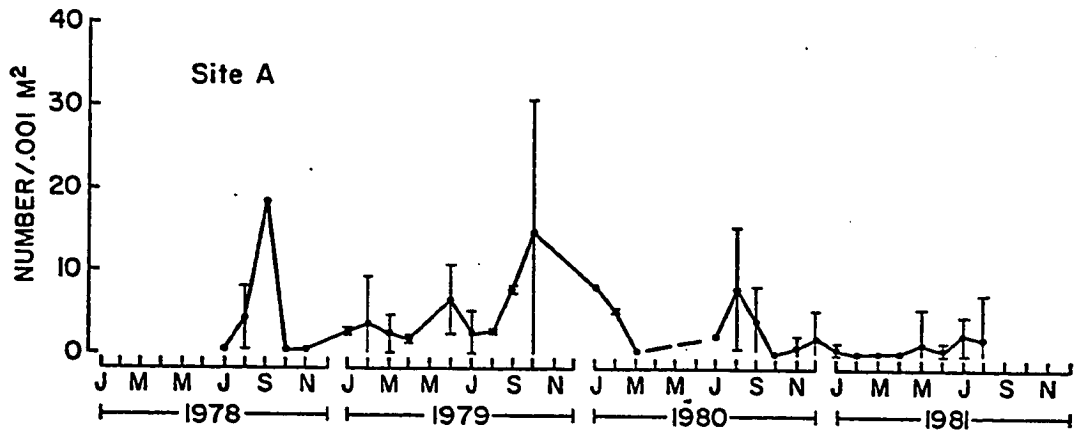


Figure 44: Fabricia limnicola benthic abundances on the  
Kendall-Frost mudflat; Sites A, B and C, 1978 - 1981.

*Fabricia limnicola*



The Fabricia population attained densities over  $100,000/m^2$  in some areas during February 1971 (Jumars, pers. comm.), June 1978, and May - July 1979, but dropped almost 2 orders of magnitude to under  $2,000/m^2$  during early and mid 1980. This decline may have resulted from deterioration of environmental conditions during severe February storms and a raw sewage spill in March. In addition, Jumars (pers. comm.) noted a tendency for this species to be highly aggregated and very patchily distributed. It is susceptible to extreme annual fluctuations in density but possesses rapid powers of recovery.

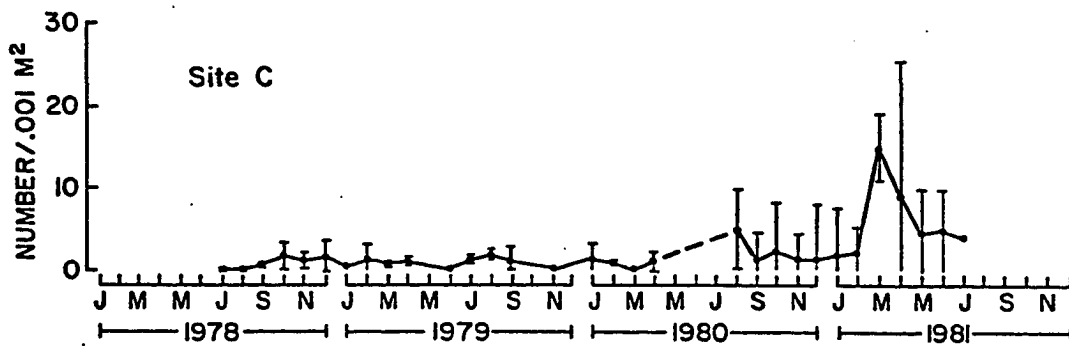
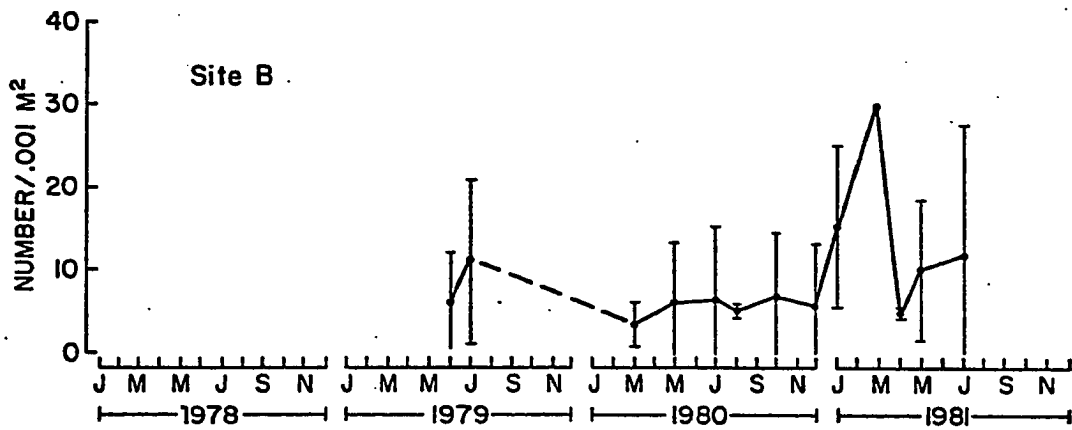
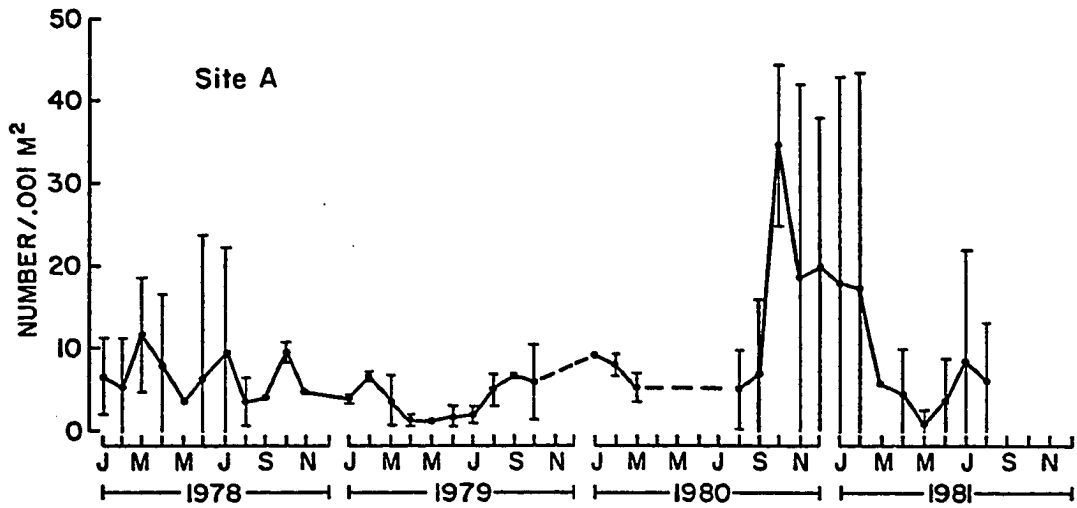
Capitella capitata occurred in moderate abundances ( $< 10,000/m$ ) at the two mid intertidal sites B and C (Figure 45) but exhibited occasional 1 - 2 month periods of elevated abundance. The same was true for the low intertidal Site A until late 1980 and early 1981 when densities more than doubled (up to  $35,000/m^2$ ) (Figure 45). At no time did this species attain the very high densities which are known to occur for Capitella capitata varieties in polluted or disturbed areas (Grassle and Grassle, 1974; Pearson and Rosenberg, 1978).

Abundance maxima for Capitella occurred at different times in the low and mid intertidal. Peak densities were attained in March - April 1981 and February - March 1981 at Sites C and B respectively. This period followed an October 1980 - February 1981 period of elevated abundance at Site A. Reproductive activity, determined from the proportion of brooding females in the population, was low throughout Sites B and C but was relatively high from November through February at Site A (Figure 38). It is likely that individuals at Sites B and C originated as offspring of adults at Site A or from Capitella dwelling subtidally.



Figure 45: Capitella capitata (Mission Bay variety) benthic abundances on the Kendall-Frost mudflat; Sites A, B and C, 1978 - 1981.

*Capitella capitata*



## Settlement and Colonization

### Midwater settling jars

One view of larval availability was provided by the settlement into gallon jars suspended in the water column at 4 stations in Mission Bay (Table 14). Only presence-absence data are presented because the gallon jars do not accurately represent absolute numbers of larvae available. Some species are more likely to settle in them than others and in general they tend to over trap larvae. (Hannan, 1981). Clearly, their presence in the jars does indicate that the larvae are available in the water column; however, absence of recruitment into these jars does not mean larvae are not present in the plankton because some species will not settle in the jars.

Pseudopolydora larvae settled at all sampling stations and Polydora ligni at 3 of 4. Post-larvae of Armandia bioculata, a species which spawns gametes into the water column and has planktotrophic development, were present in jars at all sampling stations. Rhynchospio settled into jars at Stations I (back bay) and V (Ship Channel). Exogone and Streblospio appeared only in Station I jars, near the Kendall-Frost mudflat. In general, the pattern of recruitment into the midwater jars agrees with distributions of larvae from net tows (Chapter III).

### Settling trays

Artificial settling containers were placed on the Kendall-Frost mudflat to study spatial and temporal patterns of polychaete recruitment at Sites A and C. They also provided species-specific information about the small-scale dispersal abilities of different polychaete life history stages. Larvae which entered the cartons probably came from the water

Table 14  
 Polychaete Recruitment into Gallon Jars Suspended  
 from Buoys in Mission Bay

STATION (S=near surface, B=near bottom)	I (6/79)		II (7/78)		IV (7/78)		V (7/78)		
	B	S	B	S	B	S	B	S	
<u>SPECIES</u>									
<u>Pseudopolydora paucibranchiata</u>	++	+	+	(1)	-	+	-	-	
<u>Polydora ligni</u>	++	-	+	-	+	-	-	-	
<u>Rhynchospio arenicola</u>	+	-	-	-	-	+	-	-	
<u>Streblospio benedicti</u>	(1)	-	-	-	-	-	-	-	
<u>Exogone lourei</u>	+	-	-	-	-	-	-	-	
<u>Fabricia limnicola</u>	-	-	-	-	-	-	-	-	
<u>Capitella capitata*</u>	-	(1)	(2)	-	-	-	-	(1)	
<u>Armandia bioculata</u>	++	+	+	+	+	+	+	++	
<u>Eteone sp.</u>	+	+	+	+	+	+	+	+	
<u>Prionospio malmgreni</u>	-	-	-	+	+	-	+	-	
<u>Oligochaete species</u>	-	-	++	-	-	-	-	-	

\* It was not possible to identify newly settled post-larvae as the specific variety of Capitella considered in this study.

++ = very abundant    + = present (> 2 individuals)    - = absent

( ) = number found

column (although organisms may crawl up the sides from the mud surface). Entry from the water column may occur through active swimming or passive resuspension and entrainment. Organisms commonly entering the cartons were considered to be capable of dispersal in the water column.

As with the plankton studies, the three species with planktonic development were regular recruits, either seasonally as in Pseudopolydora (Figure 46) or throughout the year in low numbers as in Polydora (Figure 47) and Rhynchospio (Figure 48). However, Streblospio and Capitella, which rarely appear in plankton samples, appeared commonly as new recruits in settling trays (Figures 49 and 51). Exogone enters the trays in low numbers, usually as adults (Figure 50) and Fabricia virtually never enters the sediment trays. Rhynchospio, Streblospio and Exogone, all body brooders, are capable of colonizing the sediment cartons as adults carrying young. Table 15 lists other species found recruiting into the sediment trays.

In some cases recruitment differs dramatically between Sites A and C. Streblospio recruits primarily into trays at the muddier Site C; Pseudopolydora and often Exogone and Capitella primarily colonize trays at the sandier Site A (Table 16). These patterns mimic benthic distributions of species at these two sites. Polydora and Rhynchospio recruit at both sites although the timing of recruitment may vary between sites. When extreme annual variation occurs in recruitment, as seen in order of magnitude differences between Pseudopolydora recruitment in 1980 and 1981, the two sites agree in timing of recruitment maxima.

The sediment trays cannot provide a complete picture of colonization in mud because some species (e.g. Fabricia) do not enter them, by choice or inability to enter the plankton. Normal benthic abundances

Figure 46: Pseudopolydora paucibranchiata recruitment into settling cartons, on the Kendall-Frost mudflat; Sites A and C, 1980 - 1981. Recruitment into 9 x 9 cm plastic cartons filled to 7 cm with azoic sediments. Number per  $.001 \text{ m}^2$  per 14 days.

*Pseudopolydora paucibranchiata* recruitment

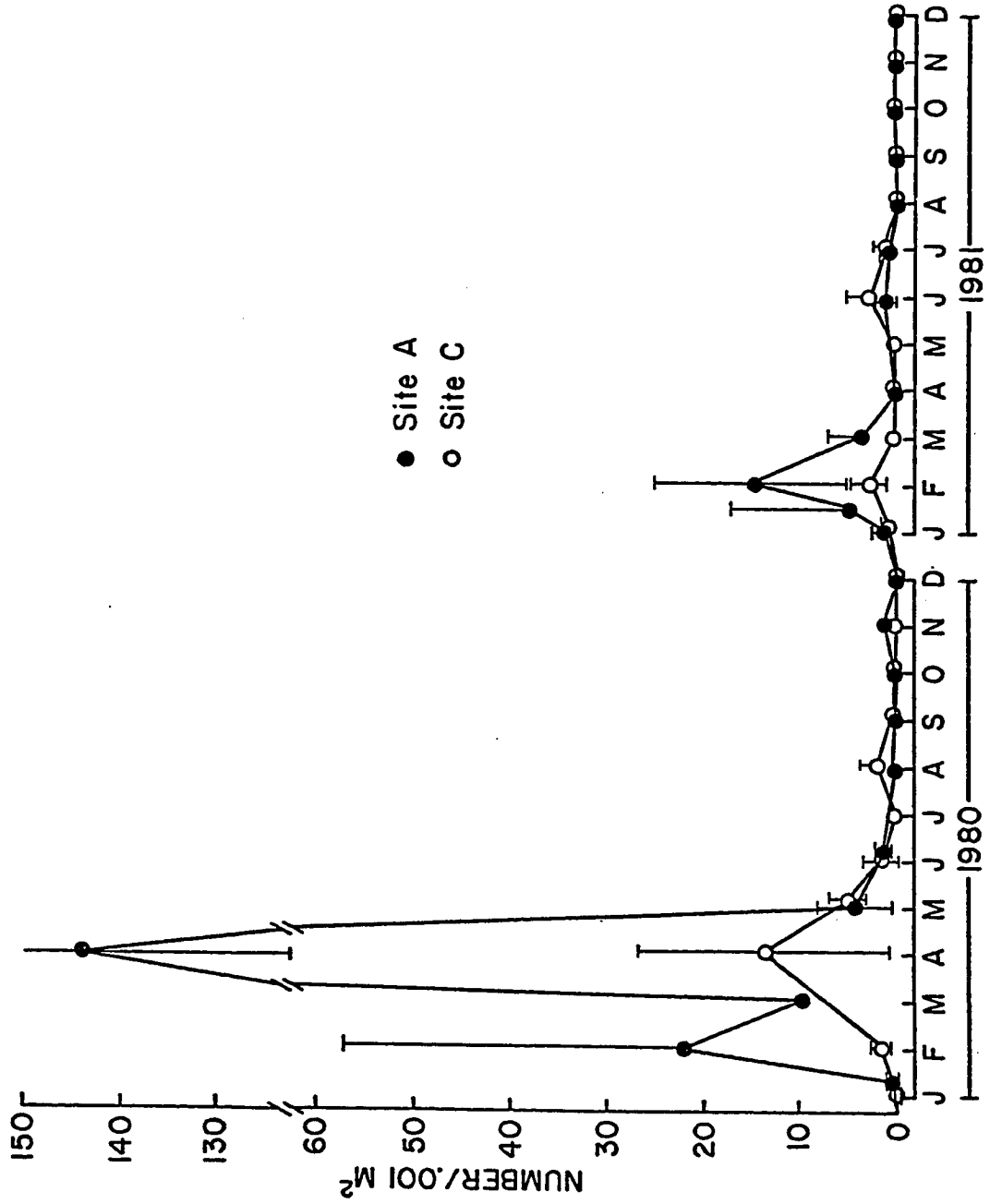


Figure 47: Polydora ligni recruitment into settling cartons on the Kendall-Frost mudflat; Sites A and C, 1980 - 1981. Recruitment into 9 x 9 cm plastic cartons filled to 7 cm with azoic sediments. Number per .001 m<sup>2</sup> per 14 days.



*Polydora ligni* recruitment

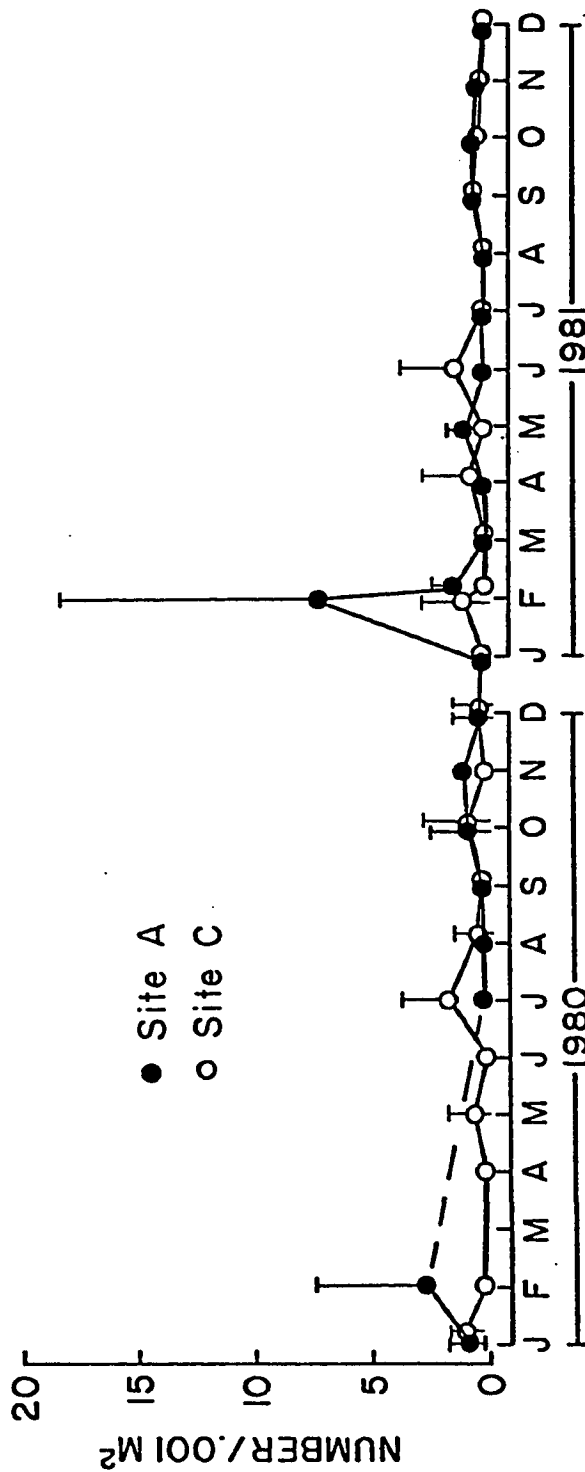


Figure 48: Rhynchospio arenicola recruitment into settling cartons on the Kendall-Frost mudflat; Sites A and C, 1980 - 1981. Recruitment into 9 x 9 cm plastic cartons filled with azoic sediments. Number per  $.001 \text{ m}^2$  per 14 days.

*Rhynchospio arenicola* recruitment

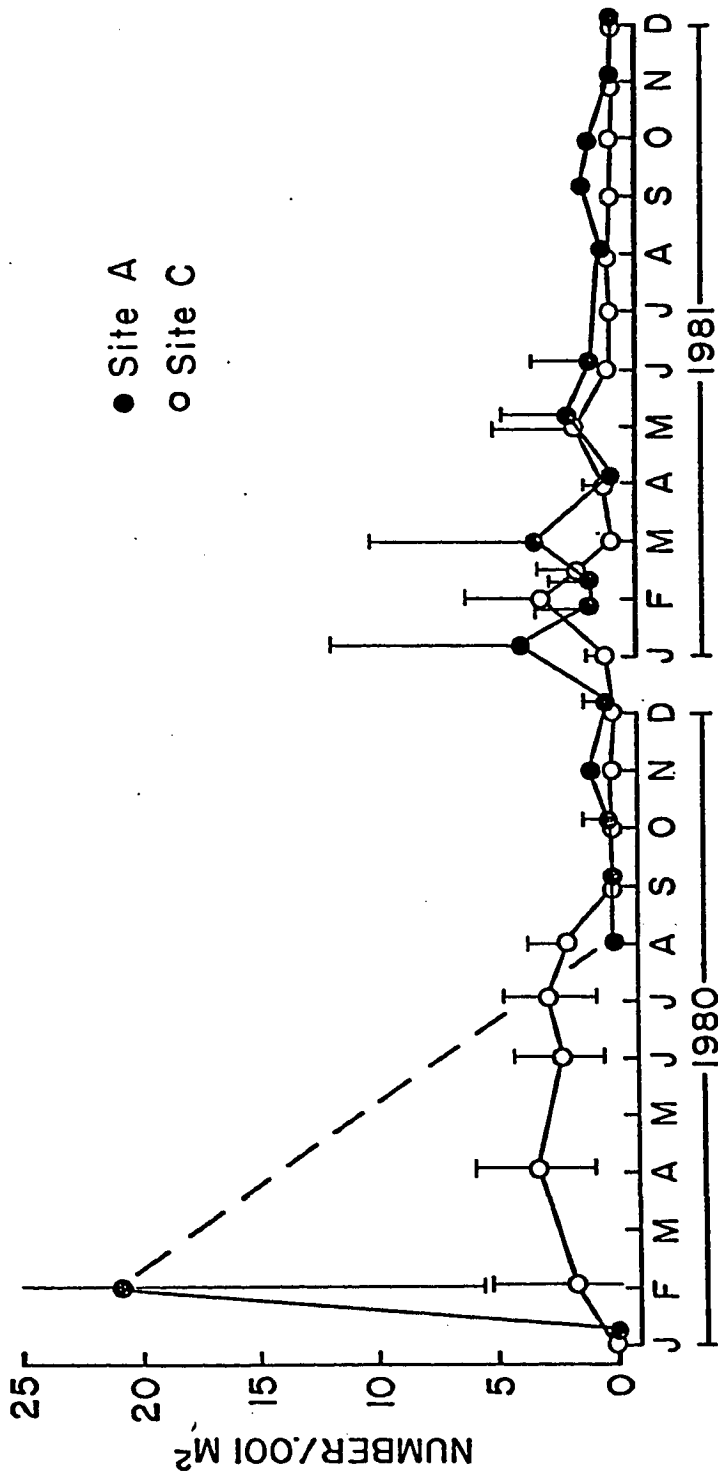


Figure 49: Streblospio benedicti recruitment into settling cartons on the Kendall-Frost mudflat; Sites A and C, 1980 - 1981. Recruitment into 9 x 9 cm plastic cartons filled to 7 cm with azoic sediments. Number per .001 m<sup>2</sup> per 14 days.

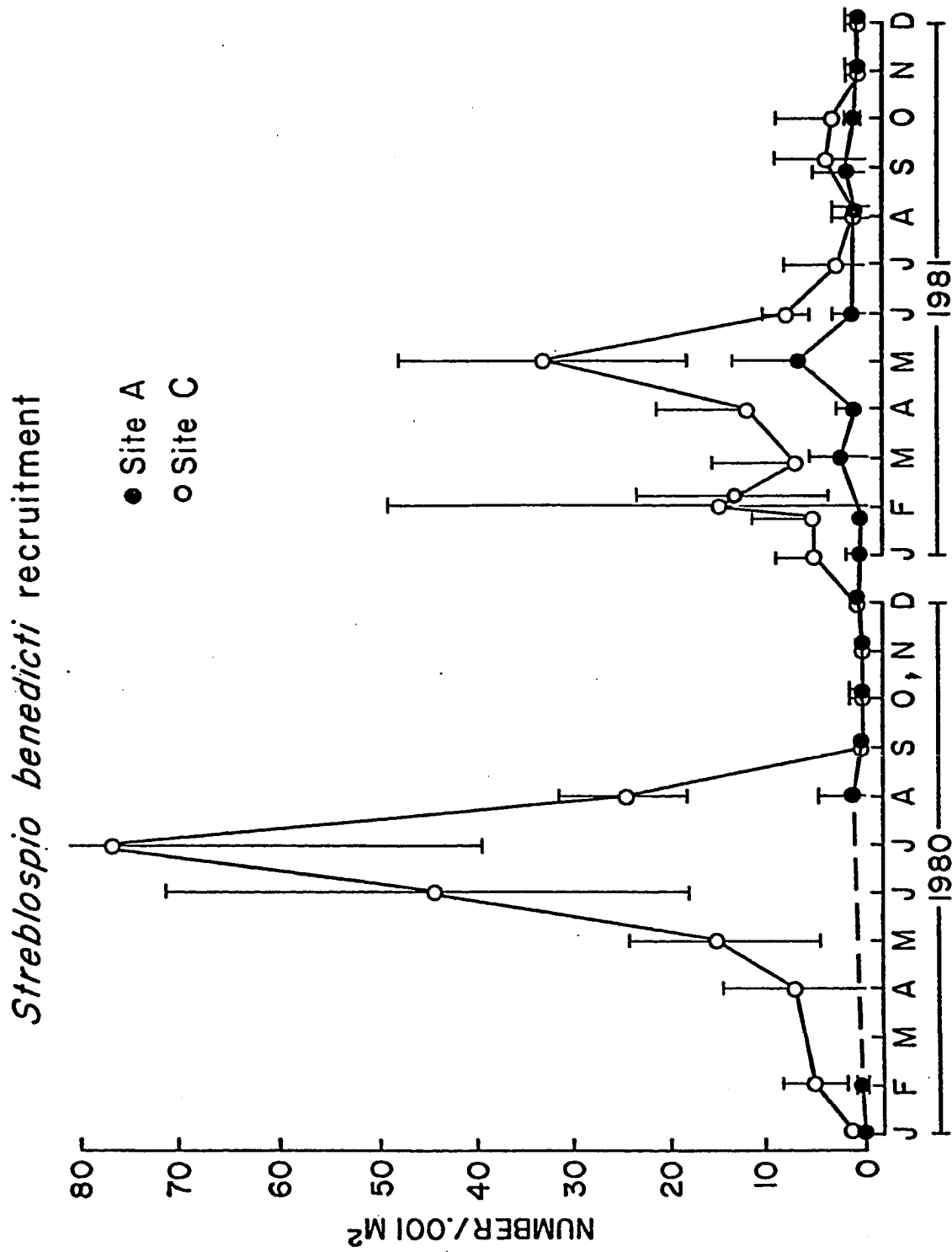


Figure 50: Exogone lourei recruitment into settling cartons on the Kendall-Frost mudflat; Sites A and C, 1980 - 1981. Recruitment into 9 x 9 cm plastic cartons filled to 7 cm with azoic sediments. Number per  $.001 \text{ m}^2$  per 14 days.

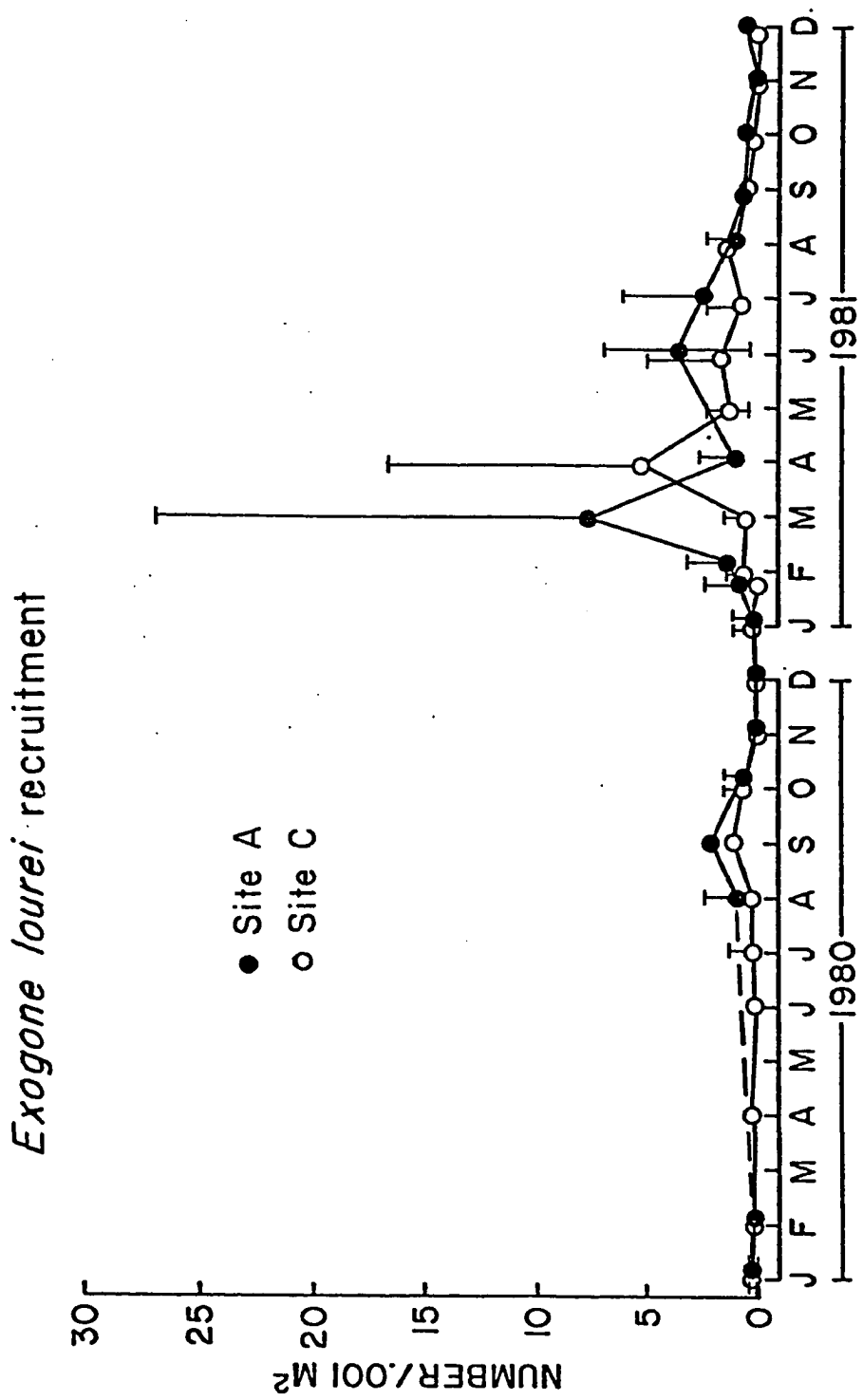


Figure 51: Capitella capitata recruitment into settling cartons on the Kendall-Frost mudflat; Sites A and C, 1980 - 1981. Recruitment into 9 x 9 cm plastic cartons filled to 7 cm with azoic sediments. Number per .001 m<sup>2</sup> per 14 days.



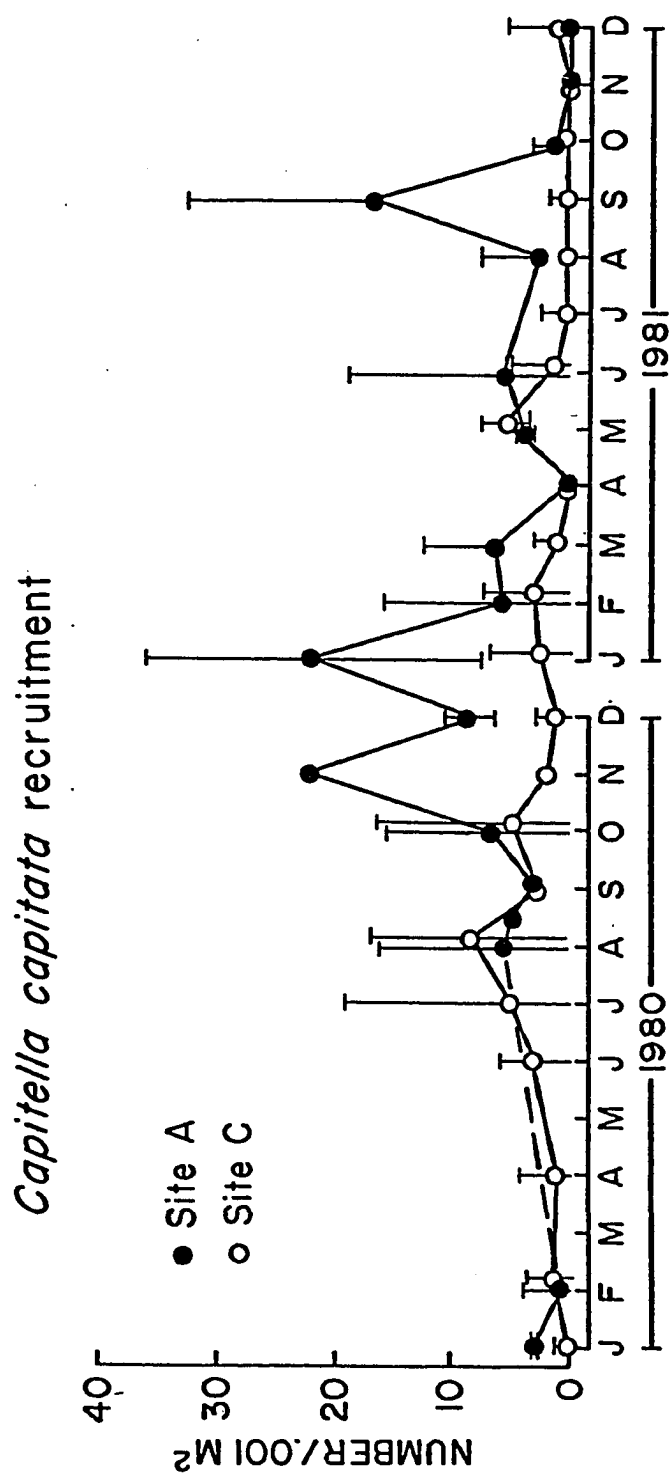


Table 15  
Species Recruiting into Settling Trays  
on the Mudflat

As Larvae:	As Juveniles or Adults:
<u>Pseudopolydora paucibranchiata</u>	* <u>Exogone lourei</u>
<u>Polydora ligni</u>	* <u>Streblospio benedicti</u>
<u>Rhynchospio arenicola</u>	* <u>Rhynchospio arenicola</u>
<u>Capitella capitata</u>	
<u>Armandia bioculata</u>	
<u>Prionospio malmgreni</u>	
<u>Eteone dilatata</u>	
<u>Nereis sp.</u>	
<u>Polydora sp.</u>	
Unid. Sabellid	
<u>Phoronis sp.</u>	Tubificid oligochaetes
<u>Musculus senhausii</u>	* <u>Leptochelia Dubia</u>
Nemertean	* <u>Corophium sp.</u>
Dipteran	* <u>Ericthonius sp.</u>
	* <u>Pontogeneia sp.</u>
	* <u>Caprella sp.</u>
	<u>Acteocina culcitella</u>
	Cumaceans
	Ostracods
	Nematodes
	Harpacticoid Copepods

\*May colonize while brooding young

Table 16  
 A Comparison of Polychaete Recruitment into Settling  
 Trays and Benthic Abundances at Sites A and C

Mean Values/.001 m<sup>2</sup>

(n = 2, 3 or 4)

SITE	<u>Streblospio</u>		<u>Capitella</u>		<u>Exocoene</u>		<u>Pseudopolydora</u>	
	A	/ C	A	/ C	A	/ C	A	/ C
Benthic: 1/13/80	0.7	< 11.9	28.0	> 4.0	84.0	> 4.0	10.0	> 0.7
Recruits: 1/13-1/27	0.06	< 2.7	22.0	> 2.7	1.5	> 0.7	3.5	> 0.7
Benthic: 2/11/80	0.5	< 68.0	25.0	> 2.5	32.0	> 0.0	33.5	> 3.5
Recruits: 2/11-2/24	0.0	< 24.7	1.3	> 0.0	-	-	11.0	> 0.0
Benthic: 8/13/80	7.0	< 12.3	5.3	> 5.0	27.0	> 1.7	29.3	> 8.0
Recruits: 7/30-8/13	1.3	< 5.0	5.8	< 8.7	0.8	> 0.0	0.3	< 2.0
Benthic: 1/6/81	1.0	< 9.0	18.0	> 1.5	29.0	> 0.0	2.8	> 0.3
Recruits: 1/6-1/20	0.8	< 5.3	16.8	> 2.5	0.3	> 0.3	1.5	> 0.8
Benthic: 2/3/81	1.0	< 24.5	17.3	> 2.0	24.0	> 4.8	9.3	> 1.3
Recruits: 2/3 - 2/17	0.0	< 11.7	5.5	> 3.0	0.8	> 0.0	5.3	> 2.7
Benthic: 4/13/81	2.0	< 50.0	4.7	> 8.0	23.3	> 9.3	21.3	> 5.3
Recruits: 4/13-4/27	0.7	< 33.7	0.0	> 0.0	1.0	> 5.3	3.5	> 0.3
Benthic: 6/9/81	3.8	< 51.7	3.5	< 4.8	31.5	> 11.8	14.5	> 2.3
Recruits: 5/25-6/9	6.7	< 7.7	3.7	< 5.3	3.7	> 1.3	1.3	> 0.0
Benthic: 7/7/81	4.7	< 51.7	13.5	< 4.0	78.3	> 6.7	12.0	> 1.0
Recruits: 6/13-7/7	1.0	< 7.7	5.2	< 1.7	5.3	> 1.7	0.75	< 2.7

were generally not attained within the 2 week period the cartons were exposed in the field.

#### Defaunation experiments

A series of defaunation experiments were conducted in spring of 1979, 1980, and 1981 on the Kendall-Frost mudflat at mid tide levels (Site B) where Pseudopolydora, Streblospio, Exogone and Fabricia all occur at relatively high densities. The experiments were intended to add to the small-scale dispersal information acquired from midwater plankton sampling jars and settling tray studies, and to provide insight into the role of small-scale dispersal abilities in response to disturbance. Organisms collected in the plankton or in the settling apparatus are assumed to be capable of dispersal through the water. Defaunated sediments, contiguous with undisturbed sediments, may be colonized through horizontal migrations of animals within the mud as well as from the water column.

The defaunation studies embraced several levels of disturbance. The artificially defaunated plots (0.4 m<sup>2</sup>) resembled natural disturbances on the mudflat: pits and puddles created by ray foraging activities, human trampling and fishermen digging for bait. These depressions are known to persist for 1 or more months (Chapter II). A large-scale perturbation— a severe storm and raw sewage spill—occurred in 1980, the middle year of this investigation. This disturbance altered the distributions and relative abundances of species over the entire mudflat. Changing abundance patterns provided the opportunity to evaluate the effects of community composition on colonization rates and patterns and to assess the regional stability of the infaunal assemblage.

Control abundance patterns (Site B): 1979, 1980, 1981

Accurate interpretation of the defaunation studies required careful analyses of the infaunal community in control (undisturbed) sediments surrounding the experimental plots. Infaunal members of the control community and their offspring were the primary source of colonizers invading disturbed patches; there was minimal colonization by larvae originating from sites other than the Kendall-Frost mudflat.

Relative abundances of the 4 dominant infaunal polychaete species at Site B (P. paucibranchiata, S. benedicti, E. lourei, and F. limnicola) remained constant during the May 27 - July 8 experimental period in each of 3 years but shifted dramatically among years, reversing order from 1979 to 1980 and returning to 1979 levels in 1981 (Figure 52). Analyses of percent similarities of control samples within and between years were carried out using data for Pseudopolydora, Streblospio, Exogone, Fabricia, Rhynchospio, Capitella and tubificid oligochaetes. These species accounted for 83.3, 85.0 and 95.8 percent of the total macrofauna in 1979, 1980 and 1981 respectively. Percent similarities (PS) between May 27 (day 0) and July 8 (day 40) control samples were 84.7, 89.4 and 85.5 for 1979, 1980 and 1981. These relatively high PS values demonstrate that within the experimental period each year, there was little change in the structure of the control community. Percent similarity between 1979 and 1981 May controls was high (PS = 78.7) and was even higher for the July 8 controls in those 2 years (PS = 92.2). However, percent similarities for 1979 and 1980, and for 1980 and 1981 were low for initial and final controls. PS = 25.0 (1979-80) and 42.0 (1980-81) for May 27 controls and PS = 68.8 (1979-80) and 66.7 (1980-81) for July 8 controls (Table 17).

Figure 52: Polychaete abundance patterns in natural sediments;  
Site B on the Kendall-Frost mudflat.

POLYCHAETE ABUNDANCE PATTERNS IN UNDISTURBED SEDIMENTS

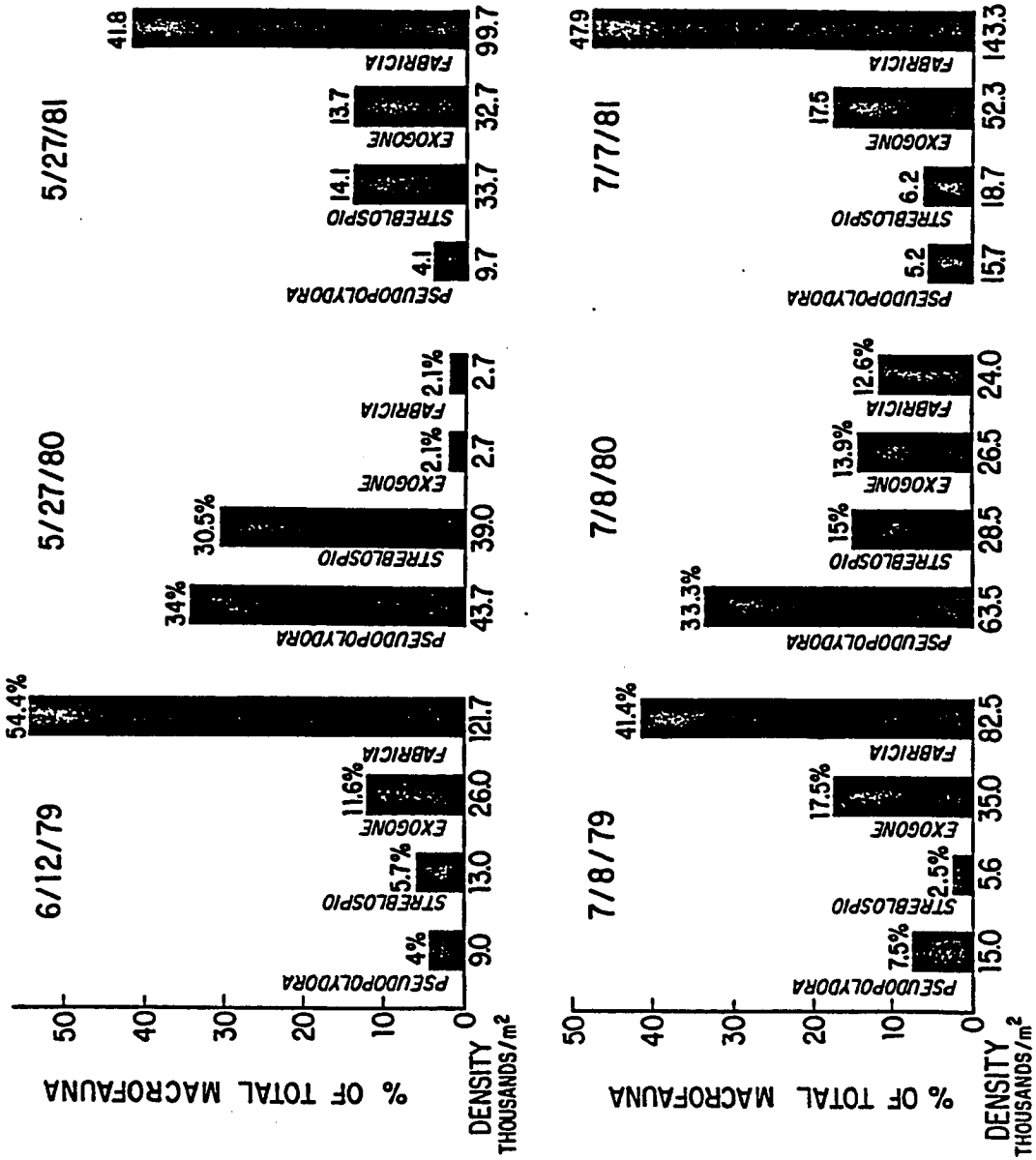


Table 17

## Percent Similiarity between Years

Controls	Initial Control (5/27)		Final Control (7/28)					
	1979 vs. 1980	25.0		68.8				
1980 vs. 1981	42.0		66.7					
1979 vs. 1981	78.7		92.2					
Colonization (Period since Defaunation)	3da		8da		21da		40da	
	1979 vs. 1980	33.8	30.7	-	62.1			
	1980 vs. 1981	33.8	62.3	63.5	64.1			
	1979 vs. 1981	85.0	71.2	-	63.0			

## 2 Way ANOVA

Controls	Years	$F_{2,2}$	= 7.093	NS
	Date	$F_{1,2}$	= 9.51	.05 < p < .10
Colonization	Years	$F_{2,6}$	= 5.063	p = .05
	Time	$F_{3,6}$	= 0.357	NS



The dissimilarity of control samples between 1980 and the other years was due to a dramatic decline in Fabricia densities and a rise in Pseudopolydora abundance. In 1971 (P. Jumars, unpublished data), 1978, 1979 and 1981, Fabricia was the numerical dominant and attained densities of over 100,000 individuals /m<sup>2</sup> at mid tide levels (Figure 44). In early 1980 Fabricia densities declined to only a few thousand per square meter. This event corresponded to a period of unusually high rainfall in San Diego, 12.76 inches in January, February and March (annual average for San Diego is 9.45 inches). In addition, broken sewer lines resulted in a large input of raw sewage into Mission Bay. The cause of Fabricia mortality is not known, but as this species is primarily a suspension feeder, the suspended sediment load in Mission Bay may have risen above tolerable levels.

Pseudopolydora was not reported at these tide levels in 1971 (Jumars, pers. comm.) and sustained fairly low mean densities of 3,330/m<sup>2</sup>, 9,000/m<sup>2</sup> and 9,700/m<sup>2</sup> in spring 1978, 1979 and 1981, though Pseudopolydora did attain much higher densities lower in the intertidal during these latter years (Figure 39). However, in March through April of 1980, Pseudopolydora larvae settled heavily in an area that had formerly been a dense Fabricia bed. By April 1980, Pseudopolydora exhibited mean abundances well over 50,000 individuals/m<sup>2</sup>, replacing Fabricia as the numerical dominant in this surface dwelling assemblage. Heavy Pseudopolydora settlement also occurred at lower tide levels during this period (Figures 39, 46).

Streblospio also increased in abundance in 1980 at Site B (Figure 42) while Exogone, like Fabricia, declined in density from previous years (Figure 43). By May 1981 community composition had shifted such

that Fabricia was again the numerical dominant. Percent composition and absolute abundances of all species resembled 1979 values (Figure 52).

#### Rates of colonization

Rates of colonization of defaunated plots were analyzed to evaluate community resilience and look for specific associations between species' life histories and their colonizing ability. The 1980 and 1981 experiments involved replicate defaunated plots designated Plot A and Plot B. No differences in colonization between replicate plots could be detected from paired t tests run separately for each species over the 3, 8, 13, 21 and 40 day sampling dates ( $t_4 = 2.776$ ,  $p > .05$ ). Colonization data for the replicate plots were subsequently pooled to increase sample sizes for 1980 and 1981.

The relative abundance of species colonizing defaunated sediments (Figure 53) reflects species abundances in control sediments (Figure 52). In 1979 and 1981 when Fabricia and Exogone were numerically dominant in surrounding sediments, they were also the most rapid and prolific colonizers, accounting for over 50% of the fauna colonizing during the first 2 weeks of the experiment. In 1980, when Pseudopolydora and Streblospio were dominant, they did most of the colonizing.

Infaunal colonization rates were rapid, but variable from one year to another and among species. The total number of macrofaunal individuals (Figure 54) did not recover to control levels within 40 days in any of the 3 experiments (1979, 80 or 81). In 1979 and 1981 total macrofaunal densities in the experimental plots attained half the control levels and in 1980 they reached only 1/4 control abundances after 40 days. In 1979 macrofaunal colonizers surpassed control densities 13

Figure 53: Colonization of defaunated sediments on the Kendall-Frost mudflat; Site B: species abundances 3, 8, 13, 21 and 40 days after defaunation.

COLONIZATION OF DEFAUNATED SEDIMENTS

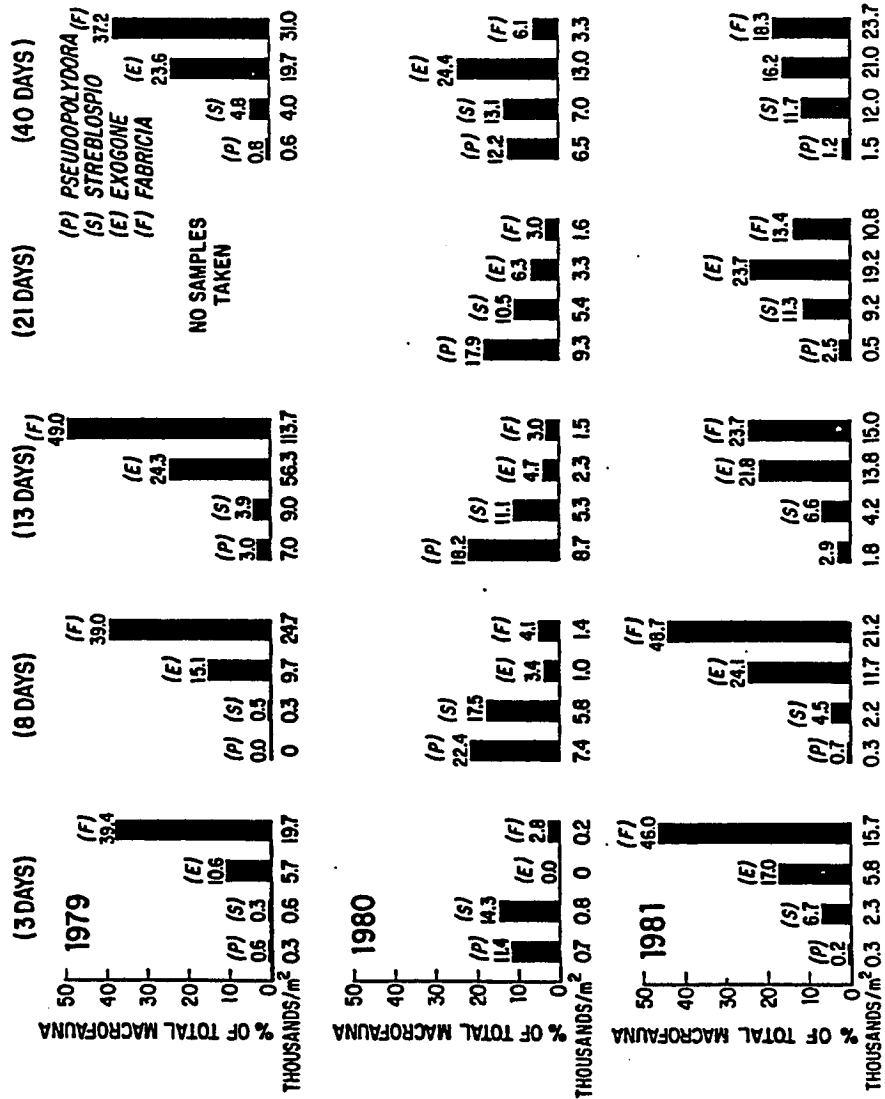
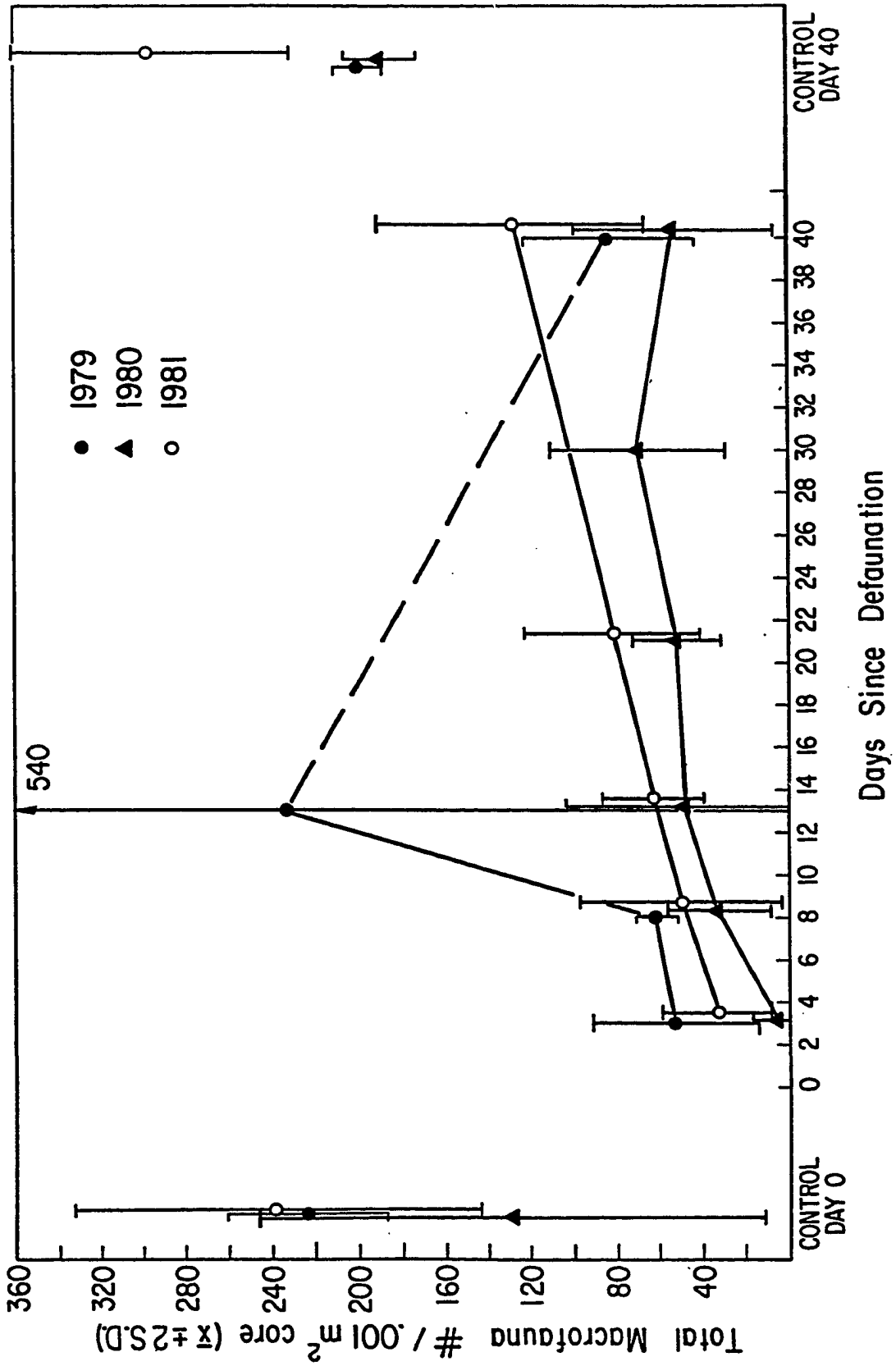


Figure 54: Colonization of control and defaunated sediments on the Kendall-Frost mudflat; Site B: total macroinfauna, #/.001 m<sup>2</sup>.



days after defaunation but rapidly declined in density in the following weeks. No overshoots of this type were seen in other years. Defaunated plots in the 1980 experiment attained control densities by August 13 (75 days after defaunation). Unfortunately, the 1979 and 1981 patches were not identifiable in months following the July 8 (40 day) sampling date, so the time required for complete community recovery could not be determined. These results suggest that macrofaunal recovery rates are fairly rapid in this community, > 40 days but < 75 days. The 1979 and 1981 assemblages, characterized by a more stable species composition, exhibited more rapid recovery than the 1980 assemblage.

While total macrofaunal densities did not reach control levels in any of the 40 day experiments, species richness (number of species present) and densities of some individual species did. Species richness of experimental plots reached control values by 8 days in 1980 ( $R = 17$ ) and 21 days in 1981 ( $R = 16$ ), but only 2/3 of the species reappeared within 40 days in 1979 (Table 18). Recovery rates varied among individual species (Table 19) and were not always consistent from year to year. The errant syllid Exogone lourei, and the burrowing Capitella capitata attained control densities within the 40 day period in all three years. Streblospio did so in 1979 and 1981 but did not attain control levels until 76 days after defaunation in 1980, when its densities were elevated relative to the other two years. Pseudopolydora and Fabricia consistently failed to recover to control densities in 40 days; the one exception was of an overshoot by Fabricia in 1979. Tubificid oligochaetes recovered to control levels 3 weeks after defaunation, but dropped again by the 40 day sampling period in 1979 and 1980. Rhynchospio was very rare in undisturbed sediments but surpassed control

Table 18

## SPECIES RICHNESS

	1979	1980	1981
5/27 Control	24	17	16
<b>Recolonization</b>			
3 days	16	7	13
8 days	18	17	15
13 days	18	18	14
21 days	-	15	17
40 days	17	18	21
7/8 Control	17	14	17



Table 19  
 Polychaete Colonization of Defaunated Sediments  
 Mean #/.001 m<sup>2</sup>

	5/27 Control	3 Day	8 Day	13 Day	21 Day	40 Day	7/8 Control (40 Day)
<u>Pseudopolydora paucibranchiata</u>							
1979	9.0	0.3	0.0	7.0	-	0.6	15.0
1980	43.7	0.7	7.4	8.7	9.3	6.5	63.5
1981	9.7	0.3	0.3	1.8	0.5	1.5	15.7
<u>Streblospio benedicti</u>							
1979	13.0	0.6	0.3	9.0	-	4.0	5.6
1980	39.0	0.8	5.8	5.3	5.4	7.0	28.5
1981	33.7	2.3	2.2	4.2	9.2	12.0	18.7
<u>Exogone lourei</u>							
1979	26.0	5.7	9.7	56.3	-	19.7	35.0
1980	2.7	0.0	1.0	2.3	3.3	13.0	26.5
1981	32.7	5.8	11.7	13.8	19.2	21.0	52.3
<u>Fabricia limnicola</u>							
1979	121.7	19.7	24.7	113.7	-	31.0	82.5
1980	2.7	0.2	1.4	1.5	1.6	3.3	24.0
1981	99.7	15.7	21.2	15.0	10.8	23.7	143.3
<u>Rhynchospio arenicola</u>							
1979	0.5	0.7	4.7	7.0	-	3.7	0.0
1980	0.0	0.0	1.6	3.0	4.3	2.5	0.0
1981	0.0	0.2	0.3	1.2	0.8	1.7	4.0
<u>Capitella capitata</u>							
1979	6.5	1.3	3.3	10.7	-	4.7	11.0
1980	5.0	0.0	3.1	4.4	5.1	8.3	9.5
1981	10.0	1.5	2.8	5.6	4.2	9.5	16.7
<u>Tubificid Oligochaetes</u>							
1979	16.5	12.3	11.7	13.0	-	9.0	23.5
1980	14.7	2.7	8.5	12.7	14.7	8.8	26.0
1981	42.7	7.3	7.7	19.6	32.5	52.2	35.3

abundances in the experimental plots each year. The three body brooding species Exogone, Streblospio and Rhynchospio, were among the most rapid colonizers. They also are capable of post-larval dispersal through the water column. These findings suggest that life history and mobility patterns influence small-scale colonization abilities.

Colonization mechanisms: adults vs. larvae

A major objective of these experiments was the identification of life history stages responsible for colonization. I hypothesized primary colonization by larvae in species possessing planktonic larval stages, and a greater dispersive role for post-larval stages in species lacking pelagic larvae. The relative ages of Pseudopolydora, Streblospio, Exogone and Fabricia individuals were estimated by measuring worm size. Individuals colonizing the experimental plots within 2 weeks of defaunation (3, 8, and 13 day samples) were measured for 1980 (Figure 55) and 1981 (Figure 56) experiments. The resulting size frequency distributions were compared to those of control worms sampled from undisturbed sediments on day 1 (May 27) of each experiment. Sizes of colonizing and control Fabricia were also measured in the 1979 experiment.

In many instances significant differences were seen between size frequencies of colonizing and control individuals. Pseudopolydora colonizers exhibited a bimodal size frequency distribution which differed significantly from worms in the controls in 1980 (K-S test,  $p < .005$ ) and 1981 (K-S test,  $p = .05$ ). Both larvae and adults colonized the experimental plots. When Pseudopolydora was very abundant and larvae were plentiful in 1980, colonization primarily occurred via newly settled larvae (K-S test,  $p < .005$ ). Streblospio also colonized primarily

Figure 55: 1980 polychaete size frequency distributions in newly colonized vs. control sediments at Site B on the Kendall-Frost mudflat.

POLYCHAETE SIZE FREQUENCY DISTRIBUTIONS IN NEWLY COLONIZED VS CONTROL SEDIMENTS

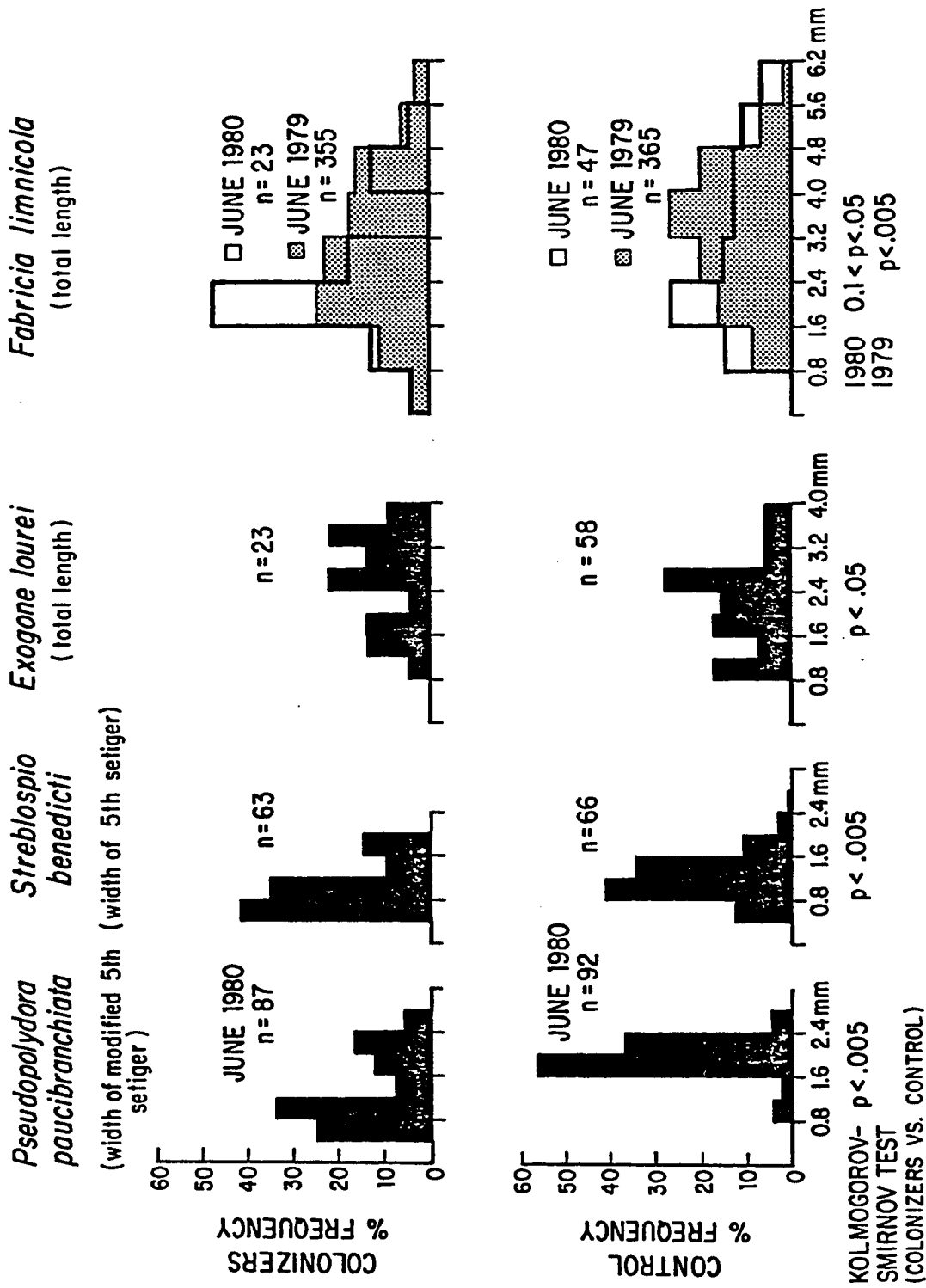
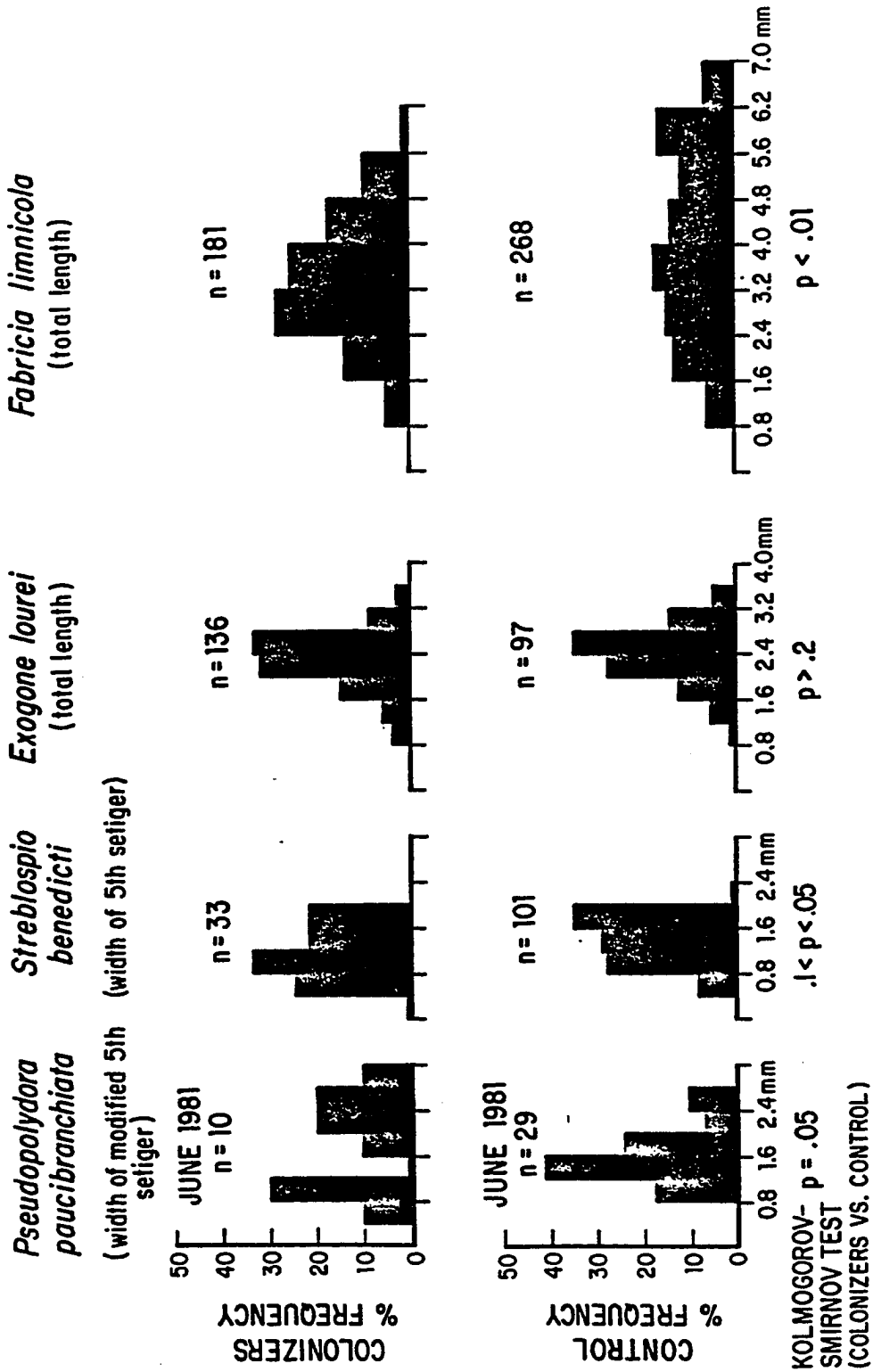


Figure 56: 1981 polychaete size frequency distributions in newly colonized vs. control sediments at Site B on the Kendall-Frost mudflat.

**POLYCHAETE SIZE FREQUENCY DISTRIBUTIONS IN NEWLY COLONIZED VS CONTROL SEDIMENTS**



as larvae, most dramatically in 1980 (K-S test,  $p < .005$ ) and to a lesser extent in 1981 (K-S test,  $.10 < p < .05$ ). The control Streblospio population in both years was mostly composed of juveniles, indicating an actively reproducing population. Exogone colonizers were larger than individuals in the control population in 1980 (K-S test,  $p < .05$ ). The adults of this species are highly mobile; they are errant in the sediments and develop specialized swimming setae for moving into the water column. All sizes of Fabricia seem to colonize defaunated plots. However, the colonizer size frequency distribution was always skewed to the left (K-S test,  $p < .005$  in 1979,  $p < .10$  in 1980 and  $p < .01$  in 1981). This suggests that the smaller individuals (juveniles) are the primary colonizers.

#### Role of brooding during colonization

In each species some adults colonized the experimental plots (Figures 55, 56); of these some were brooding offspring at the time of sampling. The number of individuals brooding embryos or larvae on the parental body or in tubes was determined for worms colonizing the experimental plots within 13 days of defaunation and for undisturbed worms sampled at the start and finish of the experimental period (Table 20). A comparison of the 2 groups suggests that brooding Exogone are active colonizers. They are significantly more common in experimental plots than in control sediments in 1980 ( $\chi^2_1 = 22.048$ ,  $p < .005$ ) and 1981 ( $\chi^2_1 = 17.61$ ,  $p < .005$ ) and more common (but not significantly so) in 1979 ( $\chi^2_1 = 2.03$ ,  $0.10 < p < 0.5$ ). An excess of brooders was observed for Streblospio colonizing in 1979 ( $\chi^2 = 3.015$ ,  $0.10 < p < .05$ ) but not in 1980 or 1981. Pseudopolydora, Fabricia, Rhynchospio and Capitella did

Table 20  
Number of Worms Brooding/ Total Number Sampled

	<u>Pseudopolydora</u> <u>paucibranchiata</u>	<u>Streblospio</u> <u>benedicti</u>	<u>Exogone</u> <u>louriei</u>	<u>Fabricia</u> <u>limnicola</u>	<u>Rhynchospio</u> <u>arenicola</u>	<u>Capitella</u> <u>capitata</u>
1979						
COLONIZERS (3+8+13 day samples)	-	7/30	5/40	32/745	0/37	1/46
CONTROL (0+40 day samples)	-	*	*	27/399	0/1	0/35
		3/40	6/86			
1980						
COLONIZERS (3+8+13 day samples)	4/136	2/84	10/21	1/22	0/7	1/56
CONTROL (0+40 day samples)	8/325	10/204	**	7/85	0/0	0/37
			4/102			
1981						
COLONIZERS (3+8+13 day samples)	1/13	6/48	37/174	1/295	1/7	0/54
CONTROL (0+40 day samples)	1/29	15/100	**	0/299	1/12	0/80
			8/98			

$\chi^2$  Comparisons of Colonizers vs Control \*  $p < 0.10$  \*\*  $p < 0.005$



not exhibit any significant differences in the proportion brooding. Many oligochaetes also appear to colonize while gravid and brooding young, however, all oligochaetes were not removed from the experimental plots by the initial defaunation procedure and these observations are equivocal. Mean oligochaete densities were  $0.25/.001 \text{ m}^2$  in 1980 and  $4.0/.001 \text{ m}^2$  in 1981 immediately after defaunation. Brooding colonizers could not be distinguished from worms remaining after defaunation and accurate counts of brooders were not made for oligochaetes.

The percent of worms brooding on each sampling date (Table 21) did not increase throughout the experimental period for any species. For most species it stabilized or declined. This suggests that brooders arrived as such, and that enhanced food supply leading to reproduction following colonization is not responsible for the elevated number of brooders seen in the experimental plots.

Many of the species under consideration here exhibit some seasonality in reproductive activity which might bias the results described above. Pseudopolydora, Streblospio, Exogone, Fabricia, and Rhynchospio all reproduce in spring and summer with peaks in reproductive activity occurring in one or more months between January and July (Figures 34 through 37). Capitella capitata reproduces primarily in fall and winter on the mudflat, between October and February (Figure 38). This probably accounts for the general absence of brooders among both control and colonizing Capitella. The reproductive cycles of all species except Capitella are such that all life history stages (larvae, juveniles, adults and brooding adults) were available for colonization during the experimental periods. Thus, the timing of the experiments introduced a bias into the colonization analysis only for Capitella,

	CONTROL 5/27	COLONIZATION					CONTROL 7/8
		3 DAYS (5/30)	8 DAYS (6/4)	13 DAYS (6/9)	21 DAYS (6/17)	40 DAUS (7/8)	
<u>Pseudopolydora paucibranchiata</u>							
1979		data not collected					
1980	3.8	0.0	5.1	1.4	0.0	0.0	1.5
1981	3.4	0.0	0.0	11.1	0.0	0.0	0.0
<u>Streblospio benedicti</u>							
1979	8.3	50.0	100.0	18.5	-	0.0	0.0
1980	6.8	20	2.2	0.0	5.3	1.5	2.3
1981	14.9	14.3	15.4	9.5	3.6	5.5	8.9
<u>Rhynchospio arenicola</u>							
1979	0.0	0.0	0.0	0.0	-	27.0	0.0
1980	0.0	0.0	0.0	0.0	0.0	0.0	0.0
1981	0.0	100.0	0.0	0.0	0.0	20.0	8.3
<u>Exogone lourei</u>							
1979	8.3	5.9	14.3	13.0	-	11.9	6.0
1980	0.0	-	33.0	58.0	26.0	25.0	4.3
1981	8.2	17.1	22.9	21.8	20.9	9.3	5.7
<u>Fabricia limnicola</u>							
1979	6.8	1.7	4.7	4.3	-	1.1	0.0
1980	12.5	0.0	0.0	10.0	18.0	4.3	7.8
1981	0.0	1.1	0.0	0.0	3.1	0.0	1.4
<u>Capitella capitata</u>							
1979	0.0	25.0	0.0	0.0	-	0.0	0.0
1980	0.0	0.0	4.0	0.0	0.0	0.0	0.0
1981	0.0	0.0	0.0	0.0	4.0	0.0	0.0

Table 21  
PERCENT BROODING

which reproduces in winter, and perhaps for Pseudopolydora, whose larval availability is greatest in spring.

The studies presented in this chapter examined a variety of processes occurring within or near the mudflat sediments. Patterns of larval development, recruitment, colonization and benthic abundance demonstrate that the Kendall-Frost community is highly dynamic and exhibits considerable spatial and temporal variability. While it is impossible to examine in detail all the processes affecting population and community dynamics, much of the observed variability can be attributed to species' responses to a constantly changing environment. Field and laboratory investigations of development, behavior, recruitment and colonization have provided a clear picture of polychaete dispersal abilities. These abilities are summarized, and their implications are discussed in the next chapter (V).

## CHAPTER V

### LIFE HISTORY AND DISPERSAL PATTERNS: IMPLICATIONS FOR POPULATION AND COMMUNITY STRUCTURE

This chapter draws together my varied approaches to the study of dispersal, including hydrographic investigations, life history studies, plankton surveys, recruitment and colonization studies and electrophoretic analyses, to present an overview of dispersal patterns in the Kendall-Frost polychaete community. These dispersal patterns, integrated with studies of life history and behavior, explain much of the temporal and spatial fluctuation in polychaete abundance observed in this study. Species-specific dispersal abilities are described first followed by a summary of community-wide trends in life history and dispersal. These patterns provide the basis for discussion of (a) species' response to disturbance, (b) population predictability and (c) community stability.

#### Dispersal Abilities

##### Pseudopolydora paucibranchiata

Pseudopolydora paucibranchiata possess excellent long distance dispersal capabilities. Though average planktonic larval life at room temperature is 1 - 2 weeks, the competent period may extend for 5 or 6 additional weeks allowing extensive transport by advection. Pseudopolydora adults are limited to the intertidal and shallow subtidal back reaches of Mission Bay but in spring and summer larvae are common in waters throughout the bay (see Chapter III). Settlement of Pseudopolydora occurred in gallon jars hung throughout the bay, including the Ship

Channel (Station V), indicating potential for flushing into the open ocean.

Despite their potential for long distance dispersal, Pseudopolydora larvae seem to oscillate back and forth with the tides in the back of Mission Bay (Figures 21 and 22). The minimal exchange of back bay waters with ocean waters acts to retain larvae and limit dispersal for many (but not all) of the larvae originating on the mudflat. Late stage larvae have been observed to remain and feed near the sediments (dish bottom) in the laboratory, a behavior which may also limit dispersal. However, intensive sampling through complete tidal cycles did not indicate retention of late stages on the mudflat during ebb tides (Figures 21 and 22).

P. paucibranchiata occurs in the water column only during larval stages. Post-larvae are never found in plankton samples and colonization of sediment trays atop the mud is only by larval settlement. In accordance, colonization of defaunated sediment patches was primarily by larvae though some adults migrated horizontally over short distances (Figures 55 and 56). Colonizing Pseudopolydora exhibited a bimodal size frequency distribution while juvenile size classes were better represented in undisturbed (control) samples. There is no tendency for females brooding larvae in their tubes to be mobile, as seen in other species on the mudflat. Individuals, once settled, tend to remain sessile and defend territories (Chapter VI), thus larvae are the primary instrument of both short and long distance dispersal.

Polydora ligni

Like Pseudopolydora, Polydora ligni possesses excellent long-distance dispersal ability. An 11 - 14 day precompetent and 35 day competent period permits advective transport of larvae over great distances. P. ligni larvae have been collected from waters throughout Mission Bay, though only a few were found in the Ship Channel. P. ligni settled abundantly into gallon jars hung near the bottom at mid and back bay stations, but none were found in jars hung in the Ship Channel. Sluggish circulation and tidal oscillations probably act to retain most larvae in the back bay.

As in Pseudopolydora, larvae are the primary mode of dispersal in this species. Polydora larvae are consistently present in low numbers in waters overlying the Kendall-Frost mudflat and they settle regularly but also in low numbers into sediment trays atop the mudflat. Juvenile or adult stages of Polydora ligni have never been collected in the water column though larvae may delay settlement to the 20 setiger stage. Post-settlement individuals seem capable of horizontal migration as they sometimes appear in defaunated bottom sediments; however, colonization by larvae is more common. Adults generally move by horizontal extension of the tube (Dauer et al., 1981). This species has flexible long distance dispersal ability. However, once recruitment has occurred, fine scale adjustments are unlikely.

Rhynchospio arenicola

Rhynchospio arenicola possesses good intermediate and small-scale dispersal abilities. Larvae have a 7-day period of obligate dispersal, and a competent period which may last up to 10 days, somewhat

shorter than that seen in the other spionids with planktotrophic larvae. Mission Bay-wide plankton samples were not sorted for Rhynchospio, however, Rhynchospio larvae are common in waters overlying the Kendall Frost mudflat and some probably disperse throughout the bay. This species did settle in gallon jars hung near the water surface in the Ship Channel in July 1978, indicating that Rhynchospio larvae are exiting to (or entering from) the ocean.

All Rhynchospio life history stages have been found to possess some planktonic dispersal ability. Rhynchospio larvae have sometimes (late winter and summer) been the most abundant component of the mudflat meroplankton. They also exhibit odd diurnal abundance patterns with maxima at high and/or low tide. Rhynchospio juveniles were collected in low numbers in plankton samples taken over the mudflat from June through September of 1981. Rhynchospio settle frequently (but in low numbers) into sediment trays atop the mudflat. Occasionally, adults and brooding females were found to enter the sediment tray (via the plankton) and the surface defaunation experiments. Rhynchospio probably migrated horizontally into the defaunated plots, and often exceeded control levels (usually close to 0) by the end of the experimental period. Migratory tendencies of larvae, juveniles, adults and brooding adults, grant this species considerable powers of small-scale dispersal and microhabitat selection.

#### Streblospio benedicti

The Mission Bay Streblospio population seems to possess very limited larval dispersal ability. Larvae spend little or no time in the plankton and have not been found in plankton samples collected

throughout Mission Bay. One Streblospio individual was obtained from a settling jar hung in midwater in the Mission Bay Ship Channel in June 1979, but it is not known whether it originated inside or outside Mission Bay. Of the jars hung at other stations in Mission Bay, only one, adjacent to the Kendall-Frost mudflat (Station I), yielded Streblospio (1 individual). This reduced dispersal ability contrasts sharply with reports of this species from the Mystic River and other New England estuaries where 10 - 12 setiger Streblospio larvae are extremely abundant in the summer plankton (Dean, 1965; Campbell, 1957). Life history traits influencing dispersal of this species vary in reports of populations from around the world.

Over short distances (meters) this species is a very flexible disperser. Like Rhynchospio, all life history stages are capable of dispersal through the water column. Streblospio juveniles have been captured repeatedly in the waters overlying the mudflat, most abundantly in spring. Sediment trays atop the mudflat, entered only via the water, are colonized primarily by larvae and juveniles, but sometimes by adults and brooding females. Sediment tray recruitment patterns reflect adult distributions, suggesting that larval movements of Streblospio are highly localized and even dispersal across the mudflat is uncommon. Size frequency analyses of colonizers of defaunated plots contiguous with undisturbed sediments, also indicate that the smallest size classes (post-larvae) are the primary colonizers. In one year (1979) of the 3-year defaunation experiment, brooding females were more common among colonizing individuals than in undisturbed sediments. This occurred on several occasions (but not consistently) in sediment trays as well.



Other investigators have reported adult Streblospio to be highly mobile (Dauer et al., 1981) and to readily leave the tube if disturbed (Foster, 1971). Dean (pers. comm.) has even collected adult Streblospio in night plankton tows from a Maine estuary.

#### Exogone lourei

Exogone lourei possesses virtually no larval dispersal ability. Newly released larvae crawl very slowly and do not enter the water column. They have never been collected in plankton samples. Older individuals are far more mobile. They are errant in the sediments and will swim up into the water column ostensibly for fertilization and possibly for dispersal purposes. Of the gallon jars hung throughout Mission Bay, only the near bottom jars situated adjacent to the Kendall-Frost mudflat collected Exogone.

Exogone are not capable of migrating long distances, but are highly mobile over short distances. Exogone, usually adults, regularly colonize (but in low numbers) sediment trays on the mudflat during spring, summer and early fall. They are capable of rapid horizontal migration over short distances and quickly recolonize disturbed sediments. Size frequency analyses of individuals migrating into sediment defaunation experiments indicate that in contrast to Pseudopolydora and Streblospio, Exogone tends to colonize as adults, many of which are brooding young.

Exogone have been observed to enter the water column carrying ova. It is possible that females are entering the water column expressly for fertilization and that subsequent dispersal is only incidental. Adults, some gravid and all with elongate swimming setae,

were collected in surface waters over the mudflat at night in summer 1981. McWilliams et al. (1981) also collected gravid Exogone sp. at night in waters over sand and coral substrates on the Great Barrier Reef. Fertilization probably occurs near the water surface and females bearing eggs demonstrate strong habitat selection during reentry to the sediments. Exogone may be attracted to reduced species densities or to the plant debris and the detritus which sometimes accumulates in the defaunated plots. In a similar sense, Van Blaricom (1978) hypothesized habitat selection by several amphipod species for ray pits which trap organic debris. In summary, adults seem to be the primary dispersal stage in this species, conferring flexible but small-scale dispersal ability only.

#### Fabricia limnicola

Fabricia is the most limited disperser among the Kendall Frost polychaetes. None of Fabricia's life history stages are known to voluntarily enter the water column and dispersal occurs through horizontal migration. Fabricia did not enter gallon jars hung in mid water, and were not collected in plankton tows taken throughout Mission Bay; one individual was collected in the plankton over the mudflat. Only 2 individuals were collected in sediment trays on the mudflat during a 3-year period. These two worms and the one collected in the plankton were probably suspended and redeposited by tidal scouring action.

Adult Fabricia are discreetly motile (sensu Fauchald and Jumars, 1979). If disturbed, they will migrate horizontally. Bottom defaunation experiments reveal that individuals of all sizes, including newly emerged juveniles and large adults, will migrate through the sediments.

However, in all 3 years the colonizer size frequency distributions were left-skewed relative to controls, indicating a tendency for smaller individuals to be migrators. Fabricia, like other small Fabricinid sabellids, are known to migrate horizontally and may even transport their tubes with them (Fauchald and Jumars, 1979).

Capitella capitata (Mission Bay Variety)

Capitella capitata is a poor disperser. Larvae develop in tubes beneath the sediment surface and have only a facultative 1 - 2 hour competent period in the plankton, offering little opportunity for pelagic dispersal.

Several varieties of Capitella capitata occur in Mission Bay and it is virtually impossible to distinguish among them during late larval and newly settled juvenile stages. Capitella larvae were not collected in plankton tows throughout Mission Bay, but some larvae did settle into near-surface and near-bottom jars hung in the Ship Channel and at Crown Point (mid bay). However, these may belong to Capitella capitata type II (as identified by Grassle and Grassle, 1976) which occurs sporadically in Mission Bay and has long-lived planktotrophic larvae. Several competent late stage Capitella larvae were present in plankton samples collected over the Kendall-Frost mudflat, though again it was not possible to positively identify the Capitella variety.

While the very short planktonic period provides this species with only limited opportunity for dispersal, small-scale colonization abilities are excellent. Recruitment into sediment trays atop the mudflat occurs year round but rises in winter. Capitella readily colonized defaunated sediments, generally as larvae. Horizontal migration of

adults occurs, but is limited. One juvenile Capitella has been collected from the plankton over the mudflat but in general juveniles and adults are not known to swim and that individual was probably resuspended by tidal motion.

#### Community Trends in Life History and Dispersal

Traits affecting both long-distance and small-scale dispersal ability are summarized for the Kendall-Frost polychaetes in Table 22. These polychaetes share many life history characteristics which limit the spatial extent of dispersal. Most striking is the prevalence of brood protection. In one form or another all the common taxa on the mudflat brood their young. The polychaetes brood larvae attached to the female ventrum, in dorsal pouches or in their tubes. Tubificid oligochaetes develop directly in capsules beneath the sediment surface and peracarid crustaceans, including amphipods, tanaids and cumaceans, brood young in marsupia to a juvenile stage. The cephalaspidean gastropod Acteocina culcitella has direct development on the adult while Aglaja sp. also a cephalaspidean, produces young which develop in jelly capsules attached to the sediment surface. As is common in brooding species, brood sizes are relatively small, generally < 200 but often < 50, and in most of the species, females produce several broods per lifetime.

Brooding of young must be highly adaptive in this environment. Infaunal predators are uncommon and brooded larvae do not experience predation in the plankton during early developmental stages. I have observed several instances in which death or partial consumption of an Exogone or Rhynchospio parent did not harm the brood; larvae were

	Larval Development				Dispersal			Colonization			General Dispersal Capability				
	Brood Protection	Stage at Release	Planktonic Period	Competent Period	Stage at Settlement	Plankton in Ship Channel	Settlement in Buoy Jars	Plankton over Kendall Frost	Recruitment into Settling Trays on mudflat	Larvae		Post-larvae, juveniles	Adult	Brooding adult	Horizontal Migration
<u>Pseudopolydora paucibranchiata</u>	in 3s tube	7- 35- 21da 40da	12s			+	+	larvae ++	+	+	+	+	+	rare	long-distance
<u>Sireblospio benedicti</u>	in 9s pouch	1da 3da 9s	9s		-	-	-	post-larvae	++	+	+	+	+	occurs	small-scale
<u>Polydora ligni</u>	in 3s tube	14da 35da 15s	15s		+	+	+	larvae +	+	+	+	+	+	rare	long-distance
<u>Rhynchospio arenicola</u>	in 3s pouch	7- 7da 10da	7s		?	+	+	larvae, juvenile	+	+	+	+	+	occurs	intermediate distance
<u>Exogone lourei</u>	ventral 6s surface	0da 0da 6s	6s		-	-	-	adults +	+	+	+	+	+	common	poor
<u>Fabricia limnicola</u>	in 11s tube	0da 0da 11s	11s		-	-	-	none	-	+	+	+	+	occurs	poor
<u>Capitella capitata</u>	in 11s tube	1da 1da 11s	11s		-	?	+	larvae rare	+	+	+	+	+	occurs	small-scale

Table 22  
Life History, Dispersal, and Colonization Characteristics  
of the Kendall-Frost Polychaete Assemblage

released normally. Brooding when followed by limited dispersal of offspring, affords the female parent the opportunity to select a habitat for her young. In situations where brooding adults are quite mobile, as in Streblospio, Exogone and the peracarid crustaceans, disturbance poses little problem. Colonization by motile adults carrying a full complement of young permits extremely rapid increases in population size.

Brooding behavior is also common in other intertidal or shallow mud communities, including False Bay, San Juan Islands, Washington; Lawson's Flat, Tomales Bay, California; and Haulover Canal, Indian River Estuary, Florida, where many of the dominant infauna (peracarid crustaceans, oligochaetes, spionid polychaetes, opisthobranch gastropods and venerid bivalves) are taxonomically constrained to (or tend towards) brooding. Many of these taxa are very small, a feature commonly associated with brooding behavior (Strathmann and Strathmann, 1982). It is possible that small size is the feature of primary adaptive value on the Kendall-Frost mudflat (and in other soft-sediment habitats) and brood protection is merely a by-product of selection for size. However, the prevalence of brooding in isolated soft-sediment habitats suggests this reproductive feature contributes in some way to the success of the infauna.

Long distance dispersal seems unlikely for the Kendall-Frost infauna. The planktonic larval period of many of the Kendall-Frost polychaetes is of short duration, as is often the case for brooding species. Fabricia and Exogone lack planktonic larval stages, Streblospio and Capitella possess brief ones, while Pseudopolydora and Polydora may remain planktonic for several weeks or more. For these planktonic species the competent period (in which larvae are capable of

settling) is equal to or more often much longer than the precompetent, obligatory planktonic phase. This trend was noted by Jackson and Strathmann (1981) for a variety of benthic invertebrates. Even in cases where lengthy competent periods would permit long-distance transport, tidal oscillations and sluggish circulation in the back bay tend to retain larvae near their place of origin. In most cases larval dispersal capabilities are limited to less than 1 km and distances of meters or tens of meters are probably the most relevant for population maintenance.

Instead of relying solely on larvae for dispersal, emphasis in mobility has shifted from larval to post-recruitment stages at Kendall-Frost, while some larvae retain facultative dispersal abilities. Juvenile stages, adults and occasionally brooding adults are surprisingly mobile, and often colonize azoic or disturbed sediments from the water column. Streblospio and Rhynchospio juveniles and Exogone adults, for example, are common constituents of the Kendall-Frost plankton. These findings contribute to the growing awareness that post-larval movements in the water column by "sessile" infauna are more common than previously believed (see Table 8). Studies of meiofaunal presence in resuspended sediments and in waters overlying intertidal mudflats indicate that benthic harpacticoid copepods, nematodes and ostracods are commonly redistributed by tidal currents (Bell and Sherman, 1980; Palmer and Brandt, 1981). As with the meiofauna, Baggerman (1953) found that young Cardium edule were resuspended and tended to accumulate in depositional muddy environments. Tyler and Banner (1977) found that hydrodynamic regimes governed the distribution of echinoderms in Oswich Bay, Bristol Channel. Newly metamorphosed echinoderm larvae were

hypothesized to be subject to the same physical laws as fine sediments in the bay.

Alternatively, infauna may actively swim up into the water column and then be transported by current or wave action. Peracarid crustaceans and polychaetes commonly enter the plankton at night and have been captured in waters overlying a variety of hard and soft substrates (Thomas and Jelley, 1972; McWilliams *et al.*, 1981; Grant, 1980; Aldredge and King, 1980). The following "benthic" polychaetes have been collected more than incidentally as juveniles or adults (but not epitokes) in coastal or bay waters: Nereis virens (Dean, 1978), Glycera sp. (Dean, 1978), Scolecopelides viridis (Dauer *et al.*, 1980), Glycinde sp., Eteone sp. (Dauer, pers. comm.), Exogone sp. (McWilliams *et al.*, 1981), and Harmothoe sarsi (Sarvala, 1971). In some cases entry into the water column may serve a reproductive function, but often immature juvenile stages are also collected in the plankton (Dauer *et al.*, 1980).

#### Response to Disturbance

Disturbances at the sediment surface are frequent on the Kendall-Frost mudflat and disturbance features range from a few centimeters (burrow openings) to tens of centimeters (pits) in diameter. The mobility of all life history stages in species such as Streblospio and Rhynchospio is adaptive in an environment where the immediate habitat is likely to be disrupted at any time. The 3 year defaunation experiment demonstrates that the Kendall-Frost polychaete fauna rapidly colonize small-scale disturbances. Pseudopolydora, Polydora and Capitella almost exclusively colonize small-scale disturbances as larvae; Rhynchospio,



Streblospio and Fabricia colonize at all life history stages, and Exogone colonizes as adults.

In several studies the relative importance of adult vs. larval colonization seems to depend on the magnitude of the disturbance and contiguous nature of surrounding sediments. Dauer and Simon (1976b) used length frequency histograms to determine that adult dispersal was the primary route of early colonization for the dominant polychaetes on a beach defaunated by hypoxia resulting from a massive fish kill. They hypothesized that the adults migrated up the beach from subtidal regions where defaunation had not taken place, again suggesting an important role for post-larval dispersal. Santos and Simon (1980a) addressed the question of adult vs. larval colonization by comparing colonization of newly defaunated bottom sediments with recruitment into sediment-filled cups and found the importance of adult colonization to vary with taxon and treatment. The platyhelminthes, cumaceans, amphipods and harpacticoid copepods always colonized the cups as adults, while the molluscs and polychaetes colonized as newly metamorphosed juveniles. However, they found that colonizers of defaunated bottom sediments were primarily adults. Similar patterns were seen at Kendall-Frost, where defaunated bottom patches experienced more adult colonization than did the sediment filled cartons atop the mudflat. Santos and Simon (1980a) attribute the discrepancy to the larger screen size (500  $\mu$  vs. 250  $\mu$ ) used to sample the bottom and to the longer time intervals between samples (monthly vs. weekly). It is possible that at Kendall-Frost bottom sediments were more accessible to adult stages migrating horizontally from adjacent areas.

McCall (1977) like Santos and Simon, found that over 90% of individuals initially colonizing sediment trays subtidally in Long Island Sound, arrived as newly settled larvae. However, Brunswig et al. (1976) found mobile adults of the common Diastylis rathkei and the polychaete Harmothoe sarsi to be the first colonizers of sediment boxes placed on the bottom of Kiel Bay. Deep sea sediment trays placed at 1760 m in the North Atlantic for 2 months contained predominantly post-larvae or juveniles of the colonizing taxa (Grassle, 1977). In general, it appears that at all depths, polychaetes colonize sediment trays primarily as larvae. In contrast, adult polychaetes are usually the first to colonize intact bottom sediments. These differences may result from decreased infaunal access to isolated vs. non-isolated substrates.

#### Life History and Population Predictability

It is commonly assumed in much of the benthic literature that events in the plankton control long-term variability in benthic abundances (Ayers, 1956; Coe, 1956). Large fluctuations in recruitment and benthic abundance from year to year have been reported from a variety of marine populations including asteroids (Loosanoff, 1964), sand dollars (Timko, 1975), bivalves (Coe, 1956; Ayers, 1956) and polychaetes (Fager, 1964). While data for long time series are uncommon, order of magnitude (or more) fluctuations are often seen in populations after only a few years of investigation. Variability in the timing or amount of recruitment, or in peak abundances attained each year, is often attributed to the vagaries of larval life in the plankton. Such factors as food supply, planktonic predators, hydrographic and atmospheric conditions, vary from year to year and will affect the availability of competent larvae

at any place or time. If these features are important, one might predict that species with little or no planktonic development should exhibit greater benthic stability and see less fluctuation between generations than those species with long-lived larvae. My data were collected over only several years, but do offer some insight into this prediction and the related hypothesis that species possessing post-larval migratory abilities should exhibit less spatial and temporal variability in the benthos than those without them.

Between 1980 and 1981, Pseudopolydora paucibranchiata larval abundances in the plankton declined several orders of magnitude but peak recruitment values fell only one order of magnitude. Peak benthic abundances exhibited a threefold drop at Site A and a sixfold drop at Site B. These findings indicate that dramatic fluctuations in larval abundance are damped during processes of recruitment and subsequent events in the benthos. One important source of damping is the territorial behavior exhibited by Pseudopolydora, which could limit maximum densities on the mudflat. This pattern contrasts with that of Polydora ligni, which exhibited an order of magnitude decline in planktonic larval abundance, no noticeable change in recruitment (always very low) and a slight (2 - 4 fold) difference in benthic abundances (also very low) during those years. Adequate plankton data do not exist for Rhynchospio arenicola to make these comparisons, however, a threefold increase in benthic abundance from 1980 to 1981 was not matched by recruitment into settlement trays (Site A). The variations in benthic population size, seen in these planktotrophic developers over a brief period, are perhaps even more significant as the 3 species occur at densities from 10,000 to 60,000 individuals/m<sup>2</sup>. Two or threefold increases are substantial when

space is limiting, as it is likely to be in the dense assemblage considered here.

A different benthic pattern was seen for Fabricia limnicola and Exogone lourei, which lack planktonic larval stages. Colonization of settling cartons by Exogone (as adults) increased 2 - 4 times between 1980 and 1981. This species exhibited large fluctuations (within each year) in the benthos but attained similar maximum densities (around  $30,000/m^2$ ) each year at Sites A and B. However, Exogone did exhibit a fourfold increase in the benthos at Site C in 1981. Fabricia does not colonize sediment trays so no recruitment data are available; however, the benthic populations at Site B, where this species is usually dominant, fell 2 orders of magnitude in 1980 (relative to 1979 and 1981 levels) following the 1980 storm and sewage spill. Fabricia is the only suspension feeder of the surface feeding species considered here and was most susceptible to damage from increased suspended sediment loads accompanying the storm. Less annual variation occurred in the 2 species with facultative planktonic larvae, neither of which were common in plankton samples. Streblospio exhibited a threefold drop in recruitment into settling trays between 1980 and 1981, but attained similar peak benthic abundances ( $60,000/m^2$ ) at Site C (where it is most abundant) during the 2 years.

The greatest variation in benthic abundance was observed for Pseudopolydora, a species with long-lived planktonic larvae, and for Fabricia, a species with direct development and no planktonic life history phase. Pseudopolydora responded to the 1980 storm and sewage spill that destroyed the Fabricia population with a dramatic increase in numbers. Exogone and Streblospio exhibited the most consistency in

benthic abundance patterns. Perhaps the post-larval dispersal abilities of these species, plus the lack of larval mortality in the plankton, account for this apparent stability. Rhynchospio, which also possesses juvenile and adult dispersal abilities, is subject to an obligatory week in the plankton during larval development and did exhibit variation in benthic abundances. The temporal predictability of benthic abundance patterns is not simply a function of planktonic development period or post-larval mobility, however, these factors are important in understanding mechanisms of population regulation. Species exhibiting development extremes (planktotrophic or direct development) may be subject to greater environmentally induced fluctuation than those with more flexibility in larval and post-recruitment dispersal.

#### Life History and Community Stability

Frequently disturbed habitats exhibit varying degrees of community stability. Here stability refers to "the ability of a system once perturbed to return to its original state" (Sousa, 1979; Santos and Bloom, 1980). In this sense the intertidal infaunal community at Kendall-Frost is locally stable. Considering the Fabricia-Exogone dominated community present at Site B in 1971, 1978, 1979 and 1981 (none of the years between 1971 and 1978 were sampled) to be the background stable state, recovery takes place in weeks to months following a small-scale ( $< 1 \text{ m}^2$ ) perturbation and within one year after a major perturbation such as the 1980 sewage spill. These recovery rates can be attributed to the small-scale mobilities and annual life cycles of the dominant species. Resilience of this sort has been observed in several disturbed soft-bottom habitats. Recovery within one year was reported

for an intertidal sandy beach fauna killed off by a red tide induced fish kill (Dauer and Simon, 1976a), and a sandy subtidal bottom buried by dredge spoils ((Oliver, 1979).

Dauer and Simon (1976a) note that high intertidal sites regained species number and infaunal densities more rapidly than lower intertidal sites. Oliver (1979), in comparing recovery rates of disturbed sites within 2 very different soft sediment habitats, McMurdo Sound, Antarctica and Monterey Bay, California, found patch resilience (recovery rate) was highest within each place in the least complex community, though overall infaunal recovery rates were considerably slower in McMurdo Sound. Jumars and Hessler (1976) noticed a decrease in the usually high deep sea diversity at a disturbed hadal site (7000 m) subject to rapid sedimentation and seismic activity. Compared to the Antarctic or deep sea, the Mission Bay community is simple in that richness is low, ranging from 16 to 24 species during the spring - summer experimental period in all 3 years. This is comparable to species numbers reported from other disturbed habitats: central Long Island Sound (R = 18) (McCall, 1977, Site A), Goose Creek, Long Island Sound (R = 29) (Kaplan et al., 1975), and Hillsborough Bay, Tampa, Florida (R = 29) (Santos and Bloom, 1980).

While the species' list for the Mission Bay mid-intertidal site remained relatively constant over the 3 year study period, the relative contribution of each species, as discussed earlier, did not. In 1980 numerical dominance shifted from Fabricia and Exogone to Pseudopolydora and Streblospio. The return of the Mission Bay community to the Fabricia - Exogone dominated assemblage within one year suggests that the 1980 species composition was an anomalous and transient situation. Santos and

Bloom (1980) observed a similar shift in infaunal species composition in the final year of a 3 year study of annually defaunated Hillsborough Bay and suggested this represented an alternate stable state. Most long-term studies of infaunal assemblages reveal changing density relationships, particularly among density dominants, while species' lists remain fairly constant (Dauer and Simon, 1976a, 1976b; Santos and Simon, 1980b; Lie and Evans, 1973; Eagle, 1975; Dexter, 1947).

Members of the Kendall-Frost polychaete assemblage (Streblospio, Polydora and Capitella) have been described in the literature as "opportunistic", i.e., present in the initial colonizing or pioneering stages of a successional sequence. Colonizing species are characterized by high reproductive rate, short generation times and high mortality rates. They often attain extremely high densities within weeks of a disturbance, then decline rapidly in population size. These dynamics have been observed for Capitella capitata (Grassle and Grassle, 1974; Chesney, pers. comm.), Polydora ligni (Dauer and Simon, 1976a), Streblospio benedicti and Ampelisca abdita (McCall, 1977). Opportunists colonizing disturbed sediments often exhibit brood protection, an adult and/or larval dispersal stage (high availability) and relatively low fecundities (see Grassle and Grassle, 1974 for a discussion of opportunistic life histories). It has been suggested that such species lack an equilibrium population size, exhibit poor competitive ability and are small in body size (May 1976), yet the most successful species on the Kendall-Frost mudflat exhibit many of these traits.

Early colonizers do not always relinquish their density dominance. In situations where disturbance is frequent or stressed environmental conditions occur (e.g., organic enrichment), opportunistic

species may persist. This has been observed in an annually defaunated estuary (Santos and Simon, 1980b) dredged channels (Kaplan et al., 1975; Reish, 1963), a newly closed estuary (Wolff et al., 1977) and in chronically polluted sediments (Pearson and Rosenberg, 1978). The Mission Bay polychaete assemblage is comprised of opportunistic species which persist; they recover rapidly from disturbance and can therefore be considered a stable community.

#### Summary

Life history and dispersal properties of the resident species have a major influence on the population and community dynamics of the Kendall-Frost assemblage. Community-wide trends in life history, including brooding behavior, variable or reduced pelagic larval stages and well developed post-larval dispersal abilities, minimize the likelihood of long-distance dispersal and emphasize small-scale movements over the mudflat.

Small-scale mobilities enhance species' tolerance to and/or recovery from local disturbance. Dispersal of juveniles, adults and brooding adults over short distances permits rapid colonization of small disturbed sediment patches which are generated biotically on the mudflat and persist for several weeks or more. Colonization by brooding adults and limited dispersal of their newly released offspring results in rapid increases in population size following only a few colonization events, and thereby contributes to the maintenance of the dense assemblage. Colonization patterns of this sort, best developed in Streblospio and Exogone, are distinct from the distance dispersal abilities exhibited by Pseudopolydora and Polydora. These latter species, dependent on a



highly variable larval supply, are most successful in colonizing large-scale disturbances whose timing coincides with periods of maximum larval availability.

Species' mobilities influence their response to environmental fluctuation and disturbance of varying magnitudes and are therefore important determinants of population predictability. Those species exhibiting extremes in larval development (Pseudopolydora and Fabricia) experienced the largest fluctuations in population size. These 2 species also possess the least genetic polymorphism (see Appendix Four). This lack of genetic variability may be due to founder effects or frequent population bottlenecks. Less variability in population size was seen in body-brooding species with mobile post-recruitment stages. Small-scale dispersal abilities tend to damp spatial patchiness and temporal variation though seasonal patterns remain. Many of the attributes which damp population fluctuations also contribute to the resilient nature of the community. Annual life cycles, short generation times, steady larval supply and small-scale dispersal abilities are opportunistic traits which speed species' response to perturbation and confer on the assemblage considerable local stability.

CHAPTER VI  
BEHAVIORAL INTERACTIONS AND SPATIAL PATTERNS

Synopsis

This chapter examines the intraspecific (Part A) and interspecific (Part B) behavioral interactions of tube dwelling polychaetes at the sediment surface and their effect on species' dispersion. The 3 species considered, Pseudopolydora paucibranchiata Okuda, Streblospio benedicti Webster, and Fabricia limnicola Hartman, comprise over 90% of the surface feeding macrofauna at mid tide levels (Site B - +1.5 to +2.5 ft above MLLW) on the Kendall-Frost mudflat and attain combined densities of over 100,000 individuals/m<sup>2</sup>. Feeding behavior and the interactions involving feeding organs (palps and tentacular crown) were observed and quantified using a dissecting microscope under 60x and 120x magnification. Dispersion was investigated with nearest-neighbor analyses. Measurements were made from photographs of worm tubes on the mudflat and with an ocular micrometer on intact cores under magnification in the laboratory.

The highly aggressive Pseudopolydora was found to steal food from other worms and to interfere with their feeding activities, sometimes causing the opponent to withdraw into its tube. Pseudopolydora exhibits intraspecific uniform spacing of tubes which is initiated during settlement and enhanced by subsequent interactions between individuals. This behavior was documented in both the laboratory and the field. Field manipulations suggest that adult Pseudopolydora inhibit settling larvae and may contribute to observed dispersion. Pseudopolydora appears to defend territories necessary for the acquisition of food and

tube building materials. Observations of Streblospio benedicti and Fabricia limnicola show no indication of aggressive behavior or non-random dispersion.

Both intra- and interspecific contacts with Pseudopolydora occurred frequently among the three polychaetes, but interspecific interactions resulted in withdrawal 10 to 50 times more frequently than Pseudopolydora intraspecific encounters. Interference from Pseudopolydora accounted for 48% and 88% of the time spent withdrawn for Streblospio and Fabricia and less than 5% of observed withdrawal time for Pseudopolydora. This represents a 7%, 4.3% and 0.4% loss of total foraging time (in still water) for the three species respectively. Larger individuals of all species experience more interaction with Pseudopolydora. Small Fabricia and large Streblospio suffer the greatest interference.

Pseudopolydora may employ spacing mechanisms to avoid intraspecific interference, however interspecies dispersion provides no evidence for species segregation or avoidance of Pseudopolydora by the other species. A possible explanation is the relatively recent coexistence of these three species. Both Pseudopolydora and Streblospio were introduced to the eastern Pacific since 1900 and probably even more recently to Mission Bay.

The studies presented in this chapter are among the first to directly quantify interference interactions among infauna and provide one of two known cases of territorial spacing behavior in a non-nereid polychaete (Pseudopolydora paucibranchiata). The results presented here suggest that interference competition may be more important than previously believed, particularly in dense infaunal assemblages of aggressive spionids and in communities where species have recently come to coexist.

This chapter is presented as two separate papers. "Dispersion, Feeding Behavior and Competition in Two Spionid Polychaetes," published in the Journal of Marine Research in 1981, addresses intraspecific behavior and dispersion in Pseudopolydora and Streblospio. "Interference Interactions among Tube-Dwelling Polychaetes in a Dense Infaunal Assemblage" describes interspecific contact and spacing among Pseudopolydora, Streblospio and Fabricia. This manuscript is currently in press in the Journal of Experimental Marine Biology and Ecology.

## Dispersion, feeding behavior and competition in two spionid polychaetes

by Lisa Ann Levin<sup>1</sup>

### ABSTRACT

Spatial analysis, laboratory and field experiments, and feeding observations indicate contrasting patterns of aggression in the polychaetes *Pseudopolydora paucibranchiata* (Okuda) and *Streblospio benedicti* (Webster) and provide the first evidence of territoriality in a spionid polychaete (*Pseudopolydora*). On the intertidal mudflats of Mission Bay in San Diego, California, *Pseudopolydora* is spaced more evenly than expected from a random distribution, while the dispersion of *Streblospio* does not depart significantly from random. Recruitment patterns in *Pseudopolydora* indicate that uniform spacing is initiated during settlement and enhanced by subsequent interactions between individuals. Field manipulations provide evidence for adult interactions with settling larvae which may also play a role in generating non-random dispersion in *Pseudopolydora*. Differences between *Pseudopolydora* and *Streblospio* in aggressive behavior (palp fighting and biting) and feeding mechanisms are correlated with different space requirements for feeding and tube building. Laboratory observations of surface deposit and suspension feeding indicate that *Pseudopolydora* is more aggressive and frequently uses its mouth and palps to acquire food particles. These species also differ in their site of food particle selection. *Streblospio* relies primarily on lips and mouth to taste particles, while *Pseudopolydora* more frequently uses its palps. It is proposed that *Pseudopolydora* defends palp territories necessary for the acquisition of food and tube building materials. The spatial analysis, in conjunction with experimental results and behavioral observations suggest strong competition in *Pseudopolydora* but not in *Streblospio*.

### 1. Introduction

Spatial patterns created by individuals in a population or by populations in a community may be classified as aggregated, regular or random. Static patterns alone are of limited value, but can serve to alert biologists to dynamic physical and biological processes structuring communities. Aggregation may result from habitat heterogeneity, symbiosis, gregarious behavior and/or limited dispersal of progeny. Regularity may arise from such negative interactions as territoriality, avoidance behavior and/or allelopathy. Randomness may result either when specifically stochastic processes govern distributions or when no other processes come into play.

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Aggregated dispersion patterns are most common in nature, while both random and regular dispersions are rare (Pielou, 1977). This is particularly true of infaunal invertebrate populations inhabiting soft sediments, where heterogeneity of sediment organics, grain size, and other structural features, as well as local disturbances, commonly create patchy distributions.

Quadrat sampling and multiple cell corers of various sizes have been used in conjunction with indices of dispersion and autocorrelation to examine fine-scale dispersion patterns in soft sediments. Alternatively, plotless sampling, which focuses on spacing of individuals, has been used in association with nearest-neighbor statistics to analyse dispersion patterns (see Pielou, 1977 for a discussion of methods). This technique has the advantage of being independent of sample size. Both approaches measure only intensity (the extent to which density varies from place to place) and not grain (size and spacing of aggregations).

Nearest-neighbor analysis involves measurements of distances between organisms. Because infaunal organisms are difficult to observe from the sediment surface (they are usually buried), their abundance and distribution are usually determined from sediment cores. Precise positions have occasionally been determined using X-radiography (Levinton, 1972) or core dissection techniques (Whitlatch, 1976). Under some circumstances infaunal organisms may be observed from the sediment surface and photographed or drawn, as was done in this investigation.

Only a few studies have demonstrated uniform dispersion in marine infaunal organisms. Holme (1950) demonstrated overdispersion in the lamellibranch *Tellina tenuis* and correlated it with foraging activities of the inhalent siphon. Johnson (1959) attributed the even spacing of the phoronid *Phoronopsis viridis* to space requirements for lophophore expansion. Connell (1963) observed that uniform dispersion of the tubes of the amphipod *Erichthonius braziliensis* and the burrow entrances of the fiddler crab *Uca pugilator* was maintained by aggressive interaction. Of the numerous species of infaunal polychaetes studied by spatial analysis (Ekman, 1979; Jumars *et al.*, 1977; Jumars, 1978; Reise, 1979; Roe, 1975; Rosenberg, 1974) only the following members of the family Nereidae exhibit uniform spacing: *Nereis diversicolor* (Reise, 1979), *Nereis vexillosa*, *Platynereis bicaniculata*, (Roe, 1975) and *Ceratocephale pacifica* (Jumars, 1978). Several of these species are known to defend territories around their burrows.

All of the infaunal invertebrates mentioned above build permanent tubes or burrows and feed at the sediment surface. Many of them deposit feed on sediment or detritus particles, though some exhibit predatory behavior as well. Infauna of other trophic modes tend to exhibit either clumped dispersion, as in the suspension feeding bivalves *Mya arenaria*, *Petricola pholadiformis* and *Modiolus demissus* (Connell, 1956) or random dispersion, as in the motile subsurface deposit feeder *Nucula proxima* (Levinton, 1972).

This paper presents studies of behavior and resulting spatial dispersion in related

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(confamilial) infaunal species, *Pseudopolydora paucibranchiata* (Okuda) (hereafter referred to as *Pseudopolydora*) and *Streblospio benedicti* (Webster) (hereafter referred to as *Streblospio*). This investigation combines laboratory and field studies to look in depth at the mechanisms generating and maintaining the observed patterns. The results provide the first evidence for territoriality in spionid polychaetes, a ubiquitous and very abundant group in shallow soft sediment environments. Differences in the feeding biology and aggressive behavior of the two species are assessed and some implications of territoriality in *Pseudopolydora* are discussed.

## 2. Natural History

*Pseudopolydora paucibranchiata* and *Streblospio benedicti* were studied on intertidal mudflats of Mission Bay in San Diego, California. Both are introduced species, *Streblospio* from the Atlantic Ocean and *Pseudopolydora* from Japan (Carleton, 1975). The following descriptions of these species are for Mission Bay populations and based on unpublished observations by the author. *Pseudopolydora* is the most abundant (up to 60,000 individuals/cm<sup>2</sup>) macroscopic species that surface feeds in the low intertidal (-2 to +2 ft) in spring and summer. *Streblospio* (4,000-16,000 individuals/m<sup>2</sup>) dominates the mid-intertidal sediments (+2 to +4 ft) in spring. Both species are annuals. Reproductive individuals can be found all year in both populations but peak larval availability occurs from February to May for *Pseudopolydora* and January to March for *Streblospio*.

The two species are similar in size, attaining live body lengths of 15 to 20 mm. *Pseudopolydora* constructs vertical tubes (1 mm diameter × 30 mm length) of cemented organic aggregates which protrude from the sediment surface. Contrary to a previous report of multiple tube openings (Blake and Woodwick, 1975) the individuals in Mission Bay each possess only one tube. *Streblospio* constructs a more fragile tube of fine silt, which also opens at the sediment surface. Under conditions of still water both species will build tubes which extend a centimeter or more above the mud surface.

*Pseudopolydora* and *Streblospio* feed primarily on organic aggregates and detritus at the sediment surface using ciliated palps for both suspension and deposit feeding. Their feeding behavior varies with water motion and three palp configurations have been observed during feeding in the laboratory. In still water the palps wander over the sediment surface deposit feeding, picking up sediment and detritus. In moving water palps suspension feed, are held upright and are often waving. At very high water velocities palps are spiraled and held perpendicular to the direction of water flow. These behaviors have also been observed in other spionid polychaetes (P. Jumars, personal communication) and may be a general feeding strategy among bitentaculate polychaetes feeding at the sediment surface. Both species deposit similar rodlike fecal pellets outside their tubes.

### 3. Methods

#### a. Study site

Spatial analyses were performed on *Streblospio* and *Pseudopolydora* from an intertidal mudflat located adjacent to the Kendall Frost Marsh Reserve in Mission Bay, California. In April and May, 1979, *Pseudopolydora* tubes were photographed and the worms were collected from the low intertidal (0 to +2 ft) and *Streblospio* were collected from +2 to +3 ft.

#### b. Spatial analysis

1. *Benthos*. To study the spatial dispersion of *Pseudopolydora* tubes protruding above the sediment surface, six 9 × 9 cm quadrats were marked on homogeneous portions of the mudflat surface, photographed and printed at life size for nearest-neighbor measurements (Fig. 1). *Streblospio* tube openings are inconspicuous and

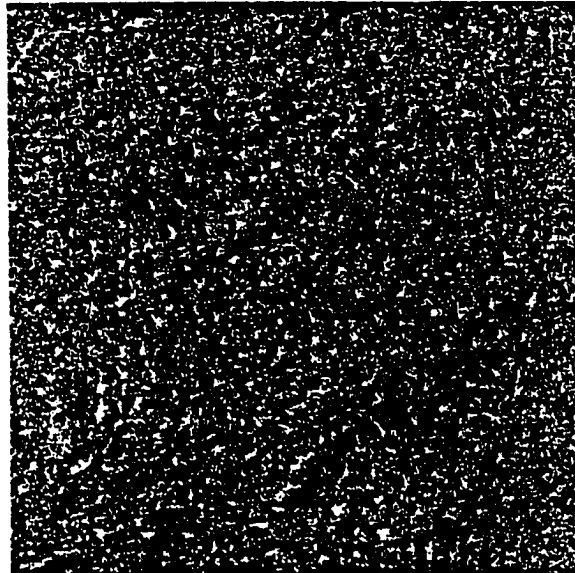


Figure 1. *Pseudopolydora paucibranchiata* tubes photographed May, 1979 at the Kendall Frost Reserve, Mission Bay, San Diego, California.

thus can not be reliably recorded by photography. Instead, 35 × 25 × 5 cm sections of the entire community were transported in plastic trays from the mudflat to the laboratory. Six 9 × 9 cm quadrats were marked in these sediments and a dissecting microscope (60× magnification) with a camera lucida was used to plot worm positions within each quadrat. Only those burrows with a worm present, or with fresh fecal pellets outside the burrow opening, were recorded. The spatial distribution studies were conducted only on quadrats in which either *Pseudopolydora* or *Streb-*



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*lospio* was the dominant species and there was little or no overlap in occurrence. The distance to nearest-neighbor was measured for every individual of these species in all quadrats to obtain six frequency distributions of nearest-neighbor distances for each species. When nearest neighbors occurred outside quadrat borders (as they sometimes did for worms on the edges of the quadrat), true nearest-neighbor distances were measured. The observed mean nearest-neighbor distance for each quadrat was compared to the expected mean nearest-neighbor distance using the Clark and Evans (1954) index:

$$R = \frac{r_{\text{observed (mean)}}}{r_{\text{expected (mean)}}$$

The difference between the observed and expected means were tested for significance using the standard normal variate:

$$C = \frac{r_{\text{observed (mean)}} - r_{\text{expected (mean)}}}{\sigma_{r_{\text{expected (mean)}}}}$$

$\sigma_{r_{\text{expected (mean)}}$  is the standard error of the mean nearest-neighbor distance. In addition each observed frequency distribution was compared to that expected in a random Poisson distribution using the Kolmogorov-Smirnov test (*K-S test*) (Sokal and Rohlf, 1969). Both Clark and Evans and Kolmogorov-Smirnov tests were employed because the mean, though a useful statistic, does not necessarily convey all the relevant information in a nearest-neighbor frequency distribution.

The ability of adult *Pseudopolydora* to regenerate uniform dispersion once disturbed was investigated by removing adults from mudflat sediments (by sieving) and reintroducing them to the sediment at various densities in 9 × 9 × 9 cm freezer cartons. The cartons were placed back on the mudflat or in the laboratory in standing or running seawater for one week.

2. *Laboratory recruitment studies.* The spatial patterns of new *Pseudopolydora* post-larvae were investigated both in the laboratory and in the field in March, 1980. Larvae were obtained for laboratory studies from net tows made over the mudflat at high water and from brooding adults which released larvae in the laboratory. Larvae fed *Monocrysis* and *Clamydomonas* were raised in still seawater at room temperature in cylindrical 15 dram vials (6.15 cm<sup>2</sup> × 6 cm deep) containing 0.3 cm of fine sediment. Upon settlement *Pseudopolydora* recruits constructed small tubes at the sediment surface. Tube positions were plotted for 6 vials of larvae at several recruitment densities, using a dissecting microscope and camera lucida. Nearest-neighbor measurements were made and both Clark and Evans and Kolmogorov-Smirnov statistics were employed to assess spatial patterns.

3. *Field recruitment studies.* Recruitment patterns of *Pseudopolydora* in the field, and the effects of adult presence on recruitment, were studied by placing plastic cartons (9 × 9 × 9 cm) filled with 7 cm of sediment on the mudflat during peak larval

availability (April, 1980). Adult *Pseudopolydora* were added to some treatments at densities of 1.5-3.9 adults/cm<sup>2</sup>. All cartons were enclosed in ½" galvanized wire mesh cages (30 × 40 × 12 cm) secured to the mudflat surface at +0.5 ft tide level. After two weeks on the mudflat the cartons were returned to the lab for immediate counts and for nearest-neighbor measurements of new recruits. A circle of area 0.001 m<sup>2</sup> was marked in the center of each carton using a plastic core of the same dimensions. In cartons without adults present positions of both tube openings and tube bases (site of tube contact with the sediment surface) were plotted for every individual within the marked area. In all other analyses in this paper *Pseudopolydora* tubes were oriented more or less vertically and positions were plotted for tube bases. Positions were plotted, nearest-neighbor distances were measured and their significance tested using the methods described above for the spatial analysis of recruitment in the laboratory. Counts of adult and recruit abundance were made visually with the aid of a dissecting microscope (60× magnification) for 0.001 m<sup>2</sup> areas marked in each treatment containing adults.

In the nearest-neighbor analysis used here, organisms are considered dimensionless (points). Although polychaete tubes are represented more accurately by circles than points, a recent assessment of spatial configurations of circles by Simberloff (1979) concludes that the classical nearest-neighbor analysis assuming points is accurate for circle diameters less than half the expected mean nearest-neighbor distance for points. The tube openings of adult *Streblospio* and *Pseudopolydora* have diameters of one millimeter and fall within the range stated above at all observed faunal densities. The tubes of new recruits are even smaller (0.2 mm) relative to nearest-neighbor distances. Thus using points instead of circles should not affect the outcome of the analysis. As an additional check  $r_{\text{observed(mean)}}$  and  $\sigma_{r_{\text{observed(mean)}}$  were corrected for the benthic quadrats having the largest ratio of tube diameter to expected mean nearest-neighbor distance (based on the computer simulation in Simberloff, 1979). Probability levels were not affected in either *Streblospio* or *Pseudopolydora* quadrats.

### c. Feeding studies

To evaluate aspects of spionid feeding biology which might affect dispersion patterns, sediment samples (9 × 9 × 9 cm) with live infauna were brought intact from the mudflat into the laboratory and maintained under running seawater. Intraspecific feeding interactions were observed for undisturbed worms in still water under 120× magnification. Small pieces of the alga *Enteromorpha* sp., commonly found on the mudflat in Mission Bay, were offered simultaneously to two individuals and the behavioral responses of the worms were recorded. This procedure was repeated for 52 pairs of *Pseudopolydora* individuals and for 25 pairs of *Streblospio* individuals. All pairs were randomly selected sets of nearest neighbors. In addition, individual worms of both species were observed in the lab to determine the site of

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Table 1. Nearest-neighbor analysis of benthic dispersion in a 9 × 9 cm quadrat.

<i>Pseudopolydora paucibranchiata</i>						<i>Streblospio benedicti</i>			
Quadrat	Density (#/cm <sup>2</sup> )	$r_{\text{mean}}$ (cm)	R	Dispersion	Quadrat	Density (#/cm <sup>2</sup> )	$r_{\text{mean}}$ (cm)	R	Dispersion
1	2.36	0.48	1.49	Uniform*	1	0.64	0.57	1.07	Random
2	2.95	0.40	1.36	Uniform*	2	0.71	0.57	1.03	Random
3	3.39	0.39	1.42	Uniform*	3	0.97	0.53	1.12	Random
4	3.72	0.40	1.54	Uniform*	4	1.32	0.42	1.03	Random
5	4.15	0.37	1.50	Uniform*	5	1.64	0.38	1.05	Random
6	5.78	0.30	1.46	Uniform*	6	1.64	0.45	1.24	Uniform*
$\bar{R}_{r(\text{mean})} = 0.39 \pm 0.10$					$\bar{R}_{r(\text{mean})} = 0.49 \pm 0.15$				

 $r_{\text{mean}}$  = mean nearest-neighbor distance.R = Clark and Evans (1954) index of dispersion =  $\frac{r_{\text{observed}(\text{mean})}}{r_{\text{expected}(\text{mean})}}$ 

R &gt; 1 indicates overdispersion

R &lt; 1 indicates underdispersion

\*p &lt; 0.001; Clark-Evans and Kolmogorov-Smirnov tests.

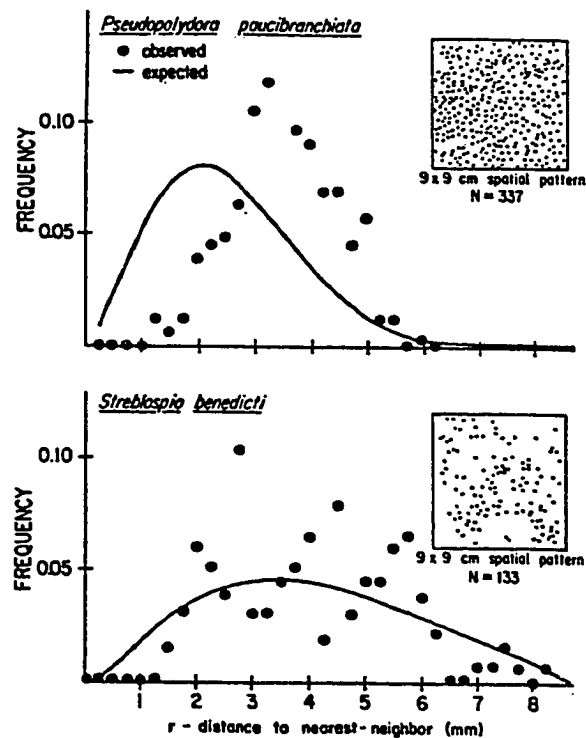


Figure 2. Sample nearest-neighbor frequency distributions for  $9 \times 9$  cm quadrats of *Pseudopolydora paucibranchiata* and *Streblospio benedicti*.

particle selection. A slurry of suspended sediment was offered to suspension feeding individuals and the rejection site was recorded for any particles initially adhering to the palps.

#### 4. Results

*a. Adult dispersion.* The results of the nearest-neighbor analysis for benthic quadrats are summarized in Table 1 and sample frequency distributions for each species are shown in Figure 2. The tubes in all six *Pseudopolydora* quadrats were more uniformly distributed than expected from the null hypothesis of Poisson randomness. The nearest-neighbor frequency distributions were right skewed ( $p < 0.001$  by the *K-S* test) and the mean nearest-neighbor distances were consistently greater ( $p < 0.001$  by the Clark and Evans test) than would be expected from a random distribution. In contrast, five out of six *Streblospio* quadrats did not depart significantly from a random distribution. However, for one quadrat the nearest-neighbor distribution was right skewed ( $p < 0.001$ , *K-S* test). Whitlatch (personal communication) has found that *Streblospio benedicti* on the east coast commonly displays aggregated

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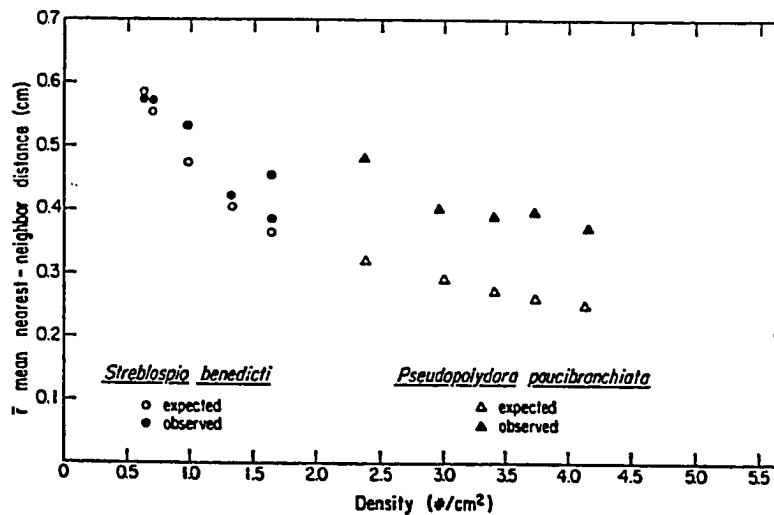


Figure 3. Nearest-neighbor distance as a function of density in *Pseudopolydora paucibranchiata* and *Streblospio benedicti*, based on analysis of  $9 \times 9$  cm quadrats.

dispersion. The Clark and Evans (1954) index of dispersion consistently fell between  $R = 1.36$  and  $R = 1.54$  for *Pseudopolydora* quadrats, indicating that the tubes were approximately one and a half times farther apart than expected.  $R$  values for *Streblospio* ranged from 1.03 to 1.24 suggesting slight overdispersion.  $R$  values differed significantly between the two species ( $p < 0.01$ , Mann-Whitney U test) indicating contrasting patterns of adult dispersion over the range of densities tested.

Figure 3 presents the relationship between spionid density and nearest-neighbor distances for both species. In both *Pseudopolydora* and *Streblospio* the observed mean nearest-neighbor distances for each quadrat varied approximately inversely with density; however, in *Pseudopolydora* observed nearest-neighbor values remained consistently greater than expected indicating that *Pseudopolydora* individuals do not maintain fixed distances between one another. Instead this distance decreases with increasing density.

The overall mean nearest-neighbor distance in benthic quadrats was 0.39 cm for *Pseudopolydora* and 0.48 cm for *Streblospio*. In randomly distributed populations one would expect very small nearest-neighbor distances,  $< 2$  mm, to be found more frequently in *Pseudopolydora*, which occurs at much greater densities, than in *Streblospio*. In fact only 2% of all *Pseudopolydora* ( $n = 1605$ ) fell within this range compared to 7% of *Streblospio* ( $n = 673$ ). Random expectations were 29% and 14% respectively. Though small nearest-neighbor distances were less frequent than expected in both species, they are far more common in *Streblospio* than in *Pseudopolydora*, indicating different patterns of dispersion.

Table 2. Nearest-neighbor analysis of *Pseudopolydora* recruitment in the laboratory. (Actual area measured is 6.16 cm<sup>2</sup>).

Vial	Density (#/cm <sup>2</sup> )	$r_{max}$ (mm)	R	Departure from Random Expectations	
				Mean (Clark-Evans test)	Frequency Distribution (Kolmogorov-Smirnov test)
1	5.24	1.90	0.89	NS*	$p < 0.01$ (aggregated)
2	6.18	1.88	0.85	$p < 0.001$ (aggregated)	NS
3	6.37	2.08	1.05	NS	NS
4	6.94	2.14	1.13	NS	$p < 0.01$ (uniform)
5	10.20	1.69	1.10	NS	NS
6	10.90	1.55	1.02	NS	NS

\* Not significant ( $p > 0.05$ )

Adult *Pseudopolydora* appeared capable of regenerating uniform dispersion following severe disturbance. Disrupted individuals (at densities above 0.60/cm<sup>2</sup>) which were returned to the field or left in the laboratory in still water had reassumed the appearance of even spacing within a week. *Pseudopolydora* maintained in the laboratory under unidirectional running seawater did not reconstruct tubes in a uniform arrangement, even at high densities (3.0/cm<sup>2</sup>). Spatial homogeneity of food supply and/or hydrodynamic factors may be necessary for spacing behavior to occur.

*b. Post-larval dispersion.* Nearest-neighbor analysis of *Pseudopolydora* recruitment patterns in the laboratory (Table 2) revealed mean nearest-neighbor distances ranging from 1.55 to 2.14 mm, only one of which differed significantly from random expectation toward overdispersion. In two out of six replicates the nearest-neighbor frequency distributions differed from expected significantly at  $p < 0.01$  (*K-S* test). In one case this was due to a shortage of small nearest-neighbor distances, indicating overdispersion and in the other instance to a shortage of large nearest-neighbor distances, indicating clumping. At lower densities (5/cm<sup>2</sup>) the settlement patterns tended to be aggregated and at higher densities (11/cm<sup>2</sup>) they tended toward overdispersion.

Recruitment of *Pseudopolydora* into sediment-filled cartons placed on the mudflat resulted in post-larval densities of 7.5 to 18.0 individuals/cm<sup>2</sup>. Mean nearest-neighbor distances (Table 3; measured for tube openings) ranged from 1.39 to 2.85 mm. Four out of five replicates had means significantly greater than expected ( $p < 0.002$ ) indicating overdispersion. Nearest-neighbor analysis of the same individuals based on distances between the base of their tubes (Table 3) revealed significantly smaller mean nearest-neighbor distances between tube bases than between tube openings (paired *t* test;  $t_5 = 7.13$ ,  $p < 0.01$ ). Three replicates were overdispersed ( $p < 0.001$ ), two did not differ from random and one was underdispersed ( $p < 0.025$ ). The over-

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Table 3. Nearest-neighbor analysis of *Pseudopolydora* recruiting into sediment filled  $9 \times 9$  cm cartons placed on the mudflat for 14 days. Positions of tube openings and tube bases (point of contact with the sediment surface) were analyzed for the same individuals. (Actual area measured is  $0.001 \text{ m}^2$ .)

Replicate	Density (#/cm <sup>2</sup> )	$r_{\text{max}}$ (mm)		R		Dispersion		Departure of frequency distributions from random expectation	
		Tube openings	Tube bases	Tube openings	Tube bases	Tube openings	Tube bases	Tube openings	Tube bases
1	7.47	2.85*	2.69*	1.56	1.48	Uniform	Uniform	$p < .001$	$p < .001$
2	8.61	2.07*	1.76	1.54	1.10	Uniform	Random	$p < .01$	NS
3	10.72	— <sup>1</sup>	1.87*	— <sup>1</sup>	1.22	— <sup>1</sup>	Uniform	— <sup>1</sup>	$p < .001$
4	13.00	1.47	1.15*	1.06	0.88	Random	Aggregated	$p < .05$	$p < .001$
5	15.75	1.74*	1.49*	1.39	1.21	Uniform	Uniform	$p < .001$	$p = .05$
6	18.03	1.39*	1.22	1.18	1.04	Uniform	Random	$p < .001$	NS

\* Significant departure from Poisson expectation  $p < 0.01$ , Clark-Evans (1954) test.

<sup>1</sup> Accidental (irrecoverable) omission during data collection.

Table 4. Recruitment of *Pseudopolydora* into  $9 \times 9 \times 9$  cm sediment-filled cartons placed on the mudflat for 14 days. *Pseudopolydora* adults were added to 5 of 12 cartons. Recruitment differs significantly between treatments with and without adults (Students *t* test;  $t_0 = 7.25$ ;  $p < .001$ ).

Treatment (#/.001 m <sup>2</sup> )	Replicates						
Adults present	1	2	3	4	5	6 <sup>1</sup>	$\bar{X} \pm 2 \text{ S.D.}$
New recruits	76	93	68	85	79		$80.2 \pm 16.8$
Adults	39	22	15	30	27		$26.6 \pm 16.0$
Total	115	115	83	115	106		$106.8 \pm 24.8$
Adults absent							
New recruits	126	105	117	120	134	137	$123.2 \pm 25.1$

<sup>1</sup> Carton contents were accidentally spilled in transport from the field to the laboratory.

all mean nearest neighbor distance was 1.66 mm for tube bases and 1.90 mm for tube openings.

Recruitment of *Pseudopolydora* into settling cartons containing *Pseudopolydora* adults was significantly lower than recruitment into cartons without adults (Table 4; students *t* test,  $t_0 = 7.25$ ,  $p < 0.001$ ). Mean post-larval densities were  $8.01 \pm 1.7$  individuals/cm<sup>2</sup> ( $n = 5$ ) in treatments with adults and  $12.3 \pm 2.2$  individuals/cm<sup>2</sup> ( $n = 6$ ) in treatments without adults. Total *Pseudopolydora* densities (adults & larvae) are also lower in treatments with adults ( $10.78 \pm 2.5$  individuals/cm<sup>2</sup>) than in treatments without ( $12.3 \pm 2.2$ ) (students *t* test  $t_0 = 2.35$ ,  $p < 0.05$ ).

*c. Feeding biology.* The unusual occurrence of uniform dispersion and the differences in spatial pattern between *Streblospio* and *Pseudopolydora* suggests possible species-specific behavioral differences. In other investigations, uniform dispersion has been associated with surface deposit feeding.

Results of intraspecific feeding studies in which dried particles of *Enteromorpha* sp. were offered simultaneously to two individuals revealed food fights accompanied by strongly aggressive behavior between *Pseudopolydora* individuals 98% of the time ( $N = 52$  observations). Such struggles were much less frequent (24% of the time,  $N = 21$  observations) and very weakly aggressive in *Streblospio*. A closer look at *Pseudopolydora* food struggles (Table 5) revealed a variety of behaviors which occur when their ciliated palps meet with resistance in transporting food or tube building materials toward the prostomium. Partial emergence from the tube and biting and pulling at algae with lips and mouth occurred frequently in these struggles. This behavior was also observed in *Streblospio* feeding alone, but never occurred when another worm was involved. Often direct palp contact and pulling on tubes took place between *Pseudopolydora* individuals involved in contests over large particles. In two instances *Pseudopolydora* individuals were observed to emerge from their tubes and bite off one palp of the opposing worm. The reach of



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*Levin: Spionid competition*Table 5. Feeding interactions among *Pseudopolydora paucibranchiata*, based on 52 observations of food fights between pairs of worms.

Behavior	% Occurrence
Use of mouth and lips, emergence from tube	59% (30)
Bending of worm tubes due to resistance from opposing individuals	41% (21)
Direct contact between palps of opposing individuals	39% (20)
Withdrawal of one individual into its tube following the struggle	18% (9)
One palp bitten off by the opposing individual	4% (2)

one *Pseudopolydora* palp overlaps that of several other individuals and each palp is capable of carrying on separate struggles simultaneously. Occasionally *Pseudopolydora* palps are used as a grasping organ to pick up larger particles and carry them to the mouth. It is not uncommon for three, four, or even five worms to fight over a single food particle. Groups of *Pseudopolydora* have been observed struggling over algae, invertebrate larvae and other (dead) polychaetes. *Streblospio* palps, though slightly shorter, are long enough to reach neighboring worms easily, but are rarely used in an aggressive manner.

Studies of feeding mechanisms suggest reasons for the observed differences in aggressive behavior between the two species. The palps which have a similar role in acquiring and transporting food particles in the two species, play somewhat different roles in particle acceptance. In 25 observations of particle rejection for each species, particle rejection usually (84% of the time) occurred after tasting at the mouth in *Streblospio* whereas the palps generally (72% of the time) rejected particles in *Pseudopolydora*. This pattern was observed consistently for a variety of particle types including algae, polychaete fecal pellets and organic aggregates. All of these findings suggest that *Pseudopolydora* palps have a broader biological role than *Streblospio* palps.

## 5. Discussion

Differences in the dispersion of *Pseudopolydora* and *Streblospio* in Mission Bay may be associated with their respective feeding behaviors. The uniform spacing of *Pseudopolydora* is initiated during or soon after settlement and is maintained by aggressive behaviors in the form of palp fighting and biting. Because *Pseudopolydora* palps acquire, taste and transport food particles, it may be necessary for individuals to defend palp territories. Richardson *et al.* (1979) documents a similar case in which sweeper tentacles are used aggressively by the reef coral *Montastrea cavernosa* to maintain living space. In dense assemblages of sessile deposit and suspension feeders it is difficult to distinguish space and food as separate resources. The ability

of adult *Pseudopolydora* to regenerate uniform dispersion following disruption suggests that territoriality and the resulting spacing enhances fitness.

*Pseudopolydora* palps are quite long (up to 15 mm) and territory overlap occurs between individuals. The degree of dispersion (represented by the Clark and Evans index  $R$ ) remains fairly constant (approximately 1.5) with changing worm densities across the mudflat (Table 1). Variability in territory size has been documented by Roe (1975) for the territorial polychaete *Nereis vexillosa* and by Crisp (1961) for the territorial barnacle *Eliminius modestus*. Reise (1979) notes that the dispersion of territorial species responds to habitat heterogeneity in soft sediments. Weinberg (1979) and Whitlatch (personal communication) found that spionids increase their foraging radius (by extending further from their tube) in response to lowered levels of surface organic matter. The variation observed in *Pseudopolydora* territory size may reflect structural sediment heterogeneity and/or changes in food resource availability.

Laboratory observations indicate that aggressive behavior in *Pseudopolydora* is not limited solely to intraspecific interactions. *Pseudopolydora* individuals were observed to fight with the spionid *Polydora ligni* over algal particles and with caprellid amphipods over dead invertebrate larvae. *Pseudopolydora* exhibits aggression toward smaller polychaetes (e.g. *Rhyncospio arenicola*, *Polydora ligni* juveniles) using its palps to push these worms back into their tubes while stealing their food and tube material. Whitlatch (personal communication) has observed similar interspecific interactions including palp intertwining and food stealing among several spionid species on the east coast. *Pseudopolydora* usually dominates interactions with other polychaete species present on the Mission Bay mudflat; however *Pseudopolydora* often loses encounters with gammarid and caprellid amphipods.

In a recent review of competition in soft sediments, Woodin and Jackson (1979) note that direct competitive interactions vary in intensity as a function of the organisms' taxonomic relationships. For example, aggressive intraspecific interactions occur among herbivorous tube building nereid species, but these nereids ignore herbivorous tube building representatives of other polychaete families. Similarly, Reish and Alosi (1968) observed that among territorial nereids intra-specific aggression was stronger than interspecific aggression and no aggression was exhibited against other polychaete families tested. *Pseudopolydora* behavior follows this pattern as well. Aggressive intraspecific interactions are common and result in uniform spacing. Similar interactions take place with other tube building spionid polychaetes but *Pseudopolydora* individuals do not appear to space themselves uniformly with other tube dwelling species (personal observation). In sandy portions of the upper intertidal region *Pseudopolydora* lives in a dense *Fabricia limnicola* bed (up to 200,000 individuals/m<sup>2</sup>) along with *Streblospio benedicti*, *Polydora ligni*, *Rhyncospio arenicola*, *Capitita ambiseta* and *Phoronis* sp. The fact that *Pseudopolydora*

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tubes are frequently found touching the tubes of other species (Levin, unpublished data) underscores the differences between intra- and inter-specific aggression.

Intraspecific aggression against established adult worms is probably the primary mechanism maintaining uniform dispersion in *Pseudopolydora* but does not necessarily generate the pattern. Both adult-larval and larval-larval interactions, before and shortly after larval recruitment, may initiate regular spacing. Field studies of *Pseudopolydora* recruitment (Table 4) indicate that adults interfere with recruitment success. This interference may take the form of predation on larvae or competition with newly settled individuals resulting in post-settlement mortality. *Pseudopolydora* individuals recruited early in the season may generate regular spacing by cannibalizing settling and newly settled forms. Ingestion of invertebrate larvae has been reported for several spionid species (Daro and Polk, 1973; Breese and Phibbs, 1972) and laboratory studies confirm that ingestion of conspecific larvae by adult *Pseudopolydora* does occur (Levin, unpublished data). The spatial pattern of new recruits among adults was not quantified, but appeared somewhat overdispersed. Large worms require more feeding space than new recruits. If competition is occurring between adults and new recruits, total densities (adults and post-larvae) are expected to be lower in treatments with adults than in treatments without them, and they were ( $p < 0.05$ , student's *t* test). Unfortunately the available data do not permit separation of the effects of adult-larval competition from those of predation.

Invertebrate larvae, and polychaetes in particular, are known to be capable of complex settlement behavior and substrate selection (see Scheltema, 1974 for a general review of settlement behavior and Knight-Jones, 1951; D. P. Wilson, 1958; and Doyle, 1975 for examples of substrate selection in polychaetes). Settlement behavior may generate nonrandom spatial patterns. Aggregation often results from gregarious settlement. Microscale avoidance behavior during larval settlement has been reported for newly settled larvae of the barnacles *Eliminius modestus*, *Balanus balanoides* and *Balanus crenatus* (Crisp, 1961) and for the larvae of the polychaete *Spirorbis borealis* (Wisely, 1960). When these larvae settle they are initially attracted to conspecifics and subsequent physical contact is necessary to induce territorial behavior. This results in uniform dispersion that is attributable to avoidance behavior by the invading larva and not to any aggression by established individuals. Laboratory studies of larval recruitment in *Pseudopolydora* (Table 2) revealed a tendency (though not statistically significant) toward uniform spacing by new recruits in 4/6 experimental vials. *Pseudopolydora* larvae were attracted to initial recruits and settled a small distance away from them. This gave rise to somewhat even spacing within aggregations but resulted in either under or overdispersion in each experimental vial, depending upon the density of recruits.

Laboratory recruitment closely approximates settlement patterns in the field. Mean nearest-neighbor distances of new recruits were comparable in the laboratory ( $r_{(\text{mean})} = 1.88 \text{ mm} \pm 0.33 \text{ mm}$ ) and in settlement cartons on the mudflat ( $r_{(\text{mean})} =$

1.90 mm  $\pm$  0.97 mm). Tube openings were more evenly spaced than tube bases for individuals recruited in the field over a 14 day period. The tubes were approximately 3 mm long and many of them were bent rather than vertical, suggesting that juveniles avoid their neighbors by bending or constructing their tubes away from one another. The nearest-neighbor distances of new recruits are too large for newly settled individuals to make contact with one another, so the initial tendency toward uniform spacing is probably generated by settlement behavior. However, nearest-neighbor distances at settlement are only one-half those observed among adults. Avoidance behavior and aggressive interaction among post-larvae, which widens spacing between tubes, must begin soon after settlement and continue through an individual's lifetime. The findings discussed above suggest that a combination of avoidance behavior during settlement, predation on larvae, and aggression in feeding and tube building, generate and maintain the characteristic dispersion of *Pseudopolydora*.

In contrast to *Pseudopolydora*, the dispersion of *Streblospio* does not depart from random, a result consistent with the apparently passive behavior of the species. *Streblospio* individuals are often found inhabiting burrows directly adjacent to conspecifics and contests between *Streblospio* individuals occur rarely. Interference with feeding activities and withdrawal into the tube is often caused by *Pseudopolydora* or other members of the community, never by other *Streblospio*. Passive behavior has also been observed in *Streblospio* from the Atlantic where the spionid *Spio setosa* has been observed to harass *Streblospio* by tearing its palps and pulling it from its tube (R. Whitlatch, personal communication). The shorter palps, the importance of the mouth in particle selection, and the absence of aggressive behavior in *Streblospio* suggest that feeding territories are not necessary to the population studied in Mission Bay.

*Streblospio* can occur at much higher densities than those reported for Mission Bay (e.g. 140,000/m<sup>2</sup> in Virginia; Virnstein, 1979). The spatial analysis in the present study suggests that both the behavior and dispersion of *Streblospio* may change as density increases. Only those *Streblospio* individuals in the highest density quadrat were significantly overdispersed (Table 1). Uniform spacing has been shown to become random at lowered densities in the fiddler crab *Uca* (Connell, 1963) and in the phoronid *Phoronopsis viridis* (Johnson, 1959), presumably due to a lack of intraspecific encounters. However, densities of *Streblospio* in Mission Bay are not so low that most individuals do not "see" each other. Thus observed dispersion patterns do not simply result from a low frequency of encounters.

In addition to feeding biology, other aspects of behavior contribute to differences in dispersion of the two spionid species. Both species are considered sessile tube dwellers, but *Streblospio* may be more mobile than *Pseudopolydora*. Adults of *Streblospio* have been collected in the estuarine water column over mud habitats at night (D. Dean, personal communication) and adult *Streblospio* will occasionally migrate into sediment trays placed on the intertidal mudflats in Mission Bay (Levin,

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unpublished data). There is no evidence of such movement in *Pseudopolydora*. Thus the greater mobility of *Streblospio* may eliminate the need for maintaining feeding territories by allowing more flexibility in habitat selection.

Patterns of larval release and subsequent dispersal are known to influence dispersion (Reise, 1979). *Pseudopolydora* releases 3 setiger larvae which spend 7-10 days in the plankton before settling. *Streblospio* releases 9 setiger larvae which spend a few hours to a few days in the water column. Larvae of both species are initially photopositive and settle from the water column (Levin, unpublished data). This behavior acts to cancel any possible effects of different dispersal abilities on the small scale of dispersion (mm-cm) assessed in this study.

Territorial behavior reported here for *Pseudopolydora paucibranchiata* is the first report for any polychaete outside the family Nereidae. For space limited situations, territoriality, probably in combination with environmental heterogeneity, influences recruitment success and acts to regulate populations levels. *Pseudopolydora* belongs to a dense tube-building assemblage whose members probably experience severe space limitation. The important consequences of territoriality to the organization of *Pseudopolydora* populations suggest that interference competition may be of general importance in tubicolous infaunal communities.

## 6. Summary

1. Nearest-neighbor analysis of spionid polychaete spatial distribution on an intertidal mudflat revealed uniform dispersion in *Pseudopolydora paucibranchiata* and random dispersion in *Streblospio benedicti*.
2. Field and laboratory analysis of *Pseudopolydora* recruitment patterns indicate that uniform spacing is initiated during settlement and enhanced by subsequent interactions between post-larvae.
3. Adult competition or predation on settling or newly settled larvae may also contribute to the even dispersion of *Pseudopolydora*.
4. *Pseudopolydora* is more aggressive than *Streblospio* and will fight with neighboring conspecifics during feeding and tube building.
5. Both species are surface deposit and suspension feeders but differ in mechanisms of food particle selection. *Pseudopolydora* relies primarily on palps and *Streblospio* relies primarily on lips and mouth to select or reject particles.
6. Observations of feeding behavior and spatial patterns of adults and new recruits lead to the hypothesis that *Pseudopolydora* defends palp territories for the acquisition of food and tube building materials.
7. *Pseudopolydora* territories are maintained by strong intraspecific competition: such competition is not observed in *Streblospio*. Territoriality may serve to regulate population levels of *Pseudopolydora* within space-limited tube building assemblages.
8. This paper provides the first evidence for territoriality in a non-nereid polychaete.

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Interference interactions among tube-dwelling polychaetes  
in a dense infaunal assemblage

Abstract

Interactions involving contact between feeding organs of the tube building polychaetes Pseudopolydora paucibranchiata Okuda, Streblospio benedicti Webster, and Fabricia limnicola Hartman were observed through a dissecting microscope and quantified for frequency of occurrence, and effects on foraging time and withdrawal. These surface feeding species form a dense intertidal assemblage ( $> 100,000$  individuals/m<sup>2</sup>) and can be readily transferred to the laboratory and observed in undisturbed sediment cores. Interspecific contact with Pseudopolydora often resulted in withdrawal and consequently a 4 to 7% loss of foraging time for individuals of other species, while intraspecific interactions among Pseudopolydora did so rarely. Larger individuals of all three species experience more interaction. The probability and duration of withdrawal due to contact with Pseudopolydora is size dependent in Fabricia and Streblospio: juvenile Fabricia and adult Streblospio show the greatest interference. The observation that Pseudopolydora interferes with individuals of other species more than with conspecifics contradicts the small-scale dispersion of these species as well as previous reports of interference behavior. A possible explanation is the relatively recent coexistence of these 3 species, two of which were introduced to the eastern Pacific since 1900.



### Introduction

Dense infaunal assemblages, occupying up to 90% of available surface area, occur commonly in shallow or intertidal muds and are often dominated by small tube-building forms, usually polychaetes and peracarid crustaceans. Numerous mechanisms have been implicated in the regulation of infaunal abundance patterns: physical or predator-mediated disturbance (Van Blaricom, 1978; Oliver et al., 1980; Brenchley, 1981); biogenic sediment modification (Rhoads and Young, 1971; Thistle 1980; Brenchley, 1981); adult-larval interactions (Woodin 1976; Bell and Coull, 1980); predation (Virnstein, 1977; Quammen, 1980); and competition (Peterson, 1977; Peterson and Andre, 1980). There has been practically no direct quantification of infaunal interference interaction and little evidence exists for interference competition between species in soft sediments (Peterson, 1979). Evidence for competition comes from: (a) negative correlations of species densities in the field (Ronan, 1975; Weinberg, 1979; Croker and Hatfield, 1980; Whitlatch, 1980), (b) manipulations of species densities in the field (Peterson and Andre, 1980; Wilson, 1980a), (c) manipulations in laboratory microcosms (Weinberg, 1979; Wilson, 1980b; Brenchley, 1981), (d) character displacement (Fenchel, 1977) and (e) direct observation in the laboratory (Brenchley, 1981; Dauer et al., 1981; this study). Species interactions may take place beneath the sediment surface. However, the behavioral interactions of tube dwelling infauna that feed at the sediment surface can be observed directly under magnification.

This paper describes interactions at the sediment surface among two spionid polychaetes, Pseudopolydora paucibranchiata Okuda and Streblospio benedicti Webster and one sabellid polychaete, Fabricia

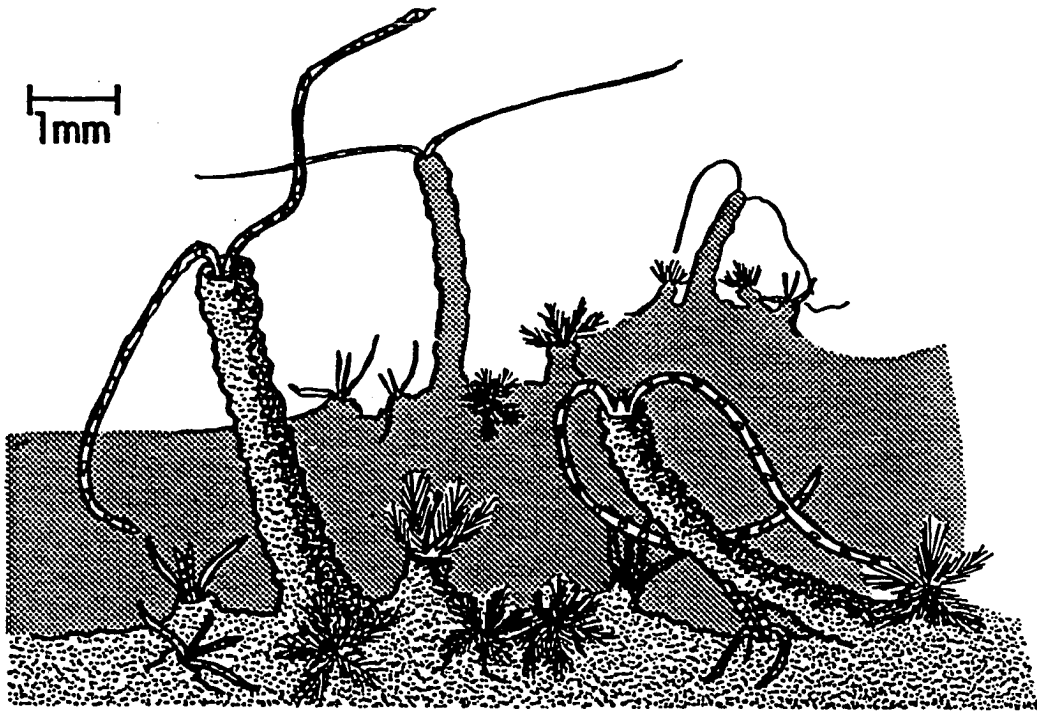
limnicola Hartman. They are depicted schematically in Figure 60. The studies presented here explore interspecific interactions involving Pseudopolydora and co-occurring surface feeding species. In this study I address the following questions: (1) Are interspecific interference interactions involving Pseudopolydora more or less frequent and severe than intraspecific interactions between Pseudopolydora individuals? (2) Is size important in determining the outcome of interactions? (3) Is the impact of interspecific interaction a function of species "relatedness"? Finally, I discuss the usefulness and interpretation of direct behavioral observations, consider a possible explanation for the behaviors observed and relate the findings of this study to abundance patterns of Pseudopolydora paucibranchiata, Streblospio benedicti and Fabricia limnicola on the Mission Bay mudflat.

#### Habitat and Species Descriptions

The intertidal mudflats of the Kendall-Frost Reserve are located in the northeast corner of Mission Bay, San Diego, California. They support a dense assemblage of polychaetes, oligochaetes, and phoronids at middle tide levels (1 - 3 ft above MLLW). Total macrofaunal density often surpasses 200,000 individuals/m<sup>2</sup>. Sediments are 75 -95% sand (> 4φ) by weight.

P. paucibranchiata, S. benedicti and F. limnicola comprise over 90% of the surface feeding macrofauna on the mudflats of Mission Bay in spring and summer. The less common spionids Rhynchospio arenicola and Polydora ligni, and the phoronid Phoronis sp., comprise much of the remainder of the macrofaunal surface feeding forms on the Kendall-Frost

Figure 57: Schematic drawing of surface feeding polychaete species at the Kendall-Frost Reserve. Pseudopolydora paucibranchiata, Streblospio benedicti and Fabricia limnicola are depicted.



mudflat. Gammarid and caprellid amphipods and tanaids are seasonally present in low numbers.

Pseudopolydora, Streblospio and Fabricia build tubes of cemented sediment which open at or above the sediment surface (Figure 60). The two spionids attain live body lengths of 10 - 30 mm, Fabricia approximately 10 mm. The spionids are facultative surface deposit feeders in still or slow moving water and suspension feeders when a strong current is present (Dauer et al., 1981; Taghon et al., 1980). They feed with paired ciliated palps on organic aggregates, phytoplankton, and detritus. Pseudopolydora palps extend over 20 mm in length and wander over the sediment surface making contact with other fauna during surface deposit feeding. Streblospio palps are shorter (< 5 mm) and also meander over the sediment. Fabricia suspension feeds with a tentacular crown < 2 mm in diameter. There are two dark palps at the center of the crown which also function in surface deposit feeding (Lewis, 1968). Fabricia processes smaller particles (< 50  $\mu$ ) than do Pseudopolydora and Streblospio.

#### Materials and Methods

Sixteen intact cores of sediment (9 x 9 x 7 cm) were collected from Mission Bay in June and July 1980 and maintained in the laboratory under running seawater until use in behavioral studies (1 - 7 days). Infauna were observed in intact cores in still seawater, illuminated with fiber optics cold lights and magnified with a Wild dissecting microscope at 60x and 120x magnification. Focal worms of each of the 3 species were selected such that individuals of all sizes were represented. Pseudopolydora interactions with Streblospio, Fabricia,

and other Pseudopolydora were studied in species pairs. Streblospio-Fabricia interactions were studied for comparison with observations involving Pseudopolydora.

For each species pair I recorded the number of encounters the focal worm experienced, the number of individuals encountered, the number of times the focal worm withdrew, the duration and the cause of the withdrawal. Observation periods on each focal worm were 3 minutes. The size of the focal worm and distances between it and interacting individuals were measured. Encounters consisted of sustained ( $> 0.5$  sec) contact between palps or tentacular crown. Very brief contact due to brushing or waving motion of palps was not recorded as an encounter. Polychaete withdrawal times were measured as seconds from the instant of withdrawal into the tube to the full reexpansion of palps or tentacular crown. Withdrawal due to interaction with another worm at the sediment surface was noted as distinct from withdrawal due to other causes.

An estimate of polychaete body length was obtained from tube diameters for Pseudopolydora (linear regression  $r = .96$ ,  $p < .01$ ), from palp length for Streblospio ( $r = .95$ ,  $p < .01$ ), and from tentacular crown diameters for Fabricia ( $r = .70$ ,  $p < .01$ ). Those few individuals regenerating palps or tentacular crowns were not included in the behavioral analysis. Worm size measurements for each species were divided into 3 size categories. Small, mid and large body length size classes for each species were: Pseudopolydora  $< 10$  mm,  $10.1 - 17.5$  mm and  $\geq 17.6$  mm; Streblospio  $< 6$  mm,  $6.1 - 8.8$  mm and  $\geq 8.9$  mm; Fabricia  $< 4.5$  mm,  $4.6 - 6.0$  mm, and  $\geq 6.0$  mm.

Intra- and interspecific nearest-neighbor distances were measured for worms collected in intact  $9 \times 9 \times 7$  cm sediment cores taken

from the mudflats of Mission Bay in May and June 1981. All measurements were made under a Wild dissecting microscope at 120x magnification using an ocular micrometer. A circular  $10 \text{ cm}^2$  area was marked in the center of each core and the densities of Pseudopolydora, Fabricia and Streblospio were recorded. For each Pseudopolydora individual in the marked  $10 \text{ cm}^2$  area the distances to the nearest individuals of Fabricia, Streblospio and Pseudopolydora were measured. For each Fabricia and Streblospio located in this manner (as being nearest to Pseudopolydora), the nearest Fabricia and Streblospio were recorded. Distances between worms were measured from tube bases at the sediment surface. Pseudopolydora tubes may open up to 1 cm above the sediment surface while Streblospio and Fabricia tubes open at or a few mm above the surface. No effort was made to measure vertical distances arising from variable tube heights.

The mean intraspecific nearest-neighbor distance expected from a Poisson (random) distribution was calculated as  $\bar{r} = 1/2\sqrt{\rho}$  where  $\rho$  = density (Clark and Evans, 1954). Interspecies expected mean nearest-neighbor distances were calculated with the assumption that the base worm represents a random individual in a randomly distributed population of the other species. The Clark and Evans (1954) index  $R = \bar{r}_{\text{obs}} / \bar{r}_{\text{exp}}$  was tested for significance with the standard normal variate  $c = \frac{\bar{r}_{\text{obs}} - \bar{r}_{\text{exp}}}{\sigma_{\bar{r}_{\text{exp}}}}$  where  $\sigma$  = the standard error of the mean nearest-neighbor distance.

## Results

### Species interactions

In all interspecific interactions involving Pseudopolydora, this species is the protagonist or aggressor. Pseudopolydora palp motion initiates and maintains contact between worms. The interactions between species pairs are summarized in Table 23. Pseudopolydora and Fabricia focal individuals on average encounter approximately the same number of Pseudopolydora (2 - 3 per observation period) and experience equal numbers of encounters with Pseudopolydora (8 - 9 per observation period) (Table 23). The number of interactions and number of individuals encountered is larger for mid and large size focal individuals than small ones. The mean number of interactions with Pseudopolydora (per 3 minute observation period) for small, mid and large size worms were 5.0, 8.9 and 12.0 for Fabricia and 1.9, 2.6 and 2.4 for small, mid and large Pseudopolydora. This size effect is highly significant for Fabricia encounters with Pseudopolydora ( $p < .0001$ , one Way ANOVA on both number of interactions ( $F_{2,57} = 16.48$ ) and number of individuals encountered ( $F_{2,57} = 8.07$ ) (Table 24).

Streblospio - Pseudopolydora and Streblospio - Fabricia interactions (with Streblospio as focal worm) took place much less frequently ( $F_{4,251} = 44.87$ ,  $p < .0001$ , One Way ANOVA and Sum of Squares STP) than Fabricia - Pseudopolydora or Pseudopolydora - Pseudopolydora interactions. Streblospio experienced an average of only 2 encounters with Pseudopolydora per observation period, usually with a single individual. As with Fabricia, the smallest Streblospio experience the fewest



interspecific encounters, 1.2, 2.3 and 1.8 per observation period for small, mid and large size worms.

Frequency, duration and probability of withdrawal indicate the severity and significance of interspecific interactions. The frequency of withdrawal due to interference by Pseudopolydora does not vary according to each species' number of encounters with Pseudopolydora (Table 23). Interspecific encounters proved more likely to result in withdrawal than intraspecific encounters involving Pseudopolydora. Small worms were more or less likely to withdraw depending on the species (Table 24). Withdrawal occurred least often in Pseudopolydora intraspecific encounters, only twice in 66 observation periods. Pseudopolydora interference caused withdrawal of Fabricia and Streblospio far more frequently, an average of 1.00 and 0.62 times per 3 minute observation period, respectively. Streblospio contact with Fabricia resulted in withdrawal only once in 34 observations.

Thirty-two percent of all Streblospio contacts with Pseudopolydora and 12% of Fabricia encounters with Pseudopolydora resulted in their withdrawal (Table 23). The probability of Pseudopolydora induced withdrawal increases with size for Streblospio and decreases with size for Fabricia (Table 25). Less than 1% of Pseudopolydora intraspecific encounters and Streblospio - Fabricia interactions resulted in withdrawal (Table 23).

Inspection of species' time budgets reveals that the spionids spent a larger portion of the observation period withdrawn into their tubes (12% for Pseudopolydora and 15% for Streblospio) than did Fabricia (just under 5%). Interference by Pseudopolydora accounted for 48% and

TABLE 23

## POLYCHAETE INTERACTIONS

Focal Species - Interacting Species	<u>Pseudopolydora- Pseudopolydora</u>	<u>Fabricia- Pseudopolydora</u>	<u>Streblospio- Pseudopolydora</u>	<u>Streblospio- Fabricia</u>
Interactions (#/3min)*	8.1 ± 4.7	8.6 ± 4.9	2.0 ± 2.0	2.0 ± 4.2
Worms encountered (#/3min)*	2.3 ± 1.1	2.5 ± 1.1	0.9 ± 0.8	0.4 ± 0.7
Withdrawals due to species interactions (#/3min)*	0.02 ± 0.12	1.0 ± 1.1	0.62 ± 1.10	0.03 ± 0.17
Probability of withdrawal following an interaction	0.002	0.12	0.32	0.015
Percent of observation time withdrawn: $\frac{\text{due to interaction}}{\text{total time withdrawn}}$	0.4/12.2	4.3/4.9	7.0/15.7	0.5/15.6
Number of individuals observed (observation period = 3 min)	66	60	63	34

\*  $\bar{x} \pm 1.S.D.$

Table 24  
Effect of Worm Size on Polychaete Interactions  
Comparison of Behavior among Species Pairs (One-Way ANOVA)

Focal Species	<u>Pseudopolydora</u>	<u>Fabricia</u>	<u>Streblospio</u>	<u>Pseudopolydora</u>	<u>Streblospio</u>	<u>Fabricia</u>	<u>Streblospio</u>	<u>Fabricia</u>
Interacting Species	<u>Pseudopolydora</u>	<u>Pseudopolydora</u>	<u>Pseudopolydora</u>	<u>Pseudopolydora</u>	<u>Pseudopolydora</u>	<u>Pseudopolydora</u>	<u>Pseudopolydora</u>	<u>Pseudopolydora</u>
<b>Behavior</b>								
Interactions (#/3min) One Way ANOVA	$F_{2,63} = 5.27$	$F_{2,57} = 16.48$ ****	$F_{2,60} = 1.98$	↕	↕	$F_{2,31} = 1.23$	$F_{4,251} = 44.87$ ****	
Worms encountered (#/3min) One Way ANOVA	$F_{2,63} = 1.76$	$F_{2,57} = 8.07$ ****	$F_{2,60} = 1.91$	↕	↕	$F_{2,31} = 1.40$	$F_{4,251} = 63.27$ ****	
Withdrawals due to species interactions (#/3min) One Way ANOVA	$F_{2,63} = 0.56$	$F_{2,57} = 6.27$ ***	$F_{2,60} = 1.08$	↕	↕	$F_{2,31} = 0.55$	$F_{4,251} = 19.04$ ****	
Seconds withdrawn due to species interactions (#/3min) One Way ANOVA	$F_{2,63} = 0.56$	$F_{2,57} = 3.50$ *	$F_{2,60} = 4.34$ **	↕	↕	$F_{2,31} = 0.55$	$F_{3,219} = 9.04$ ****	
Withdrawals due to other causes (#/3min)	$\chi^2_4 = 5.84$	$\chi^2_2 = 2.10$	$\chi^2_4 = 4.97$			---	$\chi^2_4 = 63.82$ ***	
Probability of withdrawal resulting from an encounter (pairwise arcsine transformations)	NS	****	NS			NS	****	

\*  $P < .05$   
 \*\*  $P < .025$   
 \*\*\*  $P < .005$   
 \*\*\*\*  $P < .001$

TABLE 25  
PROBABILITY OF WITHDRAWAL FOLLOWING SPECIES INTERACTION

Focal Species Interacting Species	<u>Pseudopolydora</u>		<u>Fabricia</u>		<u>Streblospio</u>	
	<u>Pseudopolydora</u>	<u>Pseudopolydora</u>	<u>Pseudopolydora</u>	<u>Pseudopolydora</u>	<u>Pseudopolydora</u>	<u>Fabricia</u>
Small*	.008		.36	.18		.021
Medium*	.007		.08	.38		.00
Large*	.000		.06	.41		.00
Statistical Significance of Size**	NS		p < .001	NS		NS

88% of the total Streblospio and Fabricia withdrawal times respectively. Intraspecific interactions accounted for only 3% of Pseudopolydora withdrawal time (Table 23).

The time spent withdrawn due to interference from Pseudopolydora was dependent on the size of the focal worm while withdrawals due to other causes were not (Table 25). Small Fabricia spent more of the total observation period withdrawn due to negative interactions with Pseudopolydora than did large Fabricia ( $F_{2,57} = 3.50, p < .05$ , One Way ANOVA). In contrast, small Streblospio spent significantly less time withdrawn ( $F_{2,60} = 4.34, p < .025$ , One Way ANOVA), and exhibited a lower probability of withdrawal due to Pseudopolydora interference, than did large Streblospio. Thus withdrawal probabilities and withdrawal time resulting from Pseudopolydora interference exhibit opposite size dependencies in Fabricia and Streblospio.

Other factors cause withdrawal in these polychaetes. Streblospio and Pseudopolydora will withdraw briefly to bring a fecal rod up out of the tube. Subsurface activity of motile infauna sometimes causes withdrawal of tube dwellers. Often the cause for withdrawal is not apparent. The time spent due to these other causes is independent of polychaete size ( $p < .05, X^2$  contingency table) for Streblospio, Pseudopolydora and Fabricia (Table 24). Pseudopolydora intraspecific encounters and Streblospio - Fabricia interactions resulted in withdrawal too infrequently to determine the effect of size. However, only small and mid-size Pseudopolydora were observed to withdraw at all, suggesting that they are subject to greater intraspecific interference.

## Spatial Patterns

The distances between tubes of Pseudopolydora, Fabricia, and Streblospio at the sediment surface were examined to determine whether the behavioral interactions reported on here influence the spacing of these worms on the mudflat. Intraspecific nearest-neighbor distances decreased for each species with increasing species density. Mean nearest-neighbor distances were 5.5 mm, 3.8 mm and 2.2 mm for Pseudopolydora, Streblospio and Fabricia respectively. In 1981, when these measurements were made, Fabricia was far more abundant than Pseudopolydora or Streblospio. Each species was slightly (but not significantly) underdispersed (uniform) with respect to conspecifics, based on the Clark and Evan's (1954) index

$$R = \frac{\text{observed mean nearest-neighbor distance}}{\text{expected mean nearest-neighbor distance}} = \frac{\bar{r}_{\text{obs}}}{r_{\text{exp}}} \quad (\text{Table 26})$$

This tendency was greatest for Pseudopolydora and is consistent with the territoriality described previously for this species (Levin, 1981).

Interspecific nearest-neighbor distances do not reflect the aggressive behavior observed in Pseudopolydora. Mean nearest-neighbor distances between all inter-species pairs ranged from 2.1 to 2.7 mm (Table 26) and did not vary significantly from random expectation. Increased density of one or the other species results in lower inter-species distances. Nearest-neighbor measurements do not suggest spatial segregation or species avoidance, but rather tend towards interspecies aggregation. Segregation might be expected if Fabricia or Streblospio were avoiding Pseudopolydora, or if Pseudopolydora was maintaining interspecific territories. Pseudopolydora individuals maintain the

Table 26  
Nearest-Neighbor Distance Measurements

Base Worm Nearest Neighbor	Intraspecific Distances			Interspecific Distances		
	Pseudopolydora Pseudopolydora	Streblospio Streblospio	Fabricia Fabricia	Pseudopolydora Streblospio	Pseudopolydora Fabricia	Streblospio Fabricia
N = 4 10cm <sup>2</sup> quadrats	7	6	7	6	7	6
Density ( $\bar{D}/\text{cm}^2$ ) ± 2 S.D.	1.19±0.47	1.85±0.71	4.51±2.54	-	-	-
* $\bar{r}$ observed (mm)	5.49	3.84	2.20	3.38	2.40	2.08
* $\bar{r}$ expected (mm)	3.81	3.06	1.99	3.63	2.40	2.40
** $\bar{R} = (\frac{\bar{r}_{obs}}{\bar{r}_{exp}})$	1.44	1.26	1.10	0.95	1.00	0.87
Significance (based on standard ) normal deviate	NS	NS	NS	NS	NS	NS

\* mean value of quadrat mean nearest-neighbor distances  
\*\* mean value of quadrat R values

greatest intraspecific distances and Streblospio - Fabricia pairs exhibit the smallest interspecific distances.

#### Discussion

Intraspecific territoriality has been previously documented for Pseudopolydora paucibranchiata in Mission Bay (Levin, 1981). The findings presented here demonstrate that interspecific encounters between Pseudopolydora and other tube building polychaetes are frequent and often result in withdrawal of the other species. Interspecific aggression has been observed in the laboratory but not quantified for the spionid polychaetes Polydora, ligni Spio setosa and Scolecopelides viridis (R. Whitlatch, pers. comm.; Levin, unpublished data). Wilson (1980a) performed density manipulations in the field which provided evidence of interference competition between the spionids Pseudopolydora kempi and Pygospio elegans.

The ecological significance of interference behavior can be more readily interpreted when it results in uniform dispersion, as seen in the intraspecific spacing of Pseudopolydora (Levin, 1981). The interpretation of withdrawal probabilities and withdrawal time, in the absence of territoriality and uniform spacing, is less straightforward. Contact among surface feeding infauna occurs with feeding structures: palps, tentacular crowns or lophophores. Spionids such as Pseudopolydora will steal food from other surface deposit feeders with their palps (Levin, 1981). Most surface feeding species feed continuously in the presence of overlying water. Loss of feeding time due to inter-animal struggles or withdrawal into a tube must decrease individual fitness. While these



losses are not translated directly into mortality, they may result in decreased reproductive activity or offspring viability. Food supply is known to influence growth and reproduction in polychaetes (Schroeder and Hermans, 1975; Tenore, 1977). Interference by Pseudopolydora accounted for a 4.3% loss of Fabricia foraging time and a 7% loss of Streblospio foraging time under laboratory conditions. If foraging time translates directly into food acquisition then these losses are probably significant.

The observed behaviors are of more interest if they can be related to abundance patterns of Pseudopolydora, Streblospio and Fabricia in the field. Unusual events in early 1980 reduced mean Fabricia densities from over 100,000 individuals/m<sup>2</sup> to less than 5,000/m<sup>2</sup> at 1.5 to 2.5 ft above MLLW on the mudflats in Mission Bay. Pseudopolydora and Streblospio settled heavily and grew quickly in the following spring months where a dense Fabricia bed once existed (Levin, 1980). Newly emerging Fabricia faced unusually high numbers of aggressive Pseudopolydora (6 to 8 times normal density) during their recruitment period in 1980. Behavioral observations made in this study suggest that Pseudopolydora does not interfere with Streblospio juveniles. The 1980 Streblospio population, composed primarily of new young in spring and summer, paralleled Pseudopolydora abundances for that year. Streblospio is more mobile than either of the other two species and commonly enters the water column as juveniles or adults (Dauer *et al.*, 1981; Levin, unpublished data). This behavior may enable Streblospio to avoid negative confrontations with Pseudopolydora.

Woodin and Jackson (1979) and Wilson (1980a) have suggested that interference competition is more prevalent and stronger among closely related taxa. The relatedness of Fabricia and Streblospio to Pseudopolydora had little bearing on the level of interference experienced by those species. In a previous discussion of Pseudopolydora dispersion (Levin, 1981), I suggested that larger intra versus interspecific distances between surface dwelling infauna implies stronger competitive relationships within than between species. In this study, interspecific encounters involving Pseudopolydora cause greater interference with feeding activity than do intraspecific Pseudopolydora encounters. Intraspecific interactions, though numerous, rarely resulted in Pseudopolydora withdrawal. Uniform spacing of Pseudopolydora initiated during settlement and maintained throughout the benthic phase (Levin, 1981) may actually lessen direct interference confrontation.

Spacing mechanisms do not appear to be operating at the same level interspecifically. Streblospio, Fabricia and Pseudopolydora occur, on average, 2 to 3 mm from one another. The smallest interspecies nearest-neighbor distances occur between Streblospio and Fabricia. This is consistent with the absence of behavioral interference between the two species. Pseudopolydora - Streblospio and Pseudopolydora - Fabricia nearest-neighbor distances are small and very similar. They provide no indication that either Fabricia or Streblospio are responding to interference of Pseudopolydora by adjusting their positions at the sediment surface.

One possible explanation for these observations is that the species involved have only recently become associated and have not

evolved spacing mechanisms to avoid interspecific interference. Both Streblospio benedicti and Pseudopolydora paucibranchiata were introduced to the eastern Pacific in the early 1900's. Streblospio was introduced with the Atlantic oyster Crassostrea virginica and Pseudopolydora was introduced from Japan, via shipping or importation of the oyster Crassostrea gigas (Carlton, 1978). Fabricia limnicola has been reported only from Newport Bay, Mission Bay (in California), San Quintin Bay and one site in the northern Gulf of California (Baja California) (Carlton, 1978). The disjunct distribution in harbors suggests that Fabricia also has been introduced through shipping or that it is a relict endemic species which once had a more continuous distribution (Carlton, pers. comm.). Pseudopolydora may have become established in Mission Bay less than 10 years ago, as Streblospio and Fabricia were abundant in a 1971 survey of the Kendall-Frost mudflat but Pseudopolydora was not observed (Jumars, pers. comm.). It is therefore unlikely that the interspecies spatial patterns or behavioral responses observed on the mudflat reflect coevolved or behaviorally fixed responses to specific community members. Novel associations such as this are likely to be common in coastal embayments where often the majority of the fauna are recent introductions (Carlton, 1978). Other factors, including species' densities, environmental heterogeneity and disturbance, recruitment patterns, and predation may mask competition induced dispersion patterns.

The behavioral observations reported here were made entirely in the laboratory. However, conditions of still water are a realistic replica of natural conditions on the mudflat 6 to 12 hours each day (during slack tides and in puddles at low tide). Polychaetes are active

on the mudflat surface in puddles of water > 1 cm deep; such puddles often cover over one-half the mudflat at low tide (Levin, unpublished data). Under conditions of rapid water flow, the spionids will shift to a suspension feeding mode with palps held upright or spiralled and species interactions will be less frequent. Dauer et al. (1981) note increased feeding rates (based on defecation rates) in the presence of current for 6 spionid species. It is possible that the most successful feeding activities occur in flowing water. This could explain the apparent lack of spatial adjustment to counter interference prevailing during still water conditions.

Quantitative visual studies, such as the one presented here, are valuable in providing researchers with a level of understanding necessary to pose reasonable and testable hypotheses. In order to ask valid questions about population regulation, resource exploitation and interference competition in soft sediment communities, we must understand how, when, where and why animals interact. These results document stronger inter- than intraspecific interference from Pseudopolydora aggression. Interspecific encounters were frequent and resulted in withdrawal and loss of foraging time whereas intraspecific encounters did not. Young and adult stages responded differently to encounters with Pseudopolydora and the response pattern varied with species. Studies of infaunal interactions must therefore be species-specific and must take life history stage into consideration. Species interactions are not reflected by interspecies dispersion possibly because these species have only recently begun to coexist. Interference competition among infauna may be more common and important than previously believed, particularly in dense assemblages with aggressive spionid polychaetes.

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## CHAPTER VII

### CONCLUSIONS

#### Benefits and Limitations of the Approach

The overriding message of this thesis is that species' life histories and associated dispersal abilities affect almost all processes important in structuring soft sediment assemblages, including predation, competitive interactions among community members, species' response to disturbance, and population variability in space and time. The ecologist working on populations in the field must become familiar with reproductive modes and mobility patterns in order to pose and adequately test hypotheses concerning population regulation. The role of life history and mobility patterns and the importance of identifying the spatial and temporal scales on which they function, cannot be overemphasized. Mode of larval development determines the setting in which the larval phase occurs, sources of larval mortality, pelagic dispersal abilities and the site and mechanisms of recruitment, all of which affect how, when and where interactions involving young can take place.

No single approach can provide a true picture of species' dispersal abilities. Laboratory studies may demonstrate the tolerance range of various traits and provide evidence of the variability introduced by environmental or genetic factors. Yet it is difficult to verify how much of this is relevant in the field. Field studies of the plankton provide only a brief glimpse of the variation and fluctuation inherent in natural systems. They offer a valuable and necessary view of existing distributions but there is no assurance that findings of one year will apply to the following year, or that dispersal events result



in successful recruitment. Hydrographic studies are valuable but have the same limits; they clarify the transport of larvae by water and the variability in transport trajectories. Laboratory and field experiments reveal the elements of choice in processes of dispersal, recruitment and colonization, and the nature of species' responses to events not easily tested by observing natural phenomena.

Electrophoretic studies can be a valuable tool to examine effects of dispersal on population structure. The substantial genetic differentiation between San Diego Bay and Mission Bay populations of Exogone lourei hint at a lack of gene flow and effective separation (see Appendix Four). However, the lack of polymorphic loci in the other polychaete species prevented similar genetic confirmation of isolation. Genetic differentiation of populations can arise from strong selective pressures as well as curtailed gene flow. The distinction can be clarified by electrophoretically examining the genetics of settling larvae and new recruits in addition to adult populations. The technology exists to do this but was not pursued in this thesis due to time constraints and an apparent lack of genetic variability among most species.

All of the above methods for studying dispersal provide inference or evidence for the presence or absence of dispersal. Ideally, in order to quantify dispersal events, one would like to label and track larvae (or post-larval dispersing stages) from their release through recruitment. Dye and radioactive tracer techniques offer promise but the obstacles to labeling and detection are enormous. The study of larval dispersal is an open field in need of major technological and theoretical advance.

### Synopsis

The problem of dispersal is an important one, and the polychaete assemblage of the Kendall-Frost mudflat provided an unusual opportunity to study dispersal phenomena in related, co-occurring species. During the century the Mission Bay wetlands have shrunk tremendously due to human modification, intensifying what was already a high degree of physically induced habitat isolation. Most of the polychaetes at the Kendall-Frost Reserve are limited to intertidal muds and occur primarily in the back of Mission Bay. The adult populations act as point sources for dissemination of larvae, and it is therefore possible to determine larval trajectories for some species inside the bay.

Hydrographic studies of temperature and salinity patterns and water flushing in Mission Bay indicate that circulation in the back of the bay is sluggish. Strong temperature and salinity gradients are maintained near the Kendall-Frost Reserve and dye, drogue and drift tube studies suggest that back-bay waters are subject to minimal oceanic influence. Drift tubes released near the Kendall-Frost Reserve exhibited a 3% probability of exiting Mission Bay, a pattern consistent with the distribution of Pseudopolydora larvae in Mission Bay in spring 1980.

The front regions of Mission Bay are subject to more extensive flushing. Those larvae which reach the front bay and are carried into the ocean may be rapidly transported up and down coast by tidal and wave induced longshore transport. Average currents in spring and summer (4 - 10 sec) could carry larvae with a 2-week planktonic phase 80 - 120 km, but the strong currents present during severe storms (such as that of May, 1980), could transport larvae 500 or more kilometers. In the absence of suitable substrate, planktotrophic larvae, such as those of

Pseudopolydora paucibranchiata or Polydora ligni, may delay settlement for 6 or 7 weeks, permitting longshore transport of several hundred kilometers and thus allowing access to many embayments along the Baja and Alta California coasts. Major storms are probably responsible for the most significant dispersal events since the long-distance transport of larvae rarely results in successful recruitment.

Invertebrate larvae of benthic species (polychaetes, bivalves, phoronids) are most abundant at back (I) or mid-bay (II, III) plankton stations. Some holoplanktonic forms (Oikopleura sp., Acartia tonsa) and demersal species (Harpacticoid copepods) also exhibit this pattern. These probably represent permanent Mission Bay populations which minimize loss to the ocean by remaining in slow moving back-bay waters.

Markedly higher densities of polychaete larvae occur in the waters overlying the Kendall-Frost mudflat than at other stations in Mission Bay. Predictably, the planktotrophic larvae of P. paucibranchiata, P. ligni, and R. arenicola are seasonally present, sometimes at high densities. More unusual is the recurrence of post-larval stages of infaunal and epibenthic forms which make short-term excursions into the water column. R. arenicola and S. benedicti juveniles, and E. lourei adults, and occasionally C. capitata are capable of small-scale planktonic dispersal. Spatial and temporal patterns of plankton abundances over the mudflat reflect in part the spatial distribution of species in the mud, annual and seasonal variation in reproduction, and lunar, diel and tidal cycles of spawning and larval activity. The bimodal abundance patterns observed for polychaete larvae in the mudflat plankton at a single station during 12-hour tidal cycles were probably generated by tidally driven oscillations of larval aggregations in the back bay.

Laboratory studies of polychaete life histories provided the information necessary to interpret and/or confirm dispersal implications of hydrographic and plankton investigations. The Kendall-Frost polychaete species share many life history characteristics which limit dispersal potential. All the species provide some form of brood protection for developing young, either in the adult tube, attached to the adult body, or within brood pouches. Exogone and Fabricia lack pelagic larval stages. Streblospio and Capitella larvae may recruit immediately following release from the parent. These development patterns explain the absence or rarity of the larvae of these species in the Mission Bay plankton. Pseudopolydora, Polydora and Rhynchospio exhibit mixed development (sensu Pechenik, 1979), with a brief period in which young are brooded and a more lengthy planktonic phase of feeding and development. Often larvae of these species are the most common meroplanktonic forms in the waters overlying the Kendall-Frost mudflat. In spring 1980 Pseudopolydora larvae were the most abundant polychaete larvae in the entire bay.

Larval development studies reveal much flexibility in planktonic period for those species whose larvae can actively enter the water column. While Streblospio and Capitella can become planktonic for brief periods, Pseudopolydora and Polydora may extend a (normally) 1 - 2 week pelagic development period for 4 or 5 additional weeks in the absence of suitable substrate for settlement. This behavior enhances the probability that larvae swept out to sea will remain viable long enough to reach an appropriate back-bay environment.

Post-larval stages have assumed a dispersive role in many of the Kendall-Frost species, possibly in response to sediment disturbance and

to compensate for the absence of planktonic larval stages. The presence of Streblospio, Rhynchospio and oligochaete juveniles and Exogone adults in the plankton, and the ability of these body brooding species to colonize while carrying young, attest to their flexible powers of small-scale dispersal.

Plankton distributions and life history studies also explain observed recruitment patterns and benthic distributions on the mudflat. The midwater jar settlement study affirms the localized settling abilities of those species lacking planktotrophic larvae and the broader dispersal abilities of Pseudopolydora, Polydora and Rhynchospio. Differences in recruitment into settling trays at Sites A and C may be due in part to the limited nature of dispersal in Streblospio, Capitella, and Exogone. The young of these species and of Fabricia recruit near the adults. Pseudopolydora larvae exhibit attraction to conspecifics during settlement (in the laboratory and the field). These behaviors enhance and perpetuate existing patterns and spatial heterogeneity in benthic distributions.

The defaunation experiments revealed horizontal patterns of infaunal migrations, further elucidating the small-scale dispersal and colonization capabilities of polychaetes. These studies demonstrate that the relative importance of larvae, juveniles or adults as colonizing agents varies between species. Colonization by brooding females is particularly important in some species (Exogone, Streblospio).

Species' response to disturbance varied with scale of the disturbance and was dependent on life history traits such as timing of reproduction, mode of development, mobility and dispersal patterns. Colonization of small defaunated sediment patches reflected larval

availability and adult abundances in surrounding sediments. Response to disturbance was rapid for most species, but Pseudopolydora and Polydora were dependent on larvae for colonization. Large-scale disturbances, such as the 1980 storm and sewage spill, result in a major change in species abundance patterns and spatial distributions. The Fabricia bed disappeared and Pseudopolydora took over the mid intertidal; but even these changes persisted less than one year. The relatively short recovery time for this assemblage (1 - 2 worm generations), was due to the annual nature of the species' life cycles and the ability of Fabricia, Exogone and Streblospio to reestablish high densities quickly and directly from the existing populations.

The ability to respond rapidly to disturbance is an important feature of the Kendall-Frost polychaete assemblage, attendant on their individual life histories. These abilities fall into 2 groups, those permitting good dispersal and response to large-scale disturbance and those enabling rapid colonization in response to small-scale disturbance (Table 27). Most of the Kendall-Frost polychaetes are excellent small-scale colonizers. Reproduction occurs for much of the year; brood sizes are small but larval supply is steady. Larvae exhibit little or no dispersal ability and often recruitment occurs from within the sediments, eliminating mortality associated with a pelagic phase. Post-larval stages may disperse through the water column, and colonization by brooding adults permits a rapid buildup in population size. Streblospio, Rhynchospio, Exogone, Fabricia and Capitella possess many of these features.

Pseudopolydora and Polydora are better able to respond to large scale disturbance. They are dependent on a highly seasonal, variable

Table 27

## Polychaete Life History and Mobility Traits

Long-Distance Dispersers

Response to large-scale disturbance

Seasonal reproduction

Variable larval supply

Long-distance dispersal by larvae

Recruitment from the water column

Sessile post-larval stages

Small-Scale Colonizers

Response to small-scale disturbance

Year-round reproduction

Steady larval supply

Limited dispersal by larvae

Recruitment from within sediments

Small-scale dispersal of post-larval stages: juveniles, adults, brooding adults

supply of larvae which must recruit from the water column for successful colonization and population maintenance. The larvae possess good long-distance dispersal abilities. If the timing of a large-scale disturbance coincides with a period of peak larval availability, intense recruitment and invasion can occur.

The 2 species groups exhibit different competitive abilities as well. Studies of dispersal and behavioral interactions in Pseudopolydora reveal strong intraspecific territoriality and a high degree of interspecific interference with other surface feeding polychaetes. This territoriality, the first described for a non-nereid polychaete, is initiated during settlement and maintained through subsequent palp contact. This behavior results in uniform spacing which ultimately acts to reduce interference behavior (withdrawal, inhibition of feeding activities) such as that experienced by the more passive species Streblospio and Fabricia.

Interspecific interference effects are highly dependent on the life history stages involved. Juvenile Fabricia and adult Streblospio experience the greatest loss of feeding time from Pseudopolydora aggression. However, a tube mat of adult Fabricia inhibits Pseudopolydora settlement, reversing the direction of the interspecies effect. The relatively recent coexistence of the Kendall-Frost polychaetes, many of which have been introduced to the eastern Pacific since 1900, may account for the lack of coevolved spatial or behavioral adjustments which counter interspecific interference.

Several key contributions emerge from this research. (1) Successful species in an isolated back-bay habitat are those which exhibit life history characteristics conferring reduced dispersal ability:



small size, brood protection, reduced or flexible pelagic larval stages. (2) When life histories constrain dispersal to small scales, post-larval stages assume a dispersive role. The resulting suppression of gene flow is likely to enhance rates of differentiation and speciation. (3) Observed life histories and mobility patterns enable species to respond rapidly to fine-grained disturbance and maintain very high infaunal densities. (4) Intra- and interspecific behavioral interactions influence spatial structure and the relative success of surface-feeding infauna. The importance of life histories, dispersal and interference competition has been largely ignored in past studies of dense assemblages. In Mission Bay behavioral interactions combine with life history patterns to determine species' distributions and abundances, and these factors are likely to be of ecological importance in many other infaunal communities as well.

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**APPENDICES**

## Appendix One

## Mission Bay Temperature Measurements

Temperature °C

Station #	10/18/79	2/14/80	5/12/80	8/25/80
1	21.42	15.50	18.30	23.50
2	21.42	15.65	18.09	23.65
3	21.38	15.65	18.11	23.45
4	21.30	16.00	18.04	23.30
5	21.15	-	18.20	23.30
*6	20.70	16.10	18.09	23.80
7	-	16.10	18.10	23.30
8	20.20	16.00	17.50	23.10
9	20.40	16.20	17.97	22.90
10	20.40	-	18.14	23.00
11	-	16.32	18.00	22.50
12	19.75	16.30	17.51	22.30
13	19.62	16.33	17.36	22.15
14	18.92	16.30	16.63	21.45
15	19.25	16.45	17.30	21.50
16	19.55	16.40	17.35	21.85
17	19.70	16.48	18.30	21.85
18	20.42	16.40	18.23	-
19	19.15	16.35	17.08	21.90
20	19.17	16.50	-	21.90
21	19.25	16.28	17.18	21.60
22	19.88	16.55	17.11	21.60
23	20.00	-	17.20	21.70
24	-	16.72	-	22.65
25	19.97	-	18.40	22.40
26	-	16.23	18.03	22.55
27	19.85	16.80	17.90	-
28	20.00	16.60	17.94	22.75
29	20.10	17.28	-	22.90
30	-	-	18.08	22.60
31	19.97	16.30	18.25	22.60
32	19.85	16.13	18.10	22.60
33	19.62	16.20	18.17	22.35
34	19.60	16.78	17.58	22.32
35	19.52	16.12	17.50	22.00
36	19.48	15.85	15.78	21.80
37	19.42	16.15	17.35	21.75
38	19.41	15.95	16.23	20.90
39	19.15	15.70	16.35	21.00
40	18.80	16.10	17.13	21.20
41	18.40	16.00	16.79	20.90

## Temperature °C

Station #	10/18/79	2/14/80	5/12/80	8/25/80
42	-	16.15	17.06	21.35
43	18.40	16.20	17.42	22.60
44	18.35	16.31	17.56	21.80
45	18.30	16.22	17.35	21.40
46	19.10	16.15	17.16	21.60
47	18.40	16.13	17.06	-
48	18.25	16.18	17.05	21.50
49	18.30	-	-	21.50
50	18.25	16.18	17.11	21.15
51	18.50	16.30	16.74	21.30
52	18.55	16.40	17.05	21.85
53	18.60	-	-	21.55

\* Kendall-Frost mudflat

Station #1 - 23 Back Bay

Station #24 - 53 Front Bay

(See Figure 33 for location of sampling stations.)

## Appendix Two

## Mission Bay Salinity Measurements

Salinity o/oo				
Station #	10/18/79	2/14/80	5/12/80	8/25/80
1	33.727	2.586	32.156	33.666
2	33.732	6.086	32.205	33.650
3	33.724	4.260	32.154	33.583
4	33.731	17.871	32.204	33.635
5	33.752	-	32.126	33.607
6*	33.650	25.656	32.223	33.605
7	-	10.182	32.164	33.536
8	33.590	10.342	32.362	33.434
9	33.624	23.488	32.247	33.487
10	33.609	-	32.213	33.514
11	-	26.516	32.275	33.436
12	33.502	24.753	32.400	33.353
13	33.517	29.712	32.480	33.468
14	33.476	31.008	32.605	33.416
15	33.485	28.842	32.357	33.385
16	33.495	29.130	32.386	33.401
17	33.500	27.338	32.309	33.412
18	33.614	28.123	32.309	-
19	33.503	29.995	32.456	33.417
20	33.497	29.945	-	33.413
21	33.486	31.309	32.483	33.390
22	33.513	30.773	32.438	33.397
23	33.477	-	32.492	33.370
24	-	29.040	-	33.416
25	33.548	-	32.289	33.449
26	-	31.310	32.328	33.250
27	33.478	31.066	32.220	-
28	33.485	31.696	32.269	33.264
29	33.490	30.575	-	33.313
30	-	-	32.359	33.314
31	33.492	31.894	32.574	33.332
32	33.486	31.961	32.542	33.345
33	33.477	32.091	32.532	33.337
34	33.493	29.321	32.238	33.292
35	33.497	31.60	32.273	33.317
36	33.488	32.258	32.808	33.304
37	33.477	32.090	32.345	33.333
38	33.495	32.118	32.702	33.406
39	33.487	32.253	32.629	33.404
40	33.478	31.681	32.520	33.397
41	33.453	32.110	32.542	33.406
42	-	31.638	32.483	33.350

## Salinity o/oo

Station #	10/18/79	2/14/80	5/12/80	8/25/80
43	33.457	31.990	32.577	33.359
44	33.449	31.744	32.565	33.411
45	33.450	31.768	32.544	33.411
46	33.477	31.756	32.624	33.373
47	33.450	31.847	32.636	-
48	33.458	31.825	29.813	33.410
49	33.464	-	-	33.331
50	33.456	31.765	32.610	33.411
51	33.475	29.573	32.671	32.788
52	33.471	27.357	32.163	32.851
53	33.467	-	-	33.286

\* Kendall-Frost mudflat

Station #1 - 23 Back Bay

Station #24 - 53 Front Bay

(See Figure 3 for location of sampling stations.)

Appendix Three  
Kendall-Frost Species List

Abundant - very (>25,000/m<sup>2</sup>)  
Common - (>10,000/m<sup>2</sup>)  
Present - (≥1,000/m<sup>2</sup>)  
Rare - (<1,000/m<sup>2</sup>)

<u>Species</u>	<u>Site</u>		
	A	B	C
Annelida			
Polychaeta			
<u>Pseudopolydora paucibranchiata</u>	A	C	P
<u>Streblospio benedicti</u>	P	A	A
<u>Rhynchospio arenicola</u>	C	C	P
<u>Polydora ligni</u>	P	P	P
<u>Polydora nuchalis</u>	R	P	P
<u>Nerinides tridentata</u>	R	R	R
<u>Prionospio malmgreni</u>	P	P	R
<u>Spiophanes sp.</u>	R	R	R
<u>Spio filicornis</u>	R	R	R
<u>Fabricia limnicola</u>	P	A	R
<u>Megalomma pigmentum</u>	R	-	R
<u>Euchone sp.</u>	R	R	R
<u>Capitella capitata</u> I (small)	C	C	C
<u>Capitella capitata</u> II (large)	P	R	P
<u>Capitita ambisetta</u>	C	P	C
<u>Mediomastis californiensis</u>	C	P	C
<u>Exogone lourei</u>	A	A	A
<u>Eteone dilatae</u>	R	P	P
<u>Eteone californica</u>	R	P	P
<u>Paraonis gracilis</u>	R	R	R
<u>Haploscoloplos sp.</u>	R	R	R
<u>Nereis sp.</u>	P	P	P
Oligochaeta (tubificidae, 4 species)	A	C	A
Phoronida			
<u>Phoronis sp.</u>	R	C	P
Nemertean	R	R	R

## Appendix Three

		<u>Site</u>	
	A	B	C
Mollusca			
<u>Acteocina inculta</u>	P	P	P
<u>Acteocina culcitella</u>	R	R	R
<u>Aplysia californica</u>	R	-	-
<u>Cerithidea californica</u> (abundant in salt marsh)		R	R
<u>Aglaja dromeda</u>	P	R	P
<u>Chione sp.</u>	P	P	R
<u>Tagelus sp.</u>	R	-	-
<u>Musculus senhausii</u>	P	P	P
Crustacea			
Podocopid ostracod	C	C	C
<u>Leptochelia sp.</u>	P	P	P
Caprellid amphipods	P	R	P
<u>Corophium sp.</u>	P	P	P
<u>Erichthonius sp.</u>	R	R	R
Cumacean	R	R	R
<u>Callianassa californiensis</u>	C	R	R
<u>Hemigrapsus sp.</u>	P	R	P
<u>Leptosynapta sp.</u> (holothurian)	R	-	R
Cerianthid anemone	R	-	R
Dipteran larvae	R	P	P
<u>Clevelandia ios</u> (goby)	P	-	R

Appendix Four  
Electrophoretic Studies

This study presents preliminary information on genetic variability and geographic differentiation in 4 different polychaete species: 2 spionids, Pseudopolydora paucibranchiata and Streblospio benedicti, a syllid, Exogone lourei, and a sabellid, Fabricia limnicola. These data were collected to investigate life history implications of larval dispersal, gene flow, and population genetic structure in back bay, infaunal polychaetes, and to test the prediction that species with reduced dispersal exhibit greater between-bay genetic differentiation than species with long-distance dispersal capabilities.

I present these preliminary findings in order to inform others interested in polychaete population genetics of (1) electrophoretic techniques for assaying very small worms; (2) detectable enzyme activity in polychaetes; (3) levels of polymorphism; and (4) geographic differentiation.

#### Methods

Standard horizontal slab starch gels electrophoresis was employed using 12% gel made of Sigma Starch. Whole specimens of Pseudopolydora paucibranchiata, Streblospio benedicti and Fabricia limnicola were sorted from sediments and removed from their tubes. Individual worms were macerated in 20 ml of seawater in immunology reaction wells using a small tissue grinder. The resulting crude extract was absorbed onto 3 mm x 5 mm wicks of #20 chromatography paper. Individual Exogone lourei were squashed with a ground glass stopper directly onto the wicks



wetted with seawater. Gels were run inside a refrigeration unit for 3 - 4 hours. Table A4-1 describes the buffer systems and conditions used to assay each species. After migration of enzymes, gels were sliced horizontally into 3 or 4, 1.5 mm sections, substrate was added and gels were immediately stained for activity using stain recipes and handling methods of Selander et al. (1971).

Twenty to 25 individuals were run on each gel. Once migration patterns were interpreted, and distinct loci were identified, data were recorded for each band. Alleles were named as monomorphic, fast or slow migrators at each locus. Relative mobilities were similar from one gel to another.

Intertidal polychaete collections were made in 1979 and 1980 from Mission Bay and from other California bays: P. paucibranchiata from Agua Hedionda, S. benedicti from Tijuana Slough, Morro Bay, Elkhorn Slough and Tomales Bay, F. limnicola from San Quintin Bay in Baja California, and E. lourei from San Diego Bay. Specimens of S. benedicti from Wild Harbor, Massachusetts were obtained in October 1980. Sediments were sieved in the field through a 500  $\mu$  screen at all collection sites (except Wild Harbor). All infauna retained on the screen were returned to the laboratory.

#### Results and Discussion

Table A4-2 lists the enzyme assays tested for activity. Very few systems exhibited the activity required to yield interpretable banding patterns. Some enzymes, such as PGM in Streblospio, were highly active but not consistent and were therefore uninterpretable.

TABLE A4-1  
Electrophoretic Procedures

	Pseudoptidora	Streptospio	Fabricia	Exogone	Buffer System Electrode/Gel	pH	Voltage	Time	Assays	Reference
	x	x	x	x	Tris Maleic EDTA/ 1:10 dilution	7.4	100 mv	4½ hrs	PGI	Selander <u>et. al.</u> , 1971
	x	x	x	PGM						
	x	x	x	MDH						
	x	x	x	EST						
	x		x		Tris Citrate	8.0	100 mv	3½ hrs	IDH	Selander <u>et. al.</u> , 1971
			x	LDH						
			x	x	Tris Versine Borate	8.6	200 mv	4 hrs	PGI	Selander <u>et. al.</u> , 1971
				x					PGM	
		x							EST	
	x	x	x	x	Hodgins LiOH	8.1 +6.7	350 mv	3 hrs	PGI	Hodgins <u>et. al.</u> , 1969
	x	x							EST	

TABLE A4-2  
Enzymes Assayed

- No activity  
x Activity  
+ Bands

Species	<u>Pseudopolydora</u> <u>paucibranchiata</u>	<u>Streblospio</u> <u>benedicti</u>	<u>Exogone</u> <u>loureii</u>	<u>Fabricia</u> <u>limnicola</u>
<u>Enzyme</u>				
PGI	+	+	+	+
PGM	+	+	+	+
MDH	+	+	+	+
IDH	+	x	x	x
XDH	x	x	-	-
ADH	-	x	-	-
LDH	-	-	x	+
α-GPDH	-	-	-	-
6PGDH	-	-	-	-
APH	x	x		
SDH	x	x		
ACPH	-	-		
DDH	-	-	-	-
GlyDH	-	-		x
GOT	x	x	x	x
LAP	x	-	-	-
TPI	x	x		
AO	-	-		
ME	x	-	-	x
MPI	-	-		
HK	x	x		
JOD	-	-	-	-
EST	+	+	x	+
FUM	-	x	-	-
General Protein	-	-	-	-

Table A4-3 presents allozyme frequencies for scorable enzymes of Pacific Coast populations of each species. There was surprisingly little variation in 3 of the 4 polychaete species studied. No allelic variation was seen in Pseudopolydora at 5 loci and only 1 rare allele ( $p = .01$ ) for PGI occurred in the 8 loci examined in Fabricia. Slightly more polymorphism occurs in Streblospio (PGM is polymorphic) but most populations were monomorphic for PGI, MDH and EST. This lack of variability in the 2 spionids and the sabellid contrasts sharply with the high levels of polymorphism observed in other polychaetes. The monomorphic character of PGI is unusual in that 18/20 other polychaete species assayed for this enzyme exhibited multiple alleles. The exceptions were 2 sibling species of Capitella capitata (Grassle and Grassle, 1976).

Only 2 loci, PGI and PGM, could be resolved for Exogone lourei. The small size (< 5 mm) of this worm results in low activity. However, these 2 loci were highly polymorphic and exhibited considerable differentiation between San Diego Bay and Mission Bay. Based on these loci the minimum genetic distance between adjacent Exogone lourei populations was  $D_m = .1908$  ( $p \ll .001$ ). All other species exhibit between-bay distances close to 1.0. Gooch (1975) noted a tendency for monomorphic invertebrate populations to be fixed for the same allele throughout a species' geographic range.

The mobilities of alleles at any particular enzyme locus differed among species, except for the 2 spionids which exhibited identical isozyme mobilities for PGM, MDH1 and EST. Figure A4-1 depicts the relative mobility patterns for each species. The fact that most species do



Figure A4-1: Polychaete banding patterns: starch gel electrophoresis.

*Pseudopolydora paucibranchiata*    *Streblospio benedicti*    *Exogone lourei*    *Fabricia limnicola*

Tris Malaic EDTA				
PGI	-----	-----	-----	-----
PGM	=====	-----	-----	-----
MDH	=====	-----	-----	-----
EST	-----	-----	-----	-----

not share alleles is consistent with the patterns of differentiation seen in other polychaetes.

The life histories of these species confer very limited larval dispersibility. Of the 4 polychaete species studied electrophoretically, only Pseudopolydora seems capable of long distance between-bay dispersal. In the absence of gene flow, geographic differentiation might be expected to occur via drift and selection pressure. This is seen in Exogone, however, the lack of variability in the other species indicates little between-bay divergence of populations and prevents genetic confirmation of suspected isolation.

The lack of variability in Pseudopolydora, Streblospio and Fabricia is surprising. Though relatively few genetic studies have dealt with polychaetes, the 4 families investigated (Spionidae, Glyceriidae, Spirorbidae and Capitellidae) exhibit a high proportion of polymorphic loci, 47% - 100% (Beckwitt, 1980; Grassle and Grassle, 1976; Nicklas and Hoffman, 1979; Rice and Simon, 1980).

Polychaetes appear capable of undergoing extreme genetic differentiation and changes in life histories and reproductive modes while morphological characters are conserved. Grassle and Grassle (1976) found 6 sibling species of Capitella capitata, once thought to be a single species, to have no electrophoretic alleles in common at 8 loci examined. Many of these species coexist at Wild Harbor, Massachusetts and look alike but possess distinct life histories. Later studies have distinguished at least 4 additional sibling species from other locations in the United States (Grassle, 1979). Beckwitt (1979, 1980) has found spirorbids to exhibit electrophoretic differentiation over very small



distances. Spirorbid populations in adjacent tidepools may have very different allele frequencies for some enzyme loci but not others. Sixty percent of all young settle within 20 mm of their parents. In the presence of selection and absence of substantial dispersal, differentiation might be expected to occur. Rice and Simon (1980) observed divergent populations of the spionid Polydora ligni from Florida. One population commonly found on a different substrate varied from the others with a genetic distance corresponding to sibling species.

Electrophoresis provides an exceptional tool for the study of population genetic structure. The inconclusive findings of this study may be the result of an inadequate survey of enzyme systems and a need to fine-tune electrophoretic procedures. Ultra-thin gel techniques could enhance resolution and permit a more complete investigation of polychaete genomes. However, the monomorphic character of enzymes such as PGI, PGM, and Esterases, which are polymorphic in most invertebrate populations, may be a feature associated with genetically isolated populations subject to periodic bottlenecks.