Benthic Ecology of Bahia de San Quintin Baja California

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### ABSTRACT

Barnard, J. Laurens. Benthic Ecology of Bahia de San Quintin, Baja California. Smithsonian Contributions to Zoology, 44:1-60, 1970.—Three important biotic assemblages and several minor associations occur on the soft bottoms of San Quintin Bay. The most obvious assemblage is characterized by the eelgrass, Zostera marina, that covers approximately 20 percent of the study area. A second densely populated assemblage occurs in tidal channels and on their margins and is dominated by a globular ascidian, Eugyra glutinans, and a tube-forming amphipod, Ampelisca compressa. That community merges with a poorly populated Prionospio (polychaete) community occupying sand flats in shallow, quiet water; the two are asymmetrically connected by a facies (or ecotone) characterized especially by two genera of amphipods, Acuminodeutopus and Rudilemboides. A less widespread fourth assemblage, dominated by a polychaete genus Fabricia, occurs primarily adjacent to marshes, especially in the inner reaches of the lagoon. Three phases of the Prionospio community occur, the typical phase and phases dominated by the polychaetes Scoloplos acmeceps and Cossura candida. The Ampelisca-Eugyra community also exists in extreme phases dominated by either of the principal members.

The *Prionospio* community is interpreted as a base community representing a penetration from the open sea of an analogous community in shallow waters on which is imposed the *Zostera* community where suitable banks are elevated above the surrounding flats. The *Zostera* community has few elements in common with the *Phyllospadix* (surfgrass) community of the open sea. The *Eugyra-Ampelisca* community occurs mainly in channels and at the feet of banks where water motion is highest in the bay. The *Eugyra-Ampelisca* community is unique to the literature but has affinities with open-sea *Tellina* communities.

San Quintin has few of the cosmopolitan taxa usually introduced into bays by humans. The warm-temperate lagoons of California and Baja California have few common denominators probably because of changes imposed by man. Very few species in San Quintin are obligatory inhabitants of lagoons.

San Quintin is unusual in being controlled physiographically by cinder cones; the west arm is a typical lagoon, whereas the east arm has characteristics of a drowned river valley.

A hypothetical system of lagoonal maturation and senescence is proposed in which the depositional influences are accelerated by soft-bodied benthic biota.

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# 7. Laurens Barnard

# Benthic Ecology of Bahia de San Quintin Baja California

#### Introduction

The environment and benthic macrofaunal assemblages of Bahía de San Quintín are discussed as a conclusion to a survey conducted in 1960–62. Previous papers include an Introduction by Barnard (1962), Benthic Flora (Dawson, 1962), Physiography and Sediments (Gorsline and Stewart, 1962), Isopoda (Menzies, 1962), Polychaeta (Reish, 1963), Mollusca (Keen, 1962), and Amphipoda (Barnard, 1964). Manuscripts concerning hydrography by Grady, and microbiota by Resig are in preparation.

This study is confined to the eastern, landward arm of San Quintin Bay that has been considered physiographically by Gorsline and Stewart (1962) to represent a drowned estuary. The bay now has the characteristics of a lagoon because of the arid climate. Maps printed herein include only the eastern arm of the bay except Figure 13.

Because the biotope has already been considered by Gorsline and Stewart, the presentation herein proceeds from an identification of the benthic biota to a discussion of the biotope so that facts uncovered in the biological analysis can be discussed in relation to the physical setting. The analytical procedures are described in detail (Appendix IV) as an exercise in simple methodology in hopes of stimulating further exploration of undersea bottom life in American waters. Such exploration has been neglected on level, sedimentary bottoms in the Western Hemisphere, in part because of a paucity of finances available for the large teams of researchers necessary to explore and analyze undersea biotopes and partially because of

the scarcity of expert taxonomists to identify biota. Surveys are likely to continue by utilizing simple tools and methods in the foreseeable future. The crucial focus in these early times is the necessity to describe communities in as consistent framework as possible to conform with the basic literature developed from European studies (Thorson, 1957).

### Field Methods

Water characteristics were studied in 1960 and 1961 in both arms of the bay during 5 seasonal surveys (Figure 15), whereas the bottom biota and sediments were sampled only once, in April 1960. The biotic samples were collected on an even-area grid of 90 stations in the east arm of the bay at a density of about 15 per nautical square mile utilizing an orange peel grab of 0.06 square meter coverage. Samples of sediment were also collected with this device. Gorsline and Stewart (1962) studied San Quintin sediments in terms of mean diameters of particles, but I have recalculated them as median diameters for use herein so as to correspond with procedure generally found in the literature.

The biological samples were filtered through Tyler screens of 0.7 mm mesh, sorted and identified by various specialists. The Polychaeta, Amphipoda, Isopoda, and Mollusca deserved separate reports (see list above and Appendix III). The remaining identifications are tabulated in Appendix II.

# Analytical Methods, Hypotheses, and Terms

A benthic sampling survey provides a means of describing taxonomic components of the fauna and their

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distribution and abundance in relation to their biotopes. A survey also presents the possibility of determining the cooccurrence of two or more species so that biotic associations can be discussed. Whether the terms community, association, biofacies, or assemblage deserve any categorical rank is a subject not considered in this paper because I cannot contribute anything to the problem of whether the whole ocean contains only one community or many and whether a marine community must necessarily have a visible photosynthetic base. The terms community, association, and biofacies are utilized interchangeably herein, but the term assemblage is used arbitrarily to identify a possible community in the early stages of its elaboration by statistical methods. The methods utilized in the discussion do not automatically define the taxal structure of a community nor do they circumscribe the limits of a community. These definitions are matters of judgment based on the degree of relationships among samples, the extent to which groups of samples have discontinuities among themselves, a knowledge of the environment represented by groups of samples, a knowledge of the environment adjacent to the area under study, and an appreciation of the precedents already described in the world literature of marine communities (Thorson, 1957). Other important considerations are the size of the area and the density of individuals represented by groups of samples. These characters have relevance to the matter of defining a group of samples as representative of a community or an ecotone. An ecotone is a region, usually of small extent, between two communities of large extent. In the ecotone, the principal taxa of the adjacent communities may be strongly mixed or there may occur an impoverishment of taxa and individuals of adjoining communities. If communities can be defined, or at least named, for their principal members, these members being the most frequently occurring taxa of reasonably large body size in the samples under consideration, then one finds that the community may occur in phases definable by the occurrence of secondary dominants. This may be visualized more easily by codes; two communities may be identified by their principal taxa, A and X; community A may be relatively homogeneous but community X may have other secondary species (Y and Z) nearly as abundant as X; but Y and Z may be mutually exclusive and form phases of the community; X remains the common denominator, however, and is the main member of the community. In another case community MN may have two principal species that occur together frequently but have phases in which M and N are mutually exclusive. Another community, F, may have two phases, one with F alone as dominant and one with F and G together. In this case and in the Y-Z case, it may be difficult to determine whether the Y, Z, and G phases are really ecotones unless these phases can be shown to occur on boundaries of the area of distribution of communities X and F.

Two precepts of community analysis have been abandoned in this study. The importance of standing crop as a criterion of selection for the major species in a community is considered negligible and the method unworkable. The Peterson rule of grouping samples (or bottom area) if half or more of contiguous samples (or area) have the dominant species present is abandoned in favor of a 100 percent rule. This divides the sample groups more finely. Samples are therefore grouped according to the presence of the most abundant individuals of a taxon, but taxa with high standing crops and low numbers of individuals are not ignored entirely (Table 1). The term "dominant" is accorded to a species with highest frequencies of individuals in a sample. "Subdominant" species represent taxa with secondarily high frequencies of individuals.

A synecological survey of the kind discussed in this paper requires taxonomic analysis of biota found in the samples (90). The data incorporate the names (or codes) and total numbers of specimens of each taxon in each sample and the data are arranged in five decks (Appendix IV). Initial inspection of the data of decks 1 and 2 shows that many samples can be grouped according to the presence of a few species with high numbers of individuals per sample, but most of the species have low numbers of specimens in many samples and high numbers of specimens in a few samples. By arranging the data as in deck 3 (Appendix IV), the chronology of sample numbers is lost, but each species is thereby provided with a list of samples ranked according to the number of specimens in each sample.

A working basis for community analysis is possible on the theory that the most widely distributed species or those with highest frequencies in a few samples may represent the main species of several communities. The next step is to determine whether the main species are more or less mutually exclusive in occurrence (Appendix IV, Method 1 and alternatives A-1-2, and B-1-2). Those species with highest numbers of individuals or most widely distributed (Table 1) or a few of

NUMBER 44

TABLE 1.—Dominant species of Bahia de San Quintin (abundant or large-bodied species utilized for community analyses)

POLYCHAETA Axiothella rubrocincta Brania clavata Capitita ambiseta 46 3,840 83 12 47 Chone mollis 41 516 13 6 10 Cirriformia luxuriosa 16 124 8 3 66 Cossura candida 48 3,669 76 44 60 Exogone verugera 68 10,865 160 19 89 Fabricia limnicola † 27 3,391 126 21 74 Lumbrineris minima 41 351 9 4 7 Megalomma pigmen-um 40 371 9 5 7 Neanthes caudata 46 802 17 6 11 Onuphis microcephala 13 341 26 6 16 Pista alata 34 946 28 10 19 Platynereis bicanaliculata 33 170 7 3 5 Scolpolos anemeceps 64 1,433 22 10 16 Scoloplos ohlini 39 267 7 3 3 5 Scyphoproctus oculatus 18 267 15 6 11 ANPHPODA Acuminodeutopus heteruropus Ampelisca compressa Ampelisca compressa 56 18,923 338 8 173 Amphideutopus oculatus 22 804 37 6 22 Corophium baconi 24 260 11 8 10 Ericthonius brasiliensis 21 5,892 281 82 Hyale frequens 22 2,085 95 50 73 Lembos macromanus 25 828 33 15 24 Listriella melanica 35 199 9 5 7 Microdeutopus schmitti 28 1,049 37 5 21 Orchomene magdalenensis 28 641 23 7 15 Microdeutopus schmitti 28 1,049 37 5 21 Orchomene magdalenensis 28 641 23 7 15 Microdeutopus schmitti 28 1,049 37 5 21 Orchomene magdalenensis 28 641 23 7 15 Microdeutopus schmitti 28 1,049 37 5 21 Orchomene magdalenensis 28 641 23 7 15 Microdeutopus schmitti 28 1,049 37 5 21 Orchomene magdalenensis 28 641 23 7 15 Microdeutopus schmitti 28 1,049 37 5 21 Orchomene magdalenensis 29 267 8 4 4 Microdeutopus schmitti 29 1,494 11 6 9 MoLLUSCA Acutocina carinata 30 267 8 4 6 MoLLUSCA Paranthura elegans 40 12 10,393 866 4 4 435	Name of species	Positive sample (n=90)	Total specimens	Average positive occurrence	Median positive occurrence	Midpoint between average and median	gious fre- quency"*
Axiothella rubrocincta							
Brania clavata	rubrocineta	29	141	5	3	4	9
Capitita ambiseta		9,500					10
Chone mollis		-				X-200	228
Cirriformia luxuriosa		-					14
Cossura candida				-			11
Exogone verugera	No. of the second secon	(2) E					153
Fabricia limnicola † 27 3, 391 126 21 74 Lumbrineris minima 41 331 9 4 7 Megalomma pigmenum 40 371 9 5 7 Neanthes caudata 46 802 17 6 11 Onuphis microcephala 13 341 26 6 6 16 Pista alata 34 946 28 10 19 Platynereis bicanaliculata 23 170 7 3 5 5 Prionospio malmgreni 70 5, 735 82 44 63 Scoloplos acmeceps 64 1, 433 22 10 16 Scoloplos othini 39 267 7 3 3 5 Scyphoproctus oculatus 18 267 15 6 11 Amphideutopus heteruropus 53 2, 185 41 15 28 Ampelisca compressa 56 18, 923 338 8 173 Amphideutopus oculatus 22 804 37 6 22 Corophium baconi 24 260 11 8 10 Elasmopus rapax 16 272 17 15 16 Ericthonius brasiliensis 21 5, 892 281 82 Hyale frequens 22 2, 065 95 50 73 Lembos macromanus 25 828 33 15 24 Listriella melanica 35 319 9 5 7 Lysianassa holmesi 16 1, 457 91 3 47 Microdeutopus schmitti 28 1,049 37 5 21 Orchomene magdalenensis 28 641 23 7 15 Paraphoxus obtusidens 43 850 19 9 14 Pontogeneia quinsana 17 194 11 6 9 Rudilemboides stenopropodus 48 3,040 66 21 44 Uristes entalladurus 19 265 14 2 8 MOLLUSCA Acteocina carinata 32 267 8 4 6 6 Tanandacea				(A. 1.00)		0.00	105
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<sup>\*</sup>Number of specimens in first sample above change in curve, see text.

<sup>†</sup>Including sample zero with 1340 individuals not otherwise included in this report.

the large-bodied species in San Quintin were tested in pairs among themselves and the results presented in Figures 1-3 and 5, according to variations of n in the formula of Method I. In the standard procedure, n is considered as the total number (90) of samples in the survey, but the results are diffuse (Figure 3). By restricting the number of samples considered in the comparison between any two species, the results are sharpened strongly (Figure 2). The restriction is based on the premise that several samples with the highest number of specimens for each of the species have more informational content in the test of association. These samples are termed as those in which the species is contagious, and they are selected from data deck 3 by instructions in data deck 5 (Appendix IV) or alternatively in part 5 of data deck 4. The selection of samples that are contagious for each species is controlled by the hypothesis that the rate of increase of specimens per sample along a straight line connecting the plots of specimens on arithmetic graph paper, from lowest to highest in the sample group, represents an arithmetic progression except at the high end of the plots where the line evolves into a curve. At that point a geometric progression is assumed to commence and this point defines the minimum value of contagion for a species. The minimum value of contagion is generally approximate to a number computed from the halfway point between the mean occurrence of the species per sample and the median (discarding samples in which the species is absent). These data form a part of data deck 4 (Appendix IV) and form the basis on which samples are selected for Method 1, alternative B-2. All of the commonly occurring species in San Quintin Bay, those in 10+ percent of the samples in Table 1, show statistical aggregation in the Poisson series; this aggregation is a main function of at least some of those samples embraced by the curve signifying a geometric progression in the occurrence of a species from sample to sample. For the sake of analogy one might speak of those samples arranged in an arithmetic progression as representative of environments in which the species occurs in background (endemic) frequencies. The samples in the geometric progression might be termed as epidemic or contagious and they may represent environments in which the species occurs in superoptimal densities. So as to find a level of consistency in the foci of communities in San Quintin, the descriptions of the communities have been based largely on samples in which the main species are contagious. The

number of positive samples for each species in San Quintin that are considered as contagious varies between 7 and 12 percent of the positive samples for each species.

The method of selecting contagious samples for each species is probably a workable hypothesis only in a survey in which samples have been taken on a grid system and are thus representative of evenly sized areas which include biotopes outside the range of the species. Once the perimeter of a species has been found in a survey of this kind it would be possible to design a sampling pattern almost wholly within the parts of the biotope in which the species is most highly aggregated.

Once a matrix of C-values in Method 1 is prepared, a judgment of the significance of the values is made by inspection of the data. By trial and error various levels of significance are selected so as to group several species in polygons like those of Figures 1-3. When lower levels of significant C-values are selected more species are joined to the foci. Because of field observations in San Quintin Bay, the significant C-values could be easily selected so as to include in a group those species already known to be restricted to the Zostera community. This level of significance (Figure 1) resulted also in joining together species known to be typical of the Ampelisca-Eugyra assemblage, and it revealed a third assemblage not otherwise observed in the field.

Samples in data deck 1 are rearranged on the basis of Figure 1 to extract any containing the main species in the three assemblages and then further divided into assemblages including only those samples containing the main species in contagious levels. Because only a fraction of the samples in data deck 1 is ordered into assemblages by Method 1 the remaining samples (residuals) are treated by Method 2. The disadvantage of Method 1 is the failure to pinpoint assemblages unless three or more species are involved as the main dominants.

The further determination of assemblages based on Method 2 accounted for only 72 percent of all the samples because decisions as to possible assignment of samples to primary foci could not be made with any consistency.

The next stage of analysis is an attempt to determine if the samples represent a closely knit continuum of taxal occurrences. The method of minimum faunal percentages (MFP, see Method 3 and Sanders, 1960; Barnard, 1964) compares samples by pairs to deter-

mine if both samples of a pair contain specimens of one species. An index is found (Method 3) for all the joint occurrences of species in all pairs of samples and these values are stored in matrices (trellises, like Figure 4) or in a data deck composed of cards on which are entered the pair of sample numbers (conjoint sample) and the index of faunal affinity. The cards are reordered so that a conjoint sample with a high index value is joined by another conjoint sample containing a joint sample number and having the next highest index value. Conjoint samples are thereby clustered so that a master matrix can be formed to give a visual impression of the degree of continuity among samples. Dendrograms can be constructed according to the Mountford method (Method 5, Appendix IV).

The method MFP emphasizes the internal homogeneity of a single sample because the factors in the computed indices are based on the percentage composition of each species in the sample. The method of Morisita-Ono (Method 4, Appendix IV) is an elaboration of correlative methods in which each species in terms of its frequency is independent of the others within a sample. The numbers of specimens of taxa occurring in both members of a pair of samples (conjoint) are the correlative factors, but the vagaries of comparing pairs of samples with low and high specimen frequencies are accounted for in the lambda values. Clusters of samples identified in the data deck of Ch values can be extracted, trellis diagrams constructed of the values, or dendrograms formed by Method 5 so that the results are comparable to the method of MFP.

In the chapter to follow, various incongruities in the dendrogrammatic analysis of faunal indices are discussed. Although the broad outlines of sample clustering are presentable with the dendrogrammatic method and a measure of the distance between contiguous clusters becomes evident, one must also resort to examination of the matrices of faunal indices in order to understand incongruities that result from the 2dimensional restrictions of dendrograms. Sticks and lumps of clay marked with sample numbers are utilized to reorder the dendrogrammatic clusters so that triads, quartets (. . . etc.) of samples can be better visualized. The higher a conjoint value of Cλ or MFP scores, the closer the samples are positioned to each other by pairs. From this experience one develops a visual method of arranging samples in three dimensions by coded cards (Method 6). The relative simplicity of the

San Quintin samples facilitated a view of the broad outlines of sample relationships. To compress this arrangement into two dimensions for publication, a maze-grid is adopted (Figure 11). This method of presentation has advantages as a visual memory device incorporating information on the contiguity of samples plotted as a function of the area each sample includes. Heavy walls between adjacent samples simulate a low joint faunal index, whereas lack of heavy walls indicates high conjoint indices. Windows in heavy walls indicate conjoint indices of medium levels. Several best fits are possible in the arrangement. Letters drawn in various sizes indicate the dominant and subdominant species of each sample (based on frequencies of specimens). Maze lines of Figure 18 indicate the lines of relationship of samples so that ectones can be visualized.

# The Communities

Methods 1-6 (Appendix IV) reveal 10 main foci of assemblages in the San Quintin samples, characterized by the following taxa: (1) Zostera, as represented by various amphipods and a polychaete obligatorily associated with the eelgrass; (2) Ampelisca, Eugyra; (3) Acuminodeutopus, Pista, Rudlilemboides; (4) Prionospio; (5) Fabricia; (6) Kalliapseudes; (7) Scoloplos acmeceps; (8) Cossura; (9) Cirriformia; (10) Exogone.

Three primary groups of species determined from Method 1 represent three areas of high population density in San Quintin: (1) the Zostera-community as indicated by the occurrence of Ericthonius, Capitita, Elasmopus and Platynereis; (2) the channel community with Eugyra and Ampelisca; and (3) the intermediate sandflat zone with Pista, Acuminodeutopus, and Rudilemboides. The first two associations are obvious to the field observer. Subdominant species are also strongly bound to these associations (Figures 1-3). Still other minor associations are apparent but represented by insufficient samples for extended analysis. These are focused on Cirriformia, Scoloplos, Kalliapseudes, and Fabricia. Taxa that are widely dispersed through several communities in contagious numbers are rarely as abundant in the bay as are the primary and even some secondary dominants of the primary communities. Exogone verugera is the most conspicuous exception to this rule.

The unity of the assemblages determined in Method

1 is demonstrated by the low coefficient scores among contagious dominants from one community to another. Only in contagious numbers do the communities show strong internal cohesion, whereas those indices calculated for dominant community species utilizing all samples (n=90) are very low and similar among themselves as shown on the left side of the matrix in Figure 5. Only Eugyra and Ericthonius in Figure 5 show strong exclusion from joint occurrences in noncontagious samples. Although Eugyra and Ampelisca are strongly correlated in those samples in which they are contagious (Figures 1 and 2), they occur together in subcontagious condition very frequently throughout the bay. Neither is strongly dissociated from other species-pairs that are shown to dominate samples when collected in contagious frequencies.

Method 1 fails (1) to pinpoint Prionospio as a basic dominant of the sandflat community or (2) to demonstrate that in reality the Acuminodeutopus-Rudilemboides-Pista association is intercalated between the channel community (Ampelisca-Eugyra) and the full extreme of the sandflat community represented by Prionospio. The latter taxon occurs in all of the communities and is therefore masked from any significant pairing. It occurs in the Zostera-Ericthonius community not as an integral part of the community above root level but in the mud-sand substrate on which the Zostera grows. If the zosteral elements are determined and eliminated from the calculations the Prionospio component shows more clearly in the calculations.

The strong cohesion between the Ampelisca-Eugyra association and the Acuminodeutopus association can be seen in Figure 1 in the number of lines directly connecting the two, whereas most of the lines leading from the Ericthonius-Capitita (=Zostera) association connect only with poorly associated subdominants. The superiority to the method shown in Figure 1 of another simple calculation shown in Figure 2 occurs in the preponderance of lines connecting the Ampelisca-Eugyra association with the Acuminodeutopus-Pista association. Only those samples with species in contagious condition are used in the formula with n=a+b-h. But again, Prionospio, paired only with Cirriformia, is submerged. The weakness of utilizing noncontagious samples (n=90) is shown in Figure 3.

Methods 3 and 4 of correlating species and their frequencies by intersample comparison are superior in relegating samples to clusters that pinpoint associations. The Morisita-Ono correlation method and

Sanders minimal faunal percentage methods have different results. The Morisita-Ono method excels in bonding together samples with similar dominant species, whereas the Sanders method, in accounting for internal homogeneity of a sample, occasionally displaces a sample with extreme monospecific domination to a branch outside the basic community. The dendrogrammatic presentation in either case suffers the defect of segregating certain closely related pairs of samples in favor of others. For instance, samples 78 and 67 in Figure 10 together have a higher index of association than 78 has with any other sample, yet 78 is separated from 67 by three dendrites (samples 35, 48, and 20) and is paired with 65 only at a much lower level than with the others. These are vagaries of statistics in two dimensions on binary cycles.

A pair of dendrograms summarizing 20 samples from the five major assemblages in San Quintin (Figures 9, 10) incorporates a strongly dominated, a weakly dominated, and 2 intermediate samples from each assemblage. The strong cohesion of the Zostera community again demonstrates the usefulness of the simple methods, but there emerges also the previously assumed affinity of the Zostera community to the basic Prionospio community on which it has presumably been superimposed. The Morisita-Ono method (Figure 10) of sample comparison is shown to be superior to that of minimum faunal percentages because it results in sample 78, highly dominated by Ampelisca, being joined with those of its congeners moderately dominated by both Ampelisca and Eugyra. Sample 14, numerically dominated by Prionospio but originally selected as a weak Fabricia sample, is also more properly joined to the Prionospio community in Figure 10. The method of MFP does detect, very ably, the degree of homogeneity of samples, because samples 14 and 78 are highly aberrant and have very low faunal coefficients.

The dendrogrammatic method, as is well known, does present difficulties in leading to erroneous visual impressions as to the affinity of samples. A superior presentation (Figures 11 and 18) results from visually arranging samples in clusters and dendrites in three dimensions by utilizing cards covered with symbols of taxal frequencies (Method 6). Compression of the resulting "tree" in a grid of two-dimensions (Figure 11) then necessitates forming a "maze-grid" (Figure 18) in which samples or groups of samples are separated by walls often penetrated by windows demonstrating

partial affinity between samples. A family of community foci is formed and pathways of affinity demonstrate the spectral character of community interrelationships. The *Acuminodeutopus-Rudilemboides* ecotone is reduced in prominence in favor of other ecotones or community phases of even greater importance in terms of areal distribution.

#### The Problem of Subcommunities

The Zostera community is sharply defined statistically and in physical view, but other communities need further testing to determine their internal cohesiveness and their discreteness from contiguous associations. They are communities with sediments as the only substrate.

Slightly more than half (eight) of those samples previously determined by Barnard (1964) as belonging to an Acuminodeutopus-Rudilemboides association within the amphipodan subcommunities have been allocated to the Ampelisca-Eugyra community in the analysis of all species other than amphipods. A few of the samples (six) have been assigned by previously discussed methods to the Prionospio association and one sample is probably a member of the Zostera association. Most of these samples now assigned to the Prionospio association belong to those zones primarily characterized in frequency by Exogone or Cossura. All of the samples assigned to the Ampelisca-Eugyra community have been connected with the facies in which Ampelisca is predominant. This is of course a function of the artificial procedure of analyzing only Amphipoda, for Ampelisca is an amphipod and dominates numerous samples in which Acumindeutopus and Rudilemboides are just as abundant as they are in those Eugyra samples having low Ampelisca dominance. Utilization of just one order of organisms for indication of community structure turns out to be unsatisfactory. Subdominant organisms may thus form a pattern distinct from dominant organisms and not be bound obligatorily to primary dominants. But the Acuminodeutopus-Rudilemboides association broadly binds Prionospio samples to Ampelisca-Eugyra samples once the strictly Eugyra-dominated samples are ignored (Figures 11 and 18).

The problem is to determine whether the Ampelisca-Eugyra community is linked to the Prionospio association through the facies Acuminodeutopus-Rudilemboides. Thinking in reverse suggests the possibility that Prionospio is the base of the primary lagoon community and that the Eugyra-Ampelisca facies is superimposed on a Prionospio background in response to channelization of lagoon waters. A Prionospio community occupying inshore sands along the coast of California has already been described by Barnard (1963). One might expect the Prionospio community to have penetrated into shallow lagoons but whether the Eugyra-Ampelisca association is an imposition upon that base or a discrete community that merges with Prionospio requires examination.

Prionospio has a poor coefficient of association with other taxa in San Quintin because it is widely dispersed throughout the bay. Its occurrence in the Zostera community is apparently similar to the concurrence of Ampelisca and can be explained by the grab sampler collecting not only eelgrass but surrounding substrate that is not part of the discrete Zostera-Ericthonius assemblage. The frequency of Prionospio in the core of the Eugyra-Ampelisca community (Table 3) is 876 per square meter, but in its restricted association (Table 5) it occurs in a frequency of 3130 per square meter. Prionospio is therefore reduced in frequency in the channel community, the latter not being a simple imposition on a Prionospio base.

A continuum of samples from one extreme to the other can be arranged as in Figure 6. On a basis of percentage of the fauna in each sample, Eugyra and Ampelisca are replaced by increments with Acuminodeutopus-Pista-Rudilemboides and all five taxa further replaced by Prionospio. Fifty samples qualify for inclusion in Figure 6 (but weak Prionospio samples are omitted) with each dominant comprising more than 20 percent of the specimens in the samples. Only seven samples are not clearly dominated by any of the primary members but only three of those seven have an exceptional percentage of the Acuminodeutopus-Pista associates. The other four seen in Figure 6 show clear numerical domination by Prionospio. The Acuminodeutopus-Rudilemboides ecotone is therefore only a weak link to the Prionospio community and is confined primarily and very clearly to the Eugyra-Ampelisca community.

Other tests of the continuum potential in this ecotone between Eugyra-Ampelisca and Prionospio dominated bottoms are presented in Figure 8. These dendrograms are based on MFP and  $C\lambda$  indices and are composed from 15 samples marked with asterisks in Figure 6. The dendrograms are comparable except for sample 64 alternating between the Prionospio and Eugyra den-

drites. Sample 64 is a strong mixture of specimens of Acuminodeutopus (267), Ampelisca (63), Rudilemboides (221), Capitita ambiseta (41), Chone (67), Cossura (22), Exogone (511), Pista (212), Prionospio (330), Scoloplos acmeceps (111), and Eugyra (198); therefore it is a universal sample matching with all other samples moderately well but never pairing strongly with any.

The allotment of Acuminodeutopus-Rudilemboides samples into both dendrites of the Prionospio and Ampelisca assemblages and the relatively low  $C\lambda$  indices indicate the narrow spectral character of the merger between the two assemblages.

### Description of the Communities

Communities of the San Quintin benthos can be described despite the partial continuum among various segments of the environment seen in dendrograms and the maze-grid. Samples are segregated from the clusters seen in the maze-grid (Figure 11) and the communities described by ranking species and listing their frequencies in Tables 2-8. The foci of the communities are based mainly on samples having the main species in contagious frequencies. The Eugyra-Ampelisca community is described as a unit whole in Table 3 but split into its two phases in Table 4. The Prionospio community in its purely dominant form is described in Table 5, while one of its phases characterized by Cossura (Table 6) is described separately. The Exogone-Acuminodeutopus-Rudilemboides ecotone (Table 8) forms a link strongly penetrating the Fabricia community (Table 7), but without Exogone the other dominants are found most prominently as subdominants in the Eugyra-Ampelisca community. The Zostera community is described as a unit (Table 2) and although its sedimentophilous species show considerable variations, the component directly associated with the plant seems to be the least variable and highly specific of any in the bay. The three samples dominated by Kalliapseudes (10, 13, 28) are enigmatical. Various other samples acting as intergrades (18, 49, 50, 73, 84) or several very impoverished samples are omitted or utilized in two places.

Communities are listed in emerging order from the first detected to the least clarified and the samples for each are listed in order from strongest to weakest. Samples in parentheses are very weakly categorized and usually not reported upon in various tables or in the maze-grid. Samples without dominants are 72 and 86.

Figure 15 shows the areal distribution of the communities in the east arm of Bahia de San Quintin.

# The Zostera-Ericthonius-Capitita Community

TABLE 2

Samples.—61, 62, 70, 66, 81, 79, 34, 87, 89, 53, 74, 90, 85, 83, 57.

DISTRIBUTION.—Primarily on banks in the outer third of the bay.

Zostera has not been measured either in frequency or standing crop in this community, but its presence is clearly indicated by the occurrence of various amphipods, Ericthonius brasiliensis, Hyale frequens, Pontogeneia quinsana, Elasmopus antennatus, and by the polychaete Platynereis bicanaliculata. Another polychaete, Capitita ambiseta, is a major dominant but not wholly restricted to this community. Possibly it lives in the substrate and increases enormously in abundance as a response to the presence of Zostera. A major share of the individuals of Armandia bioculata, Modiolus species, and Corophium acherusicum live in this community.

The *Prionospio* community probably forms the substrate on which this epifloral community is superimposed. *Prionospio* is almost as numerous as it is in its own community, *Cossura candida* increases fourfold, although *Scoloplos acmeceps* and *Onuphis microcephala* decrease by half, while ghost-shrimps and transennellid clams are excluded.

The Zostera community is the most highly specific of the assemblages in San Quintin Bay. It has more species fully confined to its margins and thus is most sharply defined by those distributions than any other assemblage. The low internal homogeneity of the community is nevertheless recognizable in Figures 7 and 11.

# The Eugyra-Ampelisca Community

TABLES 3, 4

SAMPLES.—Mixed community: 73, 50, merging with Prionospio 18.

Eugyra phase: 67, 60, 35, 76, 77, 51, 46, 48, 43, 56, 20, 52.

Ampelisca phase: 69, 44, 78, 65, 15, 12, 31, 22.

DISTRIBUTION.—Channels, side channels, feet and slopes of banks, the Ampelisca phase in the deepest

TABLE 2.—Rank and abundance of species in the Zostera-Ericthonius-Capitata community based on samples with the two latter dominants comprising 30+ percent of the specimens: (stations SQ 34, 53, 61, 62, 66, 70, 79, 81, 87, 89)

Rank	Name of species	Individuals per square meter	Percentag total indi viduals o study in th communit
1	Ericthonius brasiliensis	9, 160	97
2	Capitita ambiseta	4, 500	73
3	Hyale frequens	2, 950	88
4	Exogone verugera	2, 050	12
5	Cossura candida	2,000	34
6	Prionospio malmgreni	1, 860	20
7	Lembos macromanus	1, 020	77
8	caprellids	755	30
9	Pista alata	465	31
10	Elasmopus antennatus	360	83
11	Rudilemboides		
	stenopropodus	325	7
12	nebalian	278	21
13	Pontogeneia quinsana	257	86
14	Platynereis bicanaliculata	222	82
15	Ampelisca compressa	216	1
16	Neanthes caudata	211	16
17	Corophium baconi	195	47
18	Orchomene magdalenensis	188	18
19	Listriella melanica	160	31
20	Scoloplos acmeceps	142	6
21	Acuminodeutopus		
	heteruropus	125	4
22	Armandia bioculata	125	64
23	Onuphis microcephala	118	22
24	Corophium acherusicum	112	54
25	nemerteans	101	10
26	Modiolus sp.	83	67
27	holothurians	72	12
28	Lumbrineris minima	72	13
29	Chone mollis	69	8
30	Megalomma pigmentum	58	10
31	Microdeutopus schmitti	53	3

Minor species are listed in sentence order below with individuals per square meter: Amphipholis squamata 38, shrimp 35, Stenothoe valida 32, Ampithoe plumulosa 30, ?Tricolia sp. 29, Ampithoe longimana 27, Nephtys caecoides 27, Pseudokoroga rima 26, Scoloplos ohlini 24, Mitrella carinata 18, enteropneusts 16, Amphideutopus oculatus 14, Aoroides columbiae 14, Eugyra glutinans 13, Erichsonella crenulata 11, flatworm 11, Paraphoxus heterocuspidatus 10, Amphilochus neapolitanus 8, Paracerceis sculpta 8, Axiothella rubrocincta 8, Spiophanes missionensis 8, Oxyurostylis tertia 8, tanaid 8, Paraphoxus bicuspidatus 6, Haliophasma geminata 6, Lumbrineris erecta 6, Nerinides maculata 6, Notomastus magnus 6, Microjassa

parts (6-8 meters) and the *Eugyra* phase generally in depths of 3-5 meters, the evenly mixed samples in extremes of 10 and 3 meters.

Although more than 84 percent of the individuals of both Ampelisca and Eugyra occur in this community the two taxa occur in significant frequencies in the Exogone ecotone, in the Kalliapseudes samples, and in low frequencies in other communities. Lysianassa holmesi, Tellina buttoni, Uristes entalladurus, and Paranthura elegans are obligatory companions of Ampelisca, while Microdeutopus schmitti is confined primarily to the Ampelisca phase of this community. Additional indicators of the mixed community are Amphideutopus oculatus and nebalians, while numerous other species preponderantly belong with this community.

If the *Prionospio* community forms the base on which is superimposed the numerous dominant and characteristic species of the *Eugyra-Ampelisca* community, it is indicated by the presence of *Cossura candida* and *Scoloplos acmeceps* in undiminished numbers but *Prionospio malmgreni* is reduced to a third of its frequency in its own community. Significant numbers of *Capitita ambiseta*, a characteristic member of the *Zostera* community, also occur in the channels.

# The Prionospio Community

TABLE 5

Samples.—14, 16, 19, 29, 47, 71, 17, 49, 58, 36, 23, 37, 11, 21, (8), merging with Eugyra-Ampelisca 18, Exogone-Eugyra 64, and Exogone-Cossura 38.

DISTRIBUTION.—Widespread throughout the inner two thirds of the bay on sand flats in depths not favored by Zostera.

Prionospio malmgreni is generally three times more abundant than it is in any other community except that of Zostera; Cossura candida and Scoloplos acmeceps are the second and third dominants; either species also forms the dominant of a phase of this community. Onuphis microcephala is prominent, the mollusk

macrocoxa 5, Munna ubiquita 5, Acmaea depicta 5, Arenicola cristata 5, cumacean 5, crab 5, Ciliacea sp. 5, Listriella diffusa 3, Goniada littorea 3, Hypoeulalia bilineata 3, Monoculodes hartmanae 2, Paraphoxus obtusidens 2, Aequipecten c. aequisulcatus 2, Leptopecten latiauratus 2, nudibranch 2, Brania clavata 2, Chrysopetalum occidentale 2, Cirriformia luxuriosa 2, Dorvillea articulata 2, Glycera americana 2, Lepidonotus caelorus 2, Ophiodromus pugettensis 2, Polyophthalmus pictus 2, Scyphoproctus oculatus 2, Cumella sp. 2, isopod 2.

TABLE 3.—Rank and abundance of species in the Eugyra-Ampelisca channel community, based on samples with primary dominants comprising 20+ percent of the specimens: (SQ 12, 15, 18, 35, 44, 46, 48, 51, 60, 65, 67, 69, 73, 76, 77, 78)

Rank	Name of species	Individuals per square meter	Percentage of total indi- viduals of study in this community
1	Ampelisca compressa	15, 966	84
2	Eugyra glutinans	6, 550	91
3	Rudilemboides		
	stenopropodus	1, 990	65
4	Lysianassa holmesi	1, 449	99
5	Acuminodeutopus		
	heteruropus	1,000	46
6	Microdeutopus schmitti	898	86
7	Prionospio malmgreni	876	15
8	Amphideutopus oculatus	737	92
9	Capitita ambiseta	727	19
10	nebalian	641	77
11	Paraphoxus obtusidens	522	61
12	caprellids	506	32
13	Cossura candida	378	10
14	Scoloplos acmeceps	365	25
15	Oxyurostylis tertia	246	72
16	Uristes entalladurus	259	98
17	nemerteans	229	38
18	Pista alata	227	24
19	holothurians	217	59
20	Orchomene magdalenensis	211	33
21	Neanthes caudata	184	23
22	Scyphoproctus oculatus	166	62
23	Chone mollis	159	31
24	Fabricia limnicola	152	4
25	Exogone verugera	146	1.
26	Megalomma pigmentum	133	36
27	Lumbrineris minima	118	34
28	Paranthura elegans	111	84
29	Corophium baconi	107	41
30	Kalliapseudes crassus	101	1
31	Acteocina carinata	88	32
32	Lembos macromanus	83	10
33	Paraphoxus heterocuspidatus	82	58
34	Haploscoloplos elongatus	76	86
35	Axiothella rubrocincta	74	52
36	Tellina buttoni	73	84
37	Brania clavata	60	26

Minor species are listed in sentence order below with individuals per square meter. Listriella melanica 57, Lyonsia californica 53, Transennella tantilla 50, Nerinides maculata 46, Armandia bioculata 44, Corophium acherusicum 39, Pseudokoroga rima 38, Paraphoxus bicuspidatus 38, OxyuTransennella tantilla characteristic, and ghost-shrimps Callianassa species construct their major beds in this community.

# The Cossura Phase of the Prionospio Community Table 6

SAMPLES.—26, 32, 41, 9, 24, 39, 45, 27, merging with a mixed sample 54 (Eugyra-Fabricia), and Exogone-Prionospio 38, and Prionospio-Eugyra 64.

DISTRIBUTION.—At the margins of the *Prionospio* community primarily in the middle third of the bay, not occurring in the outer third.

This ecotone links the *Prionospio* community with the *Exogone* samples. *Cossura candida* is the most numerous and clearly dominant species. *Prionospio malmgreni* is the secondary dominant and *Exogone verugera* is the third most abundant species. The only phoronids collected in the bay occur in this zone, and *Cirriformia luxuriosa* is a prominent subdominant.

## The Scoloplos Phase of the Prionospio Community

Samples.—63, 88, 40, 84, (59), (68).

DISTRIBUTION.—Generally inshore, near marshes on the east side of the outer bay.

These samples, averaging 12 species each, are very impoverished. Only 5 species are of any importance: Scolopos acmeceps 812, Acteocina carinata 96, Nerinides maculata 84, Megalomma pigmentum 64, and Exogene verugera 32 individuals per square meter.

rostylis pacifica 35, tanaids 32, Nephtys caecoides 28, enteropneusts 25, Scoloplos ohlini 25, Modiolus sp. 21, flatworm 20, Ampithoe plumulosa 19, Amphipholis squamata 17, nudibranchs 12, Cirriformia luxuriosa 12, Platynereis bicanaliculata 12, Hippomedon denticulatus 11, Microjassa macrocoxa 11, Haliophasma geminata 9, Haminoea sp. 8, Spiophanes missionensis 8, Monoculodes hartmanae 7, Anaitides multiseriata 6, Metaphoxus fultoni 5, Polydora uncata 5, Cumella sp. 5, Heterophoxus oculatus 4, Hyale frequens 4, Goniada littorea 4, Macoma yoldiformis 3, Solen rosaceus 3, Anaitides williamsi 3, Glycera americana 3, Lepidonotus caelorus 3, shrimp 3, Serolis carinata 2, Parvilucina tenuisculpta 2, Trachycardium quadragenarium 2, Eteone dilatae 2, Pherusa capulata 2, Typosyllis variegata 2, Callianassa sp. 2, Corophium uenoi 1, Cooperella subdiaphana 1, Mitrella carinata 1, Eteone pacifica 1, Lumbrineris erecta 1, Polyophthalmus pictus 1, Trypanosyllis gemmipara 1, Oxyurostylis sp. 1, Odostomia fetella 1, cumacean 1.

Table 4.—Rank and abundance of dominant species in extreme phases of the Ampelisca-Eugyra community

		Individuals per	r square meter
Rank	Name of species	Ampelisca phase Samples 12, 15, 44, 65, 69, 78	Eugyra phase Samples 35, 51 60, 67, 76, 77
1	Ampelisca compressa	41, 200	470
2	Eugyra glutinans	6, 700	9, 470
3	Rudilemboides stenopropodus	2, 975	2, 220
4	Lysianassa holmesi	3, 680	165
5	Microdeutopus schmitti	2, 060	328
6	Acuminodeutopus heteruropus	1, 030	1, 486
7	Capitita ambiseta	878	1, 057
8	Prionospio malmgreni	646	1, 342
9	nebalian	1, 675	35
10	Amphideutopus oculatus	1, 167	972
11	Paraphoxus obtusidens	935	302
12	Scoloplos acmeceps	224	670
13	caprellids	300	1, 017
14	Cossura candida	123	683
15	Uristes entalladurus	1, 160	37
16	nemerteans	189	376
17	Oxyurostylis tertia	149	248
18	Orchomene magdalenensis	472	37
19	Pista alata	294	300
20	Neanthes caudata	75	412
21	holothurians	235	215
22	Scyphoproctus oculatus	350	94
23	Chone mollis	182	189

# The Fabricia Community

## TABLE 7

SAMPLES.—6, 3, 42, 55, 91, 33, 1, 2, merging with *Exogone* 5, 4, 7.

DISTRIBUTION.—Dominating fine silt sediments of the inner bay bordered by marsh and in widely scattered inshore localities of the outer bay adjacent to marshes.

The most numerous organism of this community is Exogone verugera, but it is a small bodied polychaete not dominating the standing crop. Fabricia limnicola, the second most frequent, dominates the standing crop. Over 80 percent of the individuals of Fabricia occur in this community. The most highly characteristic species are chironimid larvae (100 percent), the amphipod Corophium uenoi (99 percent), and tanaids other than Kalliapseudes (88 percent). Polydora uncata,

Acteocina carinata. Scolopos ohlini, and Acuminodeutopus heteruropus are conspicuous subdominants.

# The Kalliapseudes samples

Samples.—28, 13, 10.

DISTRIBUTION.—In deep channels of the middle bay or in shallow channels of the inner bay but deepest of their areas.

The dominant individuals per square meter of these samples are: Kalliapseudes crassus (54,800), Exogone verugera (25,000), Ampelisca compressa (12,860), Orchomene magdalenensis (1,569), Typosyllis variegata (747), Metaphoxus fultoni (577), Listriella melanica (416), Heterophoxus oculatus (315), Cirolana diminuta (277), and Scyphoproctus oculatus (277).

At its peak of abundance, Kalliapseudes has a standing numerical frequency of 140,000 individuals per

TABLE 5.—Rank and abundance of species in samples clearly dominated by Prionospio malmgreni: SQ 11, 14, 16, 17, 19, 21, 23, 29, 36, 37, 47, 58, 71

1 2 3 4 5			meter	of study in this community
3 4 5	Prionospio malmgreni	2, 541	3, 130	44
<b>4</b> 5	Cossura candida	448	550	12
5	Scoloplos acmeceps	222	273	16
	Onuphis microcephala	186	229	55
6	Acuminodeutopus heteruropus	88	108	4
	Capitella capitata	87	107	37
7	Callianassa species	74	91	89
8	Exogone verugera	70	86	negl
9	Neanthes caudata	68	84	
10	Paraphoxus obtusidens	60	74	-3
11	Transennella tantilla	50	62	50
12	nemerteans	42	52	
13	Fabricia limnicola	37	45	1
14	holothurians	36	44 39	10
15	enteropneusts	32 28	3 <del>9</del>	10
16	Scoloplos ohlini Rudilemboides stenopropodus	26 27	33	•
17 18	Cirriformia luxuriosa	24	29	19
18	Brania clavata	23	28	i
20	Pista alata	22	27	
21	caprellids	19	23	•
22	Oxyurostylis tertia	19	23	
23	Polydora uncata	19	23	
24	Listriella melanica	19	23	
25	Ampelisca compressa	17	21	
26	Megalomma pigmentun	16	20	
27	Heterophoxus oculatus	16	20	
28	Nerinides maculata	13	16	
29	Eugyra glutinans	12	15	
30	Paraphoxus heterocuspidatus	11	14	
31	Capitita ambiseta	11	14	
32	Chone mollis	10	12	
33	Lumbrineris minima	9	11	
34	Marphysa sanguinea	9	11	
35	Acteocina carinata	7	9	
36	Axiothella rubrocincta	7	9	
37	Microdeutopus schmitti	5	6	
38	Solen rosaceus	5	6	
39	Ericthonius brasiliensis	3	4	
40	Hyale frequens	3	4	
41	Listriella diffusa	3	4	
42	nudibranchs	3	4	
43	Arabella iricolor	3	4	
44	Scyphoproctus oculatus	3	4	
45	Oxyurostylis pacifica	3	4	
46	Eteone pacifica	2	2	
47	Notomastus magnus	2	2	
48 49	Amphideutopus oculatus	1	1	
50	Corophium uenoi Hippomedon denticulatus	1	1	

TABLE 5.—Rank and	abundance of	f species in	samples clearly	dominated by Prionospio
malmgreni: SQ 11	, 14, 16, 17,	19, 21, 23,	29, 36, 37, 47	7, 58, 71—Continued

Rank	Name of species	Total	Individuals per square meter	Percentage total individuals of study in this community
51	Monoculodes hartmanae	1	1	
52	Pontogeneia quinsana	1	1	
53	Uristes entalladurus	1	1	
54	Cumella species	1	1	
55	Amphipholis squamata	1	1	

square meter. Species obligatorily bound to, or charasteristic of these samples are, Kalliapseudes crassus (100 percent), Typosyllis variegata (100), Metaphoxus fultoni (88), Cirolana diminuta (100), and Heterophoxus oculatus (70).

# The Exogone-Acuminodeutopus-Rudilemboides Ecotones

#### TABLE 8

SAMPLES.—80, 25, (30), (7), (75), merging with Fabricia 5, with Eugyra-Prionospio 64, and with Prionospio-Cossura 38.

The miscellaneous samples, with mixed dominants having Exogone as a prominent numerical member comprise various strong intergrades among all the communities except Zostera. Even sample 25 has the barest indication of proximity to a Zostera bed, with an occurrence of individuals of Elasmopus, Ericthonius, and Hyale. Sample 25 is near the abandoned pier and has the majority of specimens of Capitella capitata occurring in the bay, thus indicating some history of pollution, artificial or natural, possibly from debris generated by fouling organisms on the pilings. Sample 5 is also assigned to the Fabricia community of the upper bay; the other samples are adjacent to shore, 80 near a marsh and the Fabricia zone, 38, 64, and 30 on the midwestern shore. Sample 64 is so strongly dominated by Eugyra glutinans and Prionospio malmgreni that I have assigned it to the former community also. Exogone is a poor indicator of its own ecotone for the species is widely distributed through other communities; only when extremely abundant or occurring as the superior numerical dominant does it indicate either a speciesimpoverished area or a mixed sample.

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## Relationship of Communities to Sediments

The range of sedimentary median diameters of San Quintin samples, in which community dominants have been identified, is extreme. The central tendencies of the sample-groups are determined as median points of the median diameters (Table 9) rather than averages, because of extreme skewing that results from averaging these data. There are significant differences in these median points between the Fabricia and the Eugyra-Ampelisca communities. They show that the Fabricia community occupies silts of very fine texture adjacent to marshes, whereas the Eugyra-Ampelisca community occupies medium and fine sands of the channels (Figures 13, 14). Prionospio samples have a median point in the coarse silt range and Zostera in fine sand.

The fact that the six most important Fabricia samples occur on fine silts of approximately 9 microns median diameter indicates the possibility that the other three samples occurring on sands of approximately 130 microns median diameter represented a surface veneer of fine silt on top of medium sand and that the sampling device bit into the subsurface sand resulting in a mixed sample. If this occurred in one community it may have occurred in others even though such mixing appeared to be very low during field operations. The sedimentary data are thus potentially poor but a relationship of dominant taxa occurs to median diameters and percent sand (Figure 12).

# Relationship of the Lagoonal Community to the Open Sea

Open-sea benthic communities of the eastern Pacific Ocean are poorly known. Those described from the semiarid coast of California, 300 miles north of San

TABLE 6.—Rank and abundance of species in Cossura phase of Prionospio association: SQ 9, 24, 26, 27, 32, 39, 41, 45

Rank	Name of species	Total	Individuals per squre metear	Percentage total individual: of study in this community
1	Cossura candida	1, 075	2, 150	29
2	Prionospio malmgreni	463	926	8
3	Exogone verugera	110	220	1.
4	Acuminodeutopus heteruropus	82	164	4
5	Cirriformia luxuriosa	74	148	60
6	Capitita ambiseta	65	130	2
7	Scoloplos acmeceps	64	128	4
8	Megalomma pigmentum	48	96	13
9	Chone mollis	47	94	9
10	Lumbrineris minima	45	90	13
11	Neanthes caudata	40	80	5
12	Rudilemboides stenopropodus	33	66	1
13	nemerteans	32	64	5
14	Pista alata	30	60	3
15	Brania clavata	27	54	12
16	enteropneusts	23	46	5
17	holothurians	22	44	6
18	Scoloplos ohlini	22	44	8
19	phoronids	21	42	100
20	caprellids	18	36	1
21	Scyphoproctus oculatus	13	26	5
22	Ampelisca compressa	9	18	· ·
23	Listriella melanica	6	12	
24	Nephtys caecoides	6	12	
25	Paraphoxus obtusidens	4	8	
26	Amphilochus neapolitanus	3	6	
27	Heterophoxus oculatus	3	6	
28	Oxyurostylis tertia	3	6	
29	Amphideutopus oculatus	2	4	
30	Microdeutopus schmitti	2	4	
31	Nerinides maculata	2	4	
32	Notomastus magnus	2	4	
33	Kalliapseudes crassus	2	4	
34	Callianassa spp.	2	4	
35	Ericthonius brasiliensis	_		
36	Listriella diffusa	1	2 2	
37	Orchomene madgalenensis	1	2	
38	Paraphoxus bicuspidatus	1	2	
39	Paraphoxus heterocuspidatus		2	
40	Paranthura elegans	1	2	
41	Serolis carinata	1		
42	Tellina buttoni	1	2	
43	nudibranch	1	2	
44	Eteone dilatae	1	2	
45		1	2	
46	Glycera americana	1	2	
47	Polydera uncata Cumella species	1	2 2	

TABLE 7.—Rank and abundance of species in samples assigned to the Fabricia zone: SQ 1, 2, 3, 4, 5, 6, 33, 42, 55, 91

Rank	Name of species	Individuals per square meter	Percentage total indi- viduals of study in this community
1	Exogone verugera	3, 030	17
2	Fabricia limnicola	2, 715	82
3	tanaids	1, 190	88
4	Corophium uenoi	681	99
5	Acuminodeutopus heteruropus	392	11
6	caprellids	350	14
7	Prionospio malmgreni	278	3
8	Scoloplos ohlini	185	44
9	Acteocina carinata	168	39
10	insect larvae	133	100
11	Scoloplos acmeceps	96	4
12	Polydora uncata	90	62
13	Rudilemboides stenopropodus.	85	2
14	Neanthes caudata	66	5
15	Ampelisca compressa	51	0
16	Brania clavata	51	14
17	nemerteans	35	4
18	Pontogeneia quinsana	35	11
19	Oxyurostylis tertia	34	6
20	Oxyurostylis pacifica	27	38
21	Paraphoxus obtusidens	22	2

Minor species are listed in sentence order below with individuals per square meter: Paraphoxus heterocuspidatus 18, Ampithoe pollex 16, Corophium baconi 16, Nerinides maculata 16, Paranthura elegans 16, Hyale frequens 14, Cossura candida 11, Eugyra glutinans 11, Corophium acherusicum 11, Ampithoe plumulosa 8, enteropneust 6, Lembos macromanus 5, Chone mollis 5, Axiothella rubrocincta 3, Eteone pacifica 3, Megalomma pigmentum 3, Scyphoproctus oculatus 3, Capitita ambiseta 2, Platynereis bicanaliculata 2, Callianassa sp. 2, Paraphoxus bicuspidatus 2, stenothoid 2, Uristes entalladurus 2, nudibranch 2, Amphideutopus oculatus 2, Heterophoxus oculatus 2, Listriella melanica 2.

Quintin, have been primarily conspicuous soft-bottom assemblages (Barnard and Hartman, 1959; Barnard and Ziesenhenne, 1961; Barnard, 1963). The latter paper is pertinent to this discussion because it describes benthic assemblages on shallow-water open-sea bottoms. In depths of about 10 to 30 meters, outside the surf zone on sand and fine-sand bottoms, the biota is dominated by the clam *Tellina buttoni* and the polychaete *Nothria elegans*. This megacommunity is com-

posed of two extremes dominated primarily by Tellina on fine sediments and Nothria on coarse sediments with intermediate sediments dominated by both species together. Shallow sands in depths of 4-10 meters, on the inshore margin of the 10-30 meter coastal strip, are dominated by the small polychaete Prionospio malmgreni. This animal also occurs in the Tellina-Nothria community facies, but in the 4-10 meter zone it overwhelmingly dominates the fauna. It is 4 to 13 times more abundant in the 4-10 meter zone than in the 10-30 meter zone. In the Prionospio zone, Tellina occurs sparsely, 6 to 18 times less abundant than in the 10-30 meter zone. Nothria elegans is completely absent from the Prionospio zone. Barnard (1963) thus considers the Prionospio zone as an orthodox softbottom community.

In Bahia de San Quintin the so-called Prionospio community is a "background" community on which, perhaps, are superimposed the more diversified eelgrass and channel assemblages. The lagoonal community may be compared cursorily to the open-sea community (Table 10) and in greater detail to the lists published in a limited distribution report by Hartman, Barnard, and Jones (1960). The two representations of the Prionospio community, open sea and lagoonal, differ considerably. Of the 14 most abundant species in the open-sea assemblage, only 6 occur in San Quintin and only one of those, Prionospio malmgreni, is among the 14 most frequently occurring San Quintin species. Fifty-four species of animals have been collected in the San Quintin assemblage, of which 47 have been named. Only 11 of those species also occur among the 225+ species found by Hartman, Barnard, and Jones in the open-sea assemblage. This scant comparability casts doubt on the nomenclatural usefulness of designating communities by the names of their dominant (standing crop) species, for these two assemblages of Prionospio-dominated fauna have little in common. The six most abundant San Quintin species, however, occur in the open sea or have generic counterparts there.

Hartman, Barnard, and Jones (1961) list 13 species of polychaetes as characteristic indicators of inshore sands of southern California; none of these occurs in Bahia de San Quintin. *Prionospio malmgreni* is not on the list, of course, because it occurs in environments other than inshore sands.

The frequency of individuals in the San Quintin Prionospio community is nearly twice that in the open

TABLE 8.—Rank and abundance of species in the Exogone ecotone: SQ 5, 25, 38, 64, 80

Rank	Name of species	Total	Individuals per square meter	Percentage total individuals of study in this community
1	Exogone verugera	2, 538	8, 110	25
2	Prionospio malmgreni	800	2, 560	14
3	tanaids	6 <del>4</del> 5	2,060	75
4	Acuminodeutopus heteruropus	467	1, 495	21
5	Rudilemboides stenopropodus	322	1,030	11
6	Pista alata	334	1, 068	35
7	caprellids	246	787	16
8	Eugyra glutinans	237	759	3
9	Scoloplos acmeceps	227	726	16
10	Ampelisca compressa	166	537	1
11	Chone mollis	164	525	32
12	Cossura candida	149	477	4
13	Capitella capitata	140	448	60
14	Neanthes caudata	110	352	14
15	Capitita ambiseta	63	202	2
16	nemerteans	54	173	9
17	Microdeutopus schmitti	51	163	5
70.75		45	144	12
18	Megalomma pigmentum		138	19
19	Brania clavata	43		E.150
20	Listriella melanica	42	134	13
21	Oxyurostylis tertia	41	131	12
22	Lumbrineris minima	32	102	9
23	enteropneusts	34	109	7
24	Paraphoxus obtusidens	35	112	4
25	Amphideutopus oculatus	21	67	3
26	nudibranchs	18	58	35
27	insect larvae	15	48	
28	Cumella species	11	35	73
29	Amphipholis squamata	10	32	
30	flatworm	10	32	
31	Paranthura elegans	9	29	
32	Lyonsia californica	9	29	
33	Cirriformia luxuriosa	9	29	
34	Fabricia limnicola	9	29	
35	Ampithoe plumulosa	8	26	
36	Monoculodes hartmanae	8	26	
37	Paraphoxus heterocuspidatus	8	26	
38	Elasmopus antennatus	7	22	
39	Ampithoe pollex	6	19	
40		6	19	
41	Acteocina carinata	6	19	
42		6	19	
43		6	19	
44	The state of the s	6	19	
45		2	6	
46		2	6	
47				
48		2	6	
49		2	6	
	Oxyurostylis pacifica	2	6	
50		2	6	

TABLE 8.—Rank and abundance of species in the Exogone ecotone: SQ 5, 25, 38, 64, 80—Continued

Rank	Name of species	Total	Individuals per square meter	Percentage total individuals of study in this community
52	Hippomedon denticulatus	1	3	
53	Paraphoxus bicuspidatus	1	3	
54	Uristes entalladurus	1	3	
55	Serolis carinata	1	3	
56	Modiolus species	1	3	
57	Solen rosaceus	1	3	
5 <b>8</b>	Arabella iricolor	1	3	
59	Axiothella rubrocincta	1	3	
60	Polydora punctata	1	3	
61	Kalliapseudes crassus	1	3	
62	Callianassa species	1	3	

sea. Only 2 of the 47 identified species occur in this San Quintin community more than 50 percent of the time, one of them having 73 percent and the other 54 percent of their lagoonal individuals confined to the community.

The Eugyra-Ampelisca community of channels and their margins is dominated by a pan-American amphipod from open-sea depths of 2–200 meters and a tunicate known heretofore primarily from subarctic regions but also known to occur sporadically as far south as Magdalena Bay (to the south of San Quintin). The maximum density of Ampelisca compressa in the open sea is 27 individuals per square meter in depths of 10–20 meters (average over scores of square miles). In San Quintin the species is 500 times more abundant in the channel community than in the open sea.

No community comparable to the Eugyra-Ampelisca assemblage has been reported from the open sea, and

TABLE 9.—Sedimentary characteristics in communities of Bahia de San Quintin (data quoted as median diameters in microns)

Community	Number of samples	Range of median diameters	Median of median diameters
Fabricia	9	8-145	10
Prionospio	22	22-135	47
Zostera	13	50-155	71
Ampelisca	21	50-175	87

it may be unique to lagoons having tidal rushes largely confined to channels. Ten of the 80+ identified species in the assemblage are more than 50 percent confined to the community; indeed, five of them have 85 percent or more of their individuals confined to this community. Lysianassa holmesi, with 99 percent of its individuals in the Ampelisca-Eugyra community is found

TABLE 10.—Most abundant animal species on inshore sandy bottoms of southern California, by rank and abundance (species also occurring in Bahia de San Quintin marked with asterisks)

Rank	Name of species	Individuals per square meter
1	*Prionospio malmgreni P	930
2	Diastylopsis tenuis C	101
3	*Goniada littorea P	69
4	*Tellina buttoni M	65
5	Paraphoxus epistomus C	55
6	*Nephtys caecoides P	53
7	Chaetozone nr. spinosa P	40
8	Olivella species (including boetica) M	32
9	Mandibulophoxus uncirostratus C	31
10	*Haploscoloplos elongatus P	31
11	Dendraster species, juveniles E	27
12	*Paraphoxus bicuspidatus C	25
13	Photis lacia C	25
14	Scoloplos armiger P	24

P = polychaete; C = crustacean; M = mollusk; E = echinoderm.

in the open sea in depths of about 10 to more than 200 meters, with maximum concentration of 11 individuals per square meter in a depth class of 75–92 meters.

Several open-sea Tellina communities have been described in various parts of the world (Thorson, 1957). Apparently, the Prionospio community has little connection to those Tellina communities, for in southern California, even though Tellina occurs in the Prionospio community, its abundance is reduced to less than 10 percent of that found in the Tellina-Nothria community and in San Quintin Tellina is apparently absent from the Prionospio community. On the other hand, Tellina is strongly linked to the Eugyra-Ampelisca community, for 100 percent of the Tellina-contagious samples and 85 percent of all individuals collected in San Quintin occur in that zone. In abundance, Tellina ranks only 34th in the Eugyra-Ampelisca community, although its relatively large body size brings it to high rank in standing crop values (probably within the top 7, weights not taken). The abundance of Tellina in the Ampelisca-Eugyra zone is only 15-30 percent of that found in the Tellina-Nothria community of the open sea. The occurrence of Tellina in San Quintin suggests that the Eugyra-Ampelisca community may be an ecological equivalent to, or have a close relationship with, the open-sea Tellina communities.

### Interrelationships of Warm-Temperate Lagoons

Polychaeta, like Amphipoda, have a low proportion of common denominators in the estuaries and lagoons of California and Baja California (Reish, 1959, 1963, Reish and Barnard, 1967) presumably because of latitudinal (thermal) differences, varying amounts of runoff and alterations by mankind. San Quintin shows strongest relationship to Newport Bay but several dominant members of the San Quintin fauna have not been recorded there (among polychaetes are Exogone verugera, Onuphis microcephala, Scoloplos acmeceps, and Prionospio malmgreni). San Quintin seems to have a stronger affinity with the open sea in this sense than does Newport Bay. A few common species in coastal estuaries and lagoons from San Francisco Bay or Morro Bay south to San Quintin among polychaetes, for example, are Anaitides williamsi, Platynereis bicanaliculata, Stauronereis articulata, Haploscoloplos pugettensis, Spiophanes missionensis, Armandia bioculata, Capitella capitata, and Axiothella rubrocincta, but few of these are important dominants of lagoons. Only 9 of the 13 most important species of San Quintin occur in Newport Bay and only 6 of the 13 occur abundantly in the sublittoral of the open sea (as computed from Hartman, 1966) of southern California. San Quintin has more of the abundant Californian bay species than any other lagoon studied (18 of 21, see Reish, 1963) and has four important species not in other lagoons, thus lacking only Tharyx parvus and Nereis procera, the two indicators of healthy bottoms in Los Angeles Harbor (Reish, 1959).

# Comparability of Eelgrass Community to the *Phyllospadix* Community of the Open-Sea Intertidal

The Zostera community is, to a large extent, a superimposition of a secondary substrate (the plant) upon a primary sedimentary substrate. One might presume that without the plant the substrate community would resemble that of the Prionospio community because many of the prionospionid members occur in the sediments on which the eelgrass grows. Those Prionospio bottoms lacking eelgrass, however, must differ environmentally from those on which it does occur and one would expect that the presence of eelgrass signals the presence of organisms that would not occur on noneelgrass bottoms. This naturally applies to those animals occurring only on the living plant as well as some normally occurring in the sediments and even others that immigrate into climax Zostera communities because of (e.g.) the accumulation of waste products.

Figure 17 has been prepared in order to sort out immigrant zosteral taxa. The major species of the communities are arranged on either side of a base line (0) and added cumulatively according to their frequency of individuals per square meter in the community. This gives an impression of the relative density of organisms in each community and of which species the assemblages are composed. The Prionospio community is the second most impoverished of the five and placed near the middle as a base community. Those species characteristic of the Ampelisca community are included above the base line, those of the Zostera community below. Only five major species besides Zostera are absolutely characteristic of the eelgrass community, those of the genera: Platynereis, Pontogeneia, Elasmopus, Hyale, and Ericthonius, all presumed to be oriented to the plant directly and not necessarily to the original sedimentary substrate nor to the substrate altered by the presence of Zostera. Capitita ambiseta is partially characteristic of the Zostera community but also occurs in diminished numbers in the Eugyra-Ampelisca community and of all major lagoonal species appears to be the only one strongly influenced by the development of organic oozes in the channels and the eelgrass flats. The same may be true of Fabricia limnicola on the bay margins near the marsh flats, of the Scoloplos samples also near the bay margins, and of the ubiquitous pollution indicator Capitella capitata.

In the open sea a community comparable to that of Zostera is the Phyllospadix zone of the lower intertidal. Both taxa are flowering plants and have a similar appearance. Phyllospadix, however, is a surfgrass occurring in the heaviest zones of wave-dash. Unfortunately, the Californian Phyllospadix zone has not been well studied; the fauna included in that zone is adequately reported only by Hewatt (1946) and only from the offshore Channel Islands, which undoubtedly are biotopically distinct from continental shallows. Barnard (1969) has reported upon the amphipodan constituents of Phyllospadix zones from seven localities. One of these, at Jolla, is compared in Table 11 with the inhabitants of the Zostera community of San Quintin. Only 8 of the 24 important open-sea species occur in San Quintin and only one of these, Hyale rubra frequens, has rank equivalent to its open-sea frequency. San Quintin species (of the 8) are either much less or much more frequent in occurrence than in the open sea. The open sea and lagoonal counterparts of marine grasses thus have a fauna about as incongruous as the open sea and lagoonal members of the Prionospio fauna; the biotopes of the grasses, however, are more strongly distinct than are the Prionospio and sublittoral benthic zones because of the contrast between surf dash and quiet water. Presumably the faunal members other than Amphipoda differ from open-sea to lagoonal environments as much as do Amphipoda. Only one of the eight species of San Quintin is known to be near its northern limit at La Jolla and therefore it has a strongly different frequency in the open sea than in lagoons because of zoogeographic reasons. That species is Pontogeneia quinsana.

#### The Calm-Water Element

The bay-restricted, calm-water element in amphipodan faunas of the Californias is poorly represented in Bahia de San Quintin. Barnard (1961) identified six species

TABLE 11.—Important Amphipoda of the open-sea Phyllospadix zone and the lagoonal Zostera community (data from La Jolla, California, after Barnard, 1969)

	Individuals per square meter				
Name of species	La Jolla Phyllospadix	San Quintin Zostera			
Hyale frequens	4, 890	2, 950			
Ischyrocerus litotes	2, 177				
Elasmopus rapax serricatus	1,714	_			
Photis brevipes	935				
Photis conchicola	745				
Elasmopus antennatus	736	360			
Microdeutopus schmitti	503	33			
Cerapus tubularis	498	300			
Aoroides columbiae	408	9			
Paraphoxus spinosus	303	_			
Ericthonius brasiliensis	250	9, 160			
Amphilochus litoralis	149	_			
Megamphopus effrenus	142	_			
Jassa falcata	142	_			
Megamphopus martesia	130	_			
Ampithoe pollex	107				
Cheiriphotis megacheles	90				
Ampithoe plumulosa	70	19			
Ischyrocerus species A	63	_			
Amphilochus neapolitanus	62	.5			
Parapleustes pugettensis	44	_			
Pontogeneia rostrata	44				
Synchelidium rectipalmum	33	_			
Pontogeneia quinsana	19	257			
Total species in the faunules	43	26			

as members of this element: Corophium acherusicum, C. insidiosum, Podocerus brasiliensis, (Jassa falcata), Elasmopus rapax, and Ampithoe longimana. Since that paper, Barnard (1969) has shown that Jassa falcata is an abundant open-sea member of the intertidal fauna, and that two forms of E. rapax are extremely abundant in the open sea. The bay form of E. rapax, however, remains recognizable as a bay-restricted ?phenotype. The five bay-restricted species are extremely rare in the San Quintin fauna, possibly owing to the absence of pilings. Probably all of them are widely dispersed by means of ship foulings. The development of a remarkable phenotype of J. falcata in open-sea California (Barnard, 1969) indicates the possibility that it is an immigrant to harbors and invaded the open sea of California secondarily. Corophium acherusicum is the eighteenth most abundant amphipod in San Quintin, whereas in harbors with pilings it may rank first or second. Corophium insidiosum has not been found in San Quintin; in nearby harbors it is abundant in extremely polluted zones (or in brackish waters). Podocerus brasiliensis and the bay form of E. rapax have not been found in San Quintin. Ampithoe longimana occurs sparsely in San Quintin, but it also occurs sparsely in Newport Bay and is not pollution-tolerant.

Bay and open-sea species, of higher frequency in lagoons than in open seas, are Ericthonius brasiliensis, Stenothoe valida, and Paraphoxus spinosus. The first species is extremely abundant on harbor pilings and in beds of eelgrass and in the open sea is of medium rank (Table 11). Stenothoe valida is a common piledwelling species of Newport Bay but is of low frequency in San Quintin. Paraphoxus spinosus is surprisingly sparse in San Quintin if one considers its moderate abundance in Newport Bay and that the bay is in the middle of its eastern Pacific range; instead, P. obtusidens, a closely related species not occurring in Newport Bay, is dominant in San Quintin.

Two of the three Newport Bay, host-oriented commensal amphipods, Leucothoe alata and Leucothoides pacifica, occur in San Quintin. Anamixis linsleyi apparently does not. Because of host protection these species must be considered as belonging to a "calmwater" element.

Probably Corophium uenoi and C. baconi can be added to the list of bay and open-sea forms, of higher frequency in calm water than in surf. They are widely distributed in the open sea of the North Pacific but appear to occur in higher numerical frequency in bays than in the open sea. Whether they have been dispersed by ships or transplanted accidentally with commercial marine organisms is open to question. Unlike their congeners, C. acherusicum and C. insidiosum, they have not been recorded from seas other than the Pacific.

The so-called *Pontogeneia minuta*, now believed to be distinct from the European types, has so far been found only in Newport Bay and San Quintin and must be considered a native calm-water element.

Thus, of 15 species identified in the Californias as indicators of calm water, either by their presence or their high frequencies in ponded water, the cosmopolitan forms associated with harbor pilings are poorly represented in San Quintin (six species). Three native species of epifaunas are well represented. Two native, host-oriented species occur in San Quintin. One pan-American burrower (Paraphoxus spinosus) is poorly

represented and another pan-American phycophilous species (Ampithoe longimana) is normally represented. The final species, Ericthonius brasiliensis, is ubiquitous and extremely abundant in San Quintin. One must presume that the advent of commercial development in San Quintin would change the balance from native species to cosmopolitan species as it has in Californian harbors.

# Open-Sea Distribution of Major Lagoonal Taxa

None of the dominant taxa in the soft-bottom fauna of San Quintin Bay is wholly confined to bays although 11 species of 46 in Table 12 are primarily lagoonal inhabitants. These data concern only Polychaeta, Mollusca, and Amphipoda because the further distribution of so many of the other groups (Isopoda, Tanaidacea, Cumacea) is poorly known and still other groups are very rare in Californian lagoons (e.g., Echinodermata). Another 20 of the 46 species occur frequently in intertidal zones, another 15 in shallow water sands of the open sea and only 6 species have their centers of abundance in water exceeding 11 meters in depth. More than 85 percent of the dominant (high frequency) species of San Quintin are either lagoonal forms or have immigrated from shallow open-sea waters. If all species, including so-called strays, were considered, a very much lower percentage of the total probably would be shown to have a shallow-water affinity. Unfortunately, the quantitative distribution of marine invertebrates is poorly known and very little more can be written about the zoogeography of the lagoon faunas at this time.

# Relationship of the Benthic Lagoonal Community to Pollution Faunas

Presumably parts of San Diego Bay, Newport Bay, Mission Bay, and Los Angeles Harbor, California, resembled Bahia de San Quintin Bay in the days before mankind altered them for maritime use. Some of those harbors and others of smaller extent have been studied by Reish (1955, 1959a, 1959b, 1961) and Reish and Winter (1954). Los Angeles-Long Beach harbors have been most extensively studied. Reish (1959b) found five kinds of benthic assemblages, two of them called semihealthy, one healthy, one polluted, and one very polluted (azoic). Healthy bottoms are dominated by Tharyx parvus, Cossura candida, and Nereis procera; semihealthy bottoms either by Polydora paucibran-

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TABLE 12.—Distribution of abundant Polychaeta, Mollusca, and Amphipoda from Bahia de San Quintin (primary habitats of each species marked with an "x"; geographic remarks very abbreviated; "warm-temperate" refers only to Californias)

Names of species	Pri- marily	Inter- tidal	Open Sea (meters)			Geography
States of species	Bays		2–10	11- 30	30- 100	Geography
Polychaeta						
Armandia bioculata		x	1	1		warm-temperate
Axiothella rubrocincta			x			NE Pacific
Brania clavata		x				cosmopolitan
Capitella capitata	x					cosmopolitan
Capitita ambiseta		x				warm-temperate
Chone mollis		x				warm-temperate
Cirriformia luxuriosa	x					warm-temperate
Cossura candida		x				warm-temperate
Exogone verugera	į.		x			cosmopolitan
Fabricia limnicola	x	x				warm-temperate
Haploscoloplos elongatus		x				NE Pacific
Lumbrineris minima	x					warm-temperate bays
Megalomma pigmentum	x					warm-temperate bays
Marphysa sanguinea	x (Ca	alifornia)				cosmopolitan
Neanthes caudata	x					cosmopolitan
Nephtys caecoides			x			NE Pacific
Nerinides maculata					x	warm-temperate
Onuphis microcephala			x			tropical America
Pista alata				×		warm-temperate
Platynereis bicanaliculata	x					Pacific
Prionospio malmgreni			x			cosmopolitan
Scoloplos acmeceps		x (kelp)				NE Pacific
Scoloplos ohlini		x				E Pacific
Scyphoproctus oculatus	x		x			warm-temperate
Mollusca						
Aequipecten circularis	x					tropical-warm-
aequisulcatus Acteocina carinata		_	_			temperate tropical-warm-
Acteocina carmata		x	x			temperate
Crucibulum spinosum		x				E Pacific
Cryptomya californica	×	x				NE Pacific
Hiatella arctica		x x	x			arctic-tropical
Lasaca subviridis		x	^			warm-temperate
Lyonsia californica		x				NE Pacific
Marginella californica		x				warm-temperate
Mitrella carinata		••	x (kelj	)		NE Pacific
Ostrea lurida	_ x	x	(=]	ľ		NE Pacific
Solen rosaceus	"		x			warm-temperate
Tellina buttoni			×			NE Pacific
МРНІРОВА						and the second s
Acuminodeutopus			x			warm-temperate
heteruropus			18			•
Ampelisca compressa				x		pan-America
Amphideutopus oculatus				x		warm-temperate
Ericthonius brasiliensis		x		11.00		cosmopolitan
Hyale frequens		x				warm-temperate
Lembos macromanus	1 1	×				warm-temperate

TABLE 12.—Distribution of abundant Polychaeta, Mollusca, and Amphipoda from Bahia de
San Quintin (primary habitats of each species marked with an "x"; geographic remarks
very abbreviated; "warm-temperate" refers only to Californias)—Continued

Names of species	Pri- marily Bays	Inter- tidal	Open Sea (meters)			C
			2–10	11- 30	30- 100	Geography
Lysianassa holmesi Microdeutopus schmitti Orchomene magdalenensis Paraphoxus obtusidens			x x?	x	x	warm-temperate warm-temperate warm-temperate N Pacific

chiata in combination with Dorvillea articulata or by Cirriformia luxuriosa; and polluted bottoms by Capitella capitata. All of these organisms are polychaetes. Reish (1963 Table 4) in his analysis of the polychaetes of San Quintin cites a number of species occurring in several southern Californian bays and harbors of varying polluted conditions. Three major polychaetes do not occur in San Quintin: Nereis procera, Prionospio h. newportensis, and Tharyx parvus. That their absence from San Quintin proves that they are indicators of polluted conditions in the harbors is disputed by the presumption that they probably have their southern limits in southern California and that they do not extend as far south as San Quintin. Furthermore, San Quintin has five major species of polychaetes not occurring as major dominants in the Californian harbors: Exogone verugera, Scoloplos ohlini, S. acmeceps, Prionospio malmgreni, and Axiothella rubrocincta. A sixth San Quintin species, Fabricia limnicola, occurs only in Newport Bay, California, and not in two other harbors. Only S. ohlini of the six taxa might be a southern species not occurring as far north as the California harbors; thus the absence of the others may be related to factors of pollution. Fabricia limnicola apparently is a warm-temperate, eastern Pacific bay taxon, reported only from Newport Bay, Anaheim Slough, and San Quintin; its absence in harbors also may be a factor of artificial pollution, because in San Quintin the species occurs in areas of fine sediment with high organic contents near marshes and must be existing under conditions of partial natural pollution. The same is true of Scoloplos acmecebs.

Only Cossura candida, of those polychaetes dominating the harbor healthy benthos, also occurs in San

Quintin; it is abundant in the eelgrass and Prionospio communities.

Cirriformia luxuriosa, the harbor indicator of semihealthy bottom II has nearly 80 percent of its individuals in San Quintin Bay confined to the *Prionospio* community (mostly *Cossura* phase). There it is abundant only in three samples.

Capitella capitata, the ubiquitous pollution indicator is probably also an indicator of any environmental extreme that is limiting to other Metazoa. It occurs at three stations in San Quintin, 25, 29, and 43; one of these is a Prionospio bottom, another an Eugyra-Ampelisca bottom, and the third a Capitella-Scoloplos dominated bottom. Presumably the worm occurs in these samples in a patch of environment, probably putrid, restrictive to other organisms in the samples.

Benthic Amphipoda are nearly absent in polluted harbors such as Los Angeles and Long Beach. The piling fauna is a different matter and was discussed previously; on pilings in those harbors, Amphipoda are extremely abundant.

The benthic seaward portion of Newport Bay is dominated by the Acuminodeutopus-Rudilemboides amphipod association which in San Quintin is essentially an ecotonal area between Ampelisca-Eugyra and Prionospio communities. In San Quintin the association is actually dominated in standing crop by Eugyra glutinans and Prionospio malmgreni. Neither of those species occurs in Newport Bay (or have not been detected in great abundance). The Acuminodeutopus-Rudilemboides samples of Newport Bay are dominated in numbers by the polychaetes Capitita ambiseta, Cossura candida, and Lumbrineris minima, but these are of medium to low rank in San Quintin.

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#### The Environment

## Physiography and Sediments

Bahia de San Quintin is a Y-shaped tidal lagoon with a single entrance at the foot of the Y. It is located at approximately 30.5° N on the Pacific coast of Baja California, about 255 kilometers south of the California borderline. The lagoon has a north-south orientation (Figures 13-14) which has been controlled by the development of cinder cones on its northwest perimeter and between the arms of the lagoon. The east shore of the east arm is defined by a small escarpment which may represent a minor stage shoreline of the open sea prior to or during volcanic activity and uplift (or sea lowering) (but see Gorsline and Stewart, 1962). Spit dunes, one of which is a tambolo, form a barrier to sea encroachment on the west and connect low ground between the seaward cinder cones. The arms of the lagoon are extremely shallow except for narrow channels that rarely exceed 7 meters in depth. More than 40 percent of the bay is believed to be exposed during tides lower than mean sea level. The bay bottom, especially that in the east arm, which has been studied more thoroughly than in the west arm, is characterized by the elevation of small banks dominated by the eelgrass, Zostera marina L. Perhaps 20 percent of the bay bottom is covered with this flowering plant (Dawson, 1962). Marshes have encroached on the water area in several places, but they are severely controlled by the unusual topography of the embayment.

The western arm of the bay has the characteristics of a normal seaside lagoon in being separated from the sea by a narrow spit of dunes and sand sheets and by having its axis parallel to shore. The spit is abnormal in the sense that it has been controlled by cinder cones at either end, rather than having been formed merely as a bar in reaction to changing sea levels. A few kilometers to the north of San Quintin are numerous temporary storm lagoons completely landlocked by dunes and sand sheets, and one must presume that this would have been the fate of the present bay except for the impingement of the volcanics. Indeed, the subaerial topography of the emergent coastal plain of Santa Maria must have been extended considerably seaward by the volcanics. The "central hills" (see fig. 2 in Gorsline and Stewart, 1962), composed of extrusives, probably formed a solid barrier to longshore sand movements and controlled the development of sand

sheets and storm lagoons to the north of San Quintin. Without the volcanics one would presume that the present shoreline might occur approximately at the small escarpment forming the mideastern margin of the east arm. There is a remote possibility that this escarpment (2–8 meters high) represents an old shoreline, but Gorsline and Stewart also imply that it may have been cut by pluvial erosion, since they consider the east arm to be a drowned estuary. The central hills therefore blocked direct sea access to a major arroyo during a wetter Holocene epoch, resulting in a southward deflection of the channel, now represented by the east arm.

That the embayment has not been completely filled with sediment is of course a factor of time and climate. But the aging of the seaward lagoon to some extent and the landward relict estuary to a great extent may have been lessened through protection afforded by the peculiar topography.

The central volcanic peninsula has shielded the east arm from north and westerly windblown sediments and thus helped to control the survival of a deep channel. The deep channel in the west arm fringes the west margin of the central peninsula, thus indicating that a great deal of the sediment filling the western ninetenths of the lagoon has come from the seaward dunes. Perhaps the channel survives because it is bordered on one side by "hard" rock contributing little sediment.

If the volcanics commenced subaqueously then baserock of the bay must have been deeper than in a normal lagoon of a submergent coastal plain and if the processes of aging (sedimentation) were normal, San Quintin should have had a longer life than other aridclimate lagoons.

The east arm is not only longer than west but apparently far more complex. The diagram of sediment distribution published by Gorsline and Stewart shows a far greater complexity and patchiness to sediments in the east arm than in the west (but the east was studied more intensively than the west). The west arm sediments grade regularly from sand to silt from southeast to northwest, the silt occurring just off the only major plat of marshland in the northwest corner. That marshland survives probably because of its protection by the cinder cone known as Colina del Sudoeste, whereas marshes on the lagoonal margin of the spit are becoming inundated with sand. Essentially the west arm has been filled with sediments coming from a single undirectional source and therefore a gradational simplicity is to be expected. The near absence of

marshes on the east shore of the west arm is a function of the elevated volcanic ground.

Even though sediments of the east arm are more diverse and patchy than in the west arm, the boundaries between classes of sediments are not sharp. They appear sharp only because of the artificiality imposed by drawing isopleths and other contours. Sediments of the east arm presumably have multiple origins; some may have been brought to the bay in the ancient estuary during wetter climes and have been conserved to the present by tidal reworking; more recent sediments presumably enter the bay rarely during floods of the main arroyo and sheet flow over the escarpment; silts with high organic content are related to marshes. The full east shore of the east arm, except the margins of the escarpment, is lined with marshes, some of them very broad (cf. one half nautical mile wide). A lowland drainage area between the two major cones of the central peninsula is also dominated by a marsh on the west shore of the east arm. The main channel probably has been shifted westward since wetter climes as sheet flow carried more sediments into the bay from the plateau of the coastal plain than from the central peninusla.

# Interrelationships of Sediments and Biota

Except in the deep main channels, the upper 20 centimeters of sediment during field operations appeared fairly uniform, presumably by homogenization through biotic activities. Channel sediments are highly diverse and undoubtedly strongly affected by animal populations. In some channel segments the substrate is medium to fine sand, in other segments the sand is overlain by silt, and in the channel near the abandoned pier the substrate is essentially pure slit as far as the sampler could dig. Scouring of some of the channels may be hindered by the presence of enormous numbers of globular ascidians which would tend to impede saltation of coarse particles and thus contribute to deposition. Extraordinary numbers of ampeliscid Amphipoda, building soft tubes on the substrate surface, also characterize some of the channels but presumably not those in which the tidal rush is greatest because of the fragility of the tubes. The tunicate and the amphipod are biotic partners of the overall channel community but their codominance forms a spectrum, suggesting that the ascidian occurs in greatest abundance in rapidly flowing waters and the ampeliscid in greatest abundance in fairly slow-moving water. The amphipod is essentially a "filter feeder" on fairly coarse particles and thus requires a certain minimal amount of water movement for food supply; it therefore does not occur in abundance in completely ponded or very slow-moving water. Few organisms occurring in the channels would be considered as "sediment reworkers" (infauna) so that one is left with the impression that channel filling is being hastened by activities of organisms. This does not account for the possibility of large organisms such as elasmobranchs stirring up the bottom during feeding.

There must be a very critical fulcrum of balance in the channel environment between the factors of (1) tidal rush impelling particles in an erosional-depositional cycle (2) the depositional influences of organisms essentially contributing to a self-destruction of the environment. The maintenance of the channels in this mature to senescent stage of the lagoon therefore indicates that a fairly steady state is reached in the evolution of the lagoon. The ascidians especially do not live in extremely shallow, slow-moving waters so that if deposition were to proceed to that level the organisms would be removed from the picture and the erosional part of the tidal rush would again scour the channels to suitable biotopic conditions for the tunicate. The organisms may well have contributed to the overall filling of the bay through impedance of erosion and once the water volume had been reduced by increments, the deposition of the southern (eastwest) spit could proceed through dropping of sediment load by decrease in tidal momentum. The east-west spit now restricts the tidal rush to a relatively small amount of water moving swiftly through the entrance and into the channels and may be a major cause and not necessarily the effect of the filling of the bay by sediments. The open-sea hydrographic and topographic relationships to the east-west spit require study before a measure of the balance between spit and bay can be taken. The western (north-south) spit is presumed to be fairly stable and generally unaffected by events inside the bay for it was originally controlled by cinder cones.

In considering the maturation of the bay by filling of a medium-depth sea bottom cut off by a north-south spit and induced by volcanic activity (a consideration antithetical to the drowning of the coastal plain by change in sea level), one might recognize a stage between deep channelization and complete

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shoaling. This biotope today is represented by mediumdepth flats between banks and channels and has an impoverished fauna. If one could visualize a perfect model of this bay there would be an assumption that once the channel organisms had aided in the filling of a simple deep channel to middepth flats, thereby destroying their biotope, the subsequent stage of an impoverished fauna would endure for a long period of time until physically influenced deposition had built the flats into shoals on which eelgrass could survive. Eelgrass apparently requires a level of illumination that would occur only in the upper few meters of a highly turbid bay. The immigration of eelgrass would then reaccelerate the deposition by trapping particles and slowing water movement, but again it would help to destroy its own biotope through filling the bay to sea level. Meanwhile the lateral accretion of marshes would continue to diminish the bay volume, the plants again acting as sediment traps that would elevate marsh surfaces to the upper limit of salt water.

The lagoonal characteristics of Morro Bay (Reish and Barnard, 1967) and Newport Bay (Barnard and Reish, 1959) seem to support parts of this model and previous remarks on climate. The outer lagoon of Newport Bay is represented by wide channels of middepth (4-5 meters) artificially induced by humans through dredging and filling. Those channels have relatively even bottoms and are dominated by the impoverished Acuminodeutopus-Rudilemboides-Prionospio community typical of middepth flats in San Quintin. The marshes at Morro Bay are relatively more dominant to water area than they are in San Quintin; the upper bay bottom is scarcely covered with water, has seemingly little eelgrass and an impoverished fauna with some similarities to that of Newport and San Quintin. The main seaward channel of Morro Bay is apparently dredged and composed of hard-packed, biotically impoverished sand altered by the influences of breakwater and human habitation. No channels with ascidian-amphipod communities have been found in Morro Bay. The enlarged marsh and almost completely filled inner lagoon suggest the influence of a slightly wetter climate than in arid San Quintin, bringing into the bay more particles that were trapped by former stands of marsh and eelgrass. Rainfall is apparently sufficient to carry many of the particles through the marsh where presumably they have been trapped by eelgrass and thus contributed to lagoonal senescence. There has also been a leveling of the inner Morro lagoon through establishment of oyster farms.

A model of lagoonal maturation should therefore include a period of long stability through faunal impoverishment intercalated between the eelgrass and the marsh stage. The sequence would then proceed as follows: (1) deep channels with high tidal volume brought, through assistance of biota, to (2) middepth flats with faunal impoverishment and long-term stability, followed by (3) eelgrass dominated banks with an increase in depositional rates, succeeded by (4) shoal water, level and barren mud flats of long duration, on which finally (5) marshes would encroach by lateral immigration.

This simple model is complicated by the lack of any reports on known broad-channel embayments with high tidal volume in which stage 1 biota are known to occur. The interpretation does suggest that San Quintin Bay would have a longer life than a lagoon in a slightly wetter clime, and the model presupposes a steady sea level which is contrary to the thesis of Gorsline and Stewart that San Quintin, at least the east arm, is a drowned estuary. In the drowned estuary one could propose the occurrence of a broad and deep river channel eventually dominated by tidal rush and metasaline waters in which stage 1 biota could occur. The relatively straight eastern escarpment and axis of the east arm, deflected only by hard volcanic outcrops suggest the ancient occurrence of a fairly heavy flow of water that would have created a broad channel with few meanders. A low-gradient stream with heavy sediment load and strong meanders would provide an environment already suitable for stage 3 biota.

If coastal plain submergence took place after an increase in aridity then the broad river valley, ergo estuary, would already have a sediment load and meandering channels. Channelization would then be maintained only by tidal rush and subshoal banks would be available for immediate implantation of eelgrass. A submerged estuary in an arid climate would therefore already be mature whereas a lagoon, formed immediately after stability of sea level through simple deposition of offshore bars and their rapid evolution into a spit, might have a longer life. This longer life would be controlled by storms, prevailing winds, aridity, specific composition of the spit sediments, activities of terrestrial organisms on the bar, groundwater, and a host of other factors.

Relatively rapid changes apparently occur in Sonoran lagoons of the northeast Pacific, for Gorsline and Stewart show the considerable changes known to have occurred in the erosional-depositional cycle near the tambolo of San Quintin since 1886, and Stevenson and Emery (1958) trace the extensive changes that have occurred in Newport Bay since 1825. The changes at Newport are so extensive as to suggest significant uplift in the last 200 years, but the changes shown by Gorsline and Stewart at San Quintin appear to be oscillatory.

#### Climate of Air and Water

Climate not only influences the thermal boundaries of the biogeographic province in which San Quintin occurs but it has topical effects The very low rainfall and presumedly moderate evaporation result in slightly hypersaline lagoonal water and very little continuous sedimentation. The extremely rare occurrence of pluvial sheet-flow must create catastrophic conditions from time to time, not only in diluting seawater but by roiling the water and superimposing fresh sediments. The absence of fluvial sedimentation has presumably afforded a longer life to the lagoonal environment than if the bay had occurred in wetter climes but Gorsline and Stewart believe that San Quintin did at one time exist in a wetter clime and that the east arm is a drowned estuary. A sediment load would already be present under those circumstances. Further discussion must concern present-day water conditions.

Hydroclimatic conditions of Bahia de San Quintin are less extreme than we had expected to encounter (Figure 16). In comparison with Laguna Ojo de Liebre, 315 kilometers to the south of San Quintin (Phleger and Ewing, 1962), San Quintin is colder and less hypersaline. If the years 1956-57 for Ojo de Liebre and 1960-61 for San Quintin can legitimately be compared, one can state that in November the bays have similar thermal conditions (20° C temperature at the heads of the bays) but in February Ojo de Liebre is still 20° whereas San Quintin has dropped to 16.0-16.5° C. In August the head of San Quintin has warmed to 24.4-24.7° whereas the waters in Ojo de Liebre are in excess of 26° C. Presumably much of this summer difference can be explained by the warmer water of the inshore open sea off Ojo de Liebre and the winter difference by upwelling in the inshore open sea of San Quintin (Dawson, 1951), a condition not likely to occur at Ojo de Liebre because of its situation in the large Gulf of Sebastian Viscaino. In either bay, therefore, a considerable influence is felt from open-sea conditions. The smaller San Quintin is affected more strongly and immediately by the open sea than is Ojo de Liebre. Fog and overcast, especially in early morning hours, ameliorate thermal extremes of air and water in both San Quintin and Ojo de Liebre.

#### **Avian Predators**

Four or five species of shore birds (dowitchers, godwits, sandpipers) prey extensively on polychaetes, frequently on amphipods and other small crustaceans and rarely on mollusks and crabs (juvenile crabs or legs of adults). Stomachs of about 100 birds have been processed and await final analysis; the only comment that can be made at this time is that during periods of favorable low water a few days a month the birds take enormous numbers of polychaetes and crustaceans. Birds that had been feeding on mud flats during negative tides and killed two hours after sunrise had frequently consumed between 50 and 100 individuals of the common amphipods and polychaetes, primarily in the Zostera zone or on barren banks in shallower depths. A minimum of 5,000 shorebirds in feeding behavior during a low tide has been counted in one day. These very minimal numbers indicate a prodigious effect rendered on the invertebrate fauna even if maximal feeding is confined to 25 days per year and only on the shallowest of the banks. Other than elasmobranchs, piscine predators on small invertebrates seem to be insignificant; only the local needlefish consumes neritic copepods whereas numerous other species of fish had few invertebrates in their stomachs. Many bottom-feeding elasmobranchs occur in San Quintin Bay but most of those we autopsied had empty stomachs. Bony fish stomach contents await further study.

#### Conclusions

Few estuaries or lagoons fit a simple model. The physiographic control of the San Quintin lagoon is highly abnormal but the results fit, to a large extent, the concept of a lagoon, if stringently defined (Emery, Stevenson, Hedgpeth, 1957). San Quintin is thus a shallow, semienclosed body of slightly hypersaline sea water. Its axes are parallel to the sea margin but at least in the case of the east arm, the axis is directly controlled by solid volcanics whereas the west arm is normally controlled by a spit, although the spit is an abnormal corollary of volcanic extrusions to the north and the south. San Quintin therefore resembles other Califor-

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nian lagoons which are bipartitely extinct river valleys and seaside lagoons, but the axis of the San Ouintin stream valley has been deflected to parallel the sea margin. There is some indication that floods of rare rainstorms are channeled into shallow arroyos debouching into the upper end of the east arm in San Quintin, but this kind of erosion did not control the basic structure that came during a wetter clime in the past. Spits evolved from bars characterize some of the Californian lagoons (Newport), but solid intrusives and rock faulting obviously control others (San Diego Bay). Regardless of the controlling geomorph the results in the Sonoran northeastern Pacific have been the same; the development of ponded waters open to tidal rush, with evaporative-precipitative balance affording slight hypersalinity. San Quintin differs from lagoons to the north but not to the south in the presence of deeply cut channels far from the mouth and these are probably maintained in part by the hard precipitous volcanic ground. The east arm but not the west is protected completely from effects of storm waves and windblown sediments which so often are major components controlling the physiography and water content of lagoons.

Like most estuaries the level of dissolved phosphate and silicate is high toward the inner reaches of San Quintin, but this high level of nutrient salts cannot be explained by the loading effect of rivers (Stevenson, Emery, Hedgpeth, 1957). High levels of nutrients seem to be associated with those parts of the lagoon fringed by dense marshes. Concentration of nutrients may be assisted by avian and piscine predation altering the biomass-nutrient balance common in the open sea to a level with nutrients dominating. In other words the exposable bay margins may not support a potentially maximal biomass density consistent with available nutrients because of predatory effects. A short-term increase in standing crop would probably result from civilizing influences resulting in removal of the avian predators, but those human influences then might implement the new level by increasing nutrient disposal through domestic outfalls, followed by ultimate decrease of standing crop through introduction of lethal pollutants.

The east arm of Bahia de San Quintin might be visualized as a perfectly flat bottom dominated by a highly restricted invasive *Prionospio* community with low standing crop, low diversity, and low frequency of organisms, on which has been imposed the follow-

ing modifications that in most cases increase the diversity, abundance, and standing crop of organisms: (1) the incision of channels into which are directed most of the tidal waters and in which are received most of the sedimented debris and detritus that is reworked by the Eugyra-Ampelisca community; (2) the development of eelgrass beds on suitably elevated banks that come to climactical perfection by self-generation of debris and detritus sedimented because of water-ponding by the eelgrass; (3) peripheral low-grade sedimentation bringing the bay margins to a peneplane level on which marsh plants by particle entrapment also evolve to climax and ultimate destruction through subaerial elevation but that meanwhile contribute certain components of the underwater Fabricia biotope.

The sharp definition of the eelgrass community from the purely sedimentary surroundings attests to the importance of an epifaunal substrate provided to a few organisms that would otherwise probably not occur in lagoons except where humans have constructed artificial substrates such as pilings and floating docks.

The eelgrass community is matched in the open sea only by wave-dashed Phyllospadix stands while the channel community and Fabricia zone have no opensea counterparts. The biota of the channel community consists of invaders from the open sea thrown together in unique combination; the basic Prionospio community is dominated by a strong open-sea taxon while the Fabricia zone is dominated by a lagoonal species and the Zostera community has as its basic member a lagoonal evolute. But the zosteral associates comprise strong open-sea species in combination with a few species primarily restricted to lagoons. The channel, zosteral, and marsh communities are presumably very sensitive to depth or water-volume and momentum changes made by humans; the Fabricia community, however, may survive under certain artificial conditions of pollution, while a few of the dominant zosteral foulers will survive on artificial substrates.

No important zoological effect of an axial gradient in environmental conditions is seen in Bahia de San Quintin, although water quality differs recognizably between the open mouth and the head of the bay (Figure 16). Apparently the special domination of the upper end of the bay by Fabricia is simply a positive relationship to the increased ratio of marsh to water volume, because a weak Fabricia community occurs adjacent to marshes in the outer bay, and bottoms next to precipitous volcanics in the upper bay are barren of

Fabricia. A few rarely occurring members of the biota such as Kalliapseudes may reflect other special conditions in the reaches, but these correlations have not been elucidated because they require intense study of very small areas of bottom.

An extraordinary relationship between climate and physiography is demonstrated in the present-day condition of San Quintin Bay. The effects of the two groups of conditions are so inextricably mixed in the resultant bay structure that one must suggest the ultimate understanding of these effects will come from large-scale experimental models.

In an area of regional uplit or heavy sedimentation the fate of San Quintin would be a filled marsh with a frontage of sand beaches possibly like that at Anaheim Slough, California. Even in a geostrophic steady state the process of filling the bay with sediments occurs from windblown western dunes and the rare occurrence of freshwater runoff.

Sea-farm management of San Quintin could be accomplished by experimentation in dredging, excavation, and landfill so as to increase the undersea area covered by either Zostera banks or channel communities, balancing both extremes so that the necessary rush of water feeding the channel communities is carried in suitable proportion to zosteral banks, thus eliminating unproductive middepth or supralittoral banks. Presumably creation of additional marshes by landward excavation would provide an increase in the photosynthetic base to supply debris and detritus to the undersea flats. An enlarged water volume would have to be considered. Ponds with artificial vertical surfaces to attract fouling organisms could increase the production of protoplasm in such a system. Apparently the simple dumping of shells on the bottom would not result in an increase of favorable surface, for the shelly bottoms of upper Newport Bay are very barren. The basic product of such a system would be powdered protein or cellulose with various byproducts. Because the lagoons of the Californias are predictably vulnerable to destruction by human habitation San Quintin in its present primeval condition would make an idealistic sea-farm community experiment. In the process of its ideal development a reserve of supralittoral banks for preservation of wildfowl and marine communities could be incorporated, and recreational areas developed that would not hinder the productivity. Human effluvia from the recreational area could be contributed to the nutrient base.

The natural beauty and relatively benign climate of San Quintin, would, under circumstances affording cheap fresh water, result in a dense human population that would frustrate massive reclamation for sea farming and conservation that is unfeasible for lagoons such as Newport and San Diego because of proprietary rights. To protect San Quintin from the ugly fate of the other lagoons the timing of its development must anticipate cheap fresh water and retard the importation of deleterious industries—the ultimate ideal, of course, would be the complete protection of San Quintin, the removal of its few humans to suitable employment elsewhere, and the reintroduction of the marine turtle that used to function as a top herbivore in this system.

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# Appendix I

Contagious species in each benthic sample from Bahia de San Quintin, printed in lower case Roman type. If italicized, these names also represent standing-crop dominants. Capitalized names represent standing-crop dominants that are not in contagious frequencies. Names in parentheses represent secondary crop dominants.

#### Station number

- Acteocina carinata, PRIONOSPIO MALM-GRENI, (FABRICIA LIMNICOLA).
- 2. Acteocina carinata, FABRICIA LIMNICOLA.
- Exogone verugera, Fabricia limnicola, Scoloplos ohlini, Acteocina carinata.
- Exogone verugera, Acteocina carinata, FABRI-CIA LIMNICOLA.
- 5. Exogone verugera, Fabricia limnicola.
- 6. Fabricia limnicola.
- 7. None.
- 8. PRIONOSPIO MALMGRENI.
- 9. Prionospio malmgreni, Cossura candida.
- Neanthes caudata, Scyphoproctus oculatus, MAR-PHYSA SANGUINEA, KALLIAPSEUDES CRASSUS.
- 11. PRIONOSPIO MALMGRENI.
- Prionospio malmgreni, Scoloplos acmeceps, Scyphoproctus oculatus, Acteocina carinata, Acuminodeutopus heteruropus, Ampelisca compressa, Axiothella rubrocincta, Chone mollis, Paranthura elegans, Paraphoxus obtusidens, EUGYRA GLU-TINANS, KALLIAPSEUDES CRASSUS
- 13. Exogone verugera, Kalliapseudes crassus, Ampelisca compressa, Listriella melanica, Orchomene magdalenensis, Paranthura elegans, Paraphoxus obtusidens, (MARPHYSA SANGUINEA).
- 14. Prionospio malmgreni.
- Scoloplos acmeceps, Scyphoproctus oculatus, Acteocina carinata, Acuminodeutopus heteruropus, Ampelisca compressa, Paranthura elegans, Paraphoxus obtusidens, Scoloplos ohlini, EUGYRA GLUTINANS.
- 16. Prionospio malmgreni.

- 17. Prionospio malmgreni, COSSURA CANDIDA.
- Prionospio malmgreni, Scoloplos acmeceps, Axiothella, rubrocincta, Megalomma pigmentum, Paranthura elegans, Paraphoxus obtusidens, EU-GYRA GLUTINANS, AMPELISCA COM-PRESSA.
- 19. Prionospio malmgreni, Scoloplos acmeceps.
- Acuminodeutopus heteruropus, Paraphoxus obtusidens, EUGYRA GLUTINANS, PRIONOS-PIO MALMGRENI.
- Scoloplos ohlini, (PRIONOSPIO MALMGRE-NI).
- 22. None.
- 23. Prionospio malmgreni, Cossura candida, Pista alata.
- Megalomma pigmentum, PRIONOSPIO MALM-GRENI.
- 25. Exogone verugera, Scoloplos acmeceps, Acuminodeutopus heteruropus, Neanthes caudata, Paraphoxus obtusidens, CAPITELLA CAPITATA.
- Cirriformia luxuriosa, Cossura candida, Prionospio malmgreni.
- Scoloplos acmeceps, Scoloplos ohlini, PRIONOS-PIO MALMGRENI.
- 28. Exogone verugera, Kalliapseudes crassus, Listriella melanica, Lumbrineris minima, Orchomene magdalenensis, Paranthura elegans.
- Cirriformia luxuriosa, Prionospio malmgreni, Listriella melanica, Neanthes caudata, Scoloplos ohlini.
- 30. (MARPHYSA SANGUINEA).
- 31. None.
- 32. Lumbrineris minima, Pista alata, Scoloplos ohlini, Scyphoproctus oculatus.
- Fabricia limnicola, Acuminodeutopus heteruropus, Brania clavata, PRIONOSPIO MALMGRENI.
- 34. Capitita ambiseta, Corophium baconi, Ericthonius brasiliensis, Exogone verugera, Pista alata, Platynereis bicanaliculata.
- 35. Eugyra glutinans, Fabricia limnicola, (Prionospio malmgreni), Acuminodeutopus heteruropus, Amphideutopus oculatus, Axiothella rubrocincta,

- Cossura candida, Listriella melanica, Lumbrineris minima, Megalomma pigmentum, Pista alata, Paraphoxus obtusidens, Rudilemboides stenopropodus.
- Prionospio malmgreni, Brania clavata, Cirriformia luxuriosa, Neanthes caudata, Scolopos acmeceps.
- 37. Prionospio malmgreni, (Cossura candida).
- 38. (Cossura candida), (Pista alata), (Prionospio malmgreni), Acuminodeutopus heteruropus, Brania clavata, Chone mollis, Cirriformia luxuriosa, Exogone verugera, Listriella melanica, Lumbrineris minima, Megalomma pigmentum, Neanthes caudata, Rudilemboides stenopropodus, Scoloplos acmeceps.
- Chone mollis, (Lumbrineris minima), (Scoloplos acmeceps), Capitita ambiseta, Cossura candida, Megalomma pigmentum, Pista alata, PRIONOS-PIO MALMGRENI.
- 40. (Scoloplos acmeceps), Paraphoxus obtusidens.
- 41. Prionospio malmgreni, (Neanthes caudata), Cossura candida.
- 42. Prionospio malmgreni, (Fabricia limnicola), Brania clavata.
- 43. Eugyra glutinans, Megalomma pigmentum, Acuminodeutopus heteruropus, Amphideutopus oculatus, Brania clavata, Exogone verugera, Microdeutopus schmitti, Paraphoxus obtusidens, Pista alata, Rudilemboides stenopropodus, (PRIONOS-PIO MALMGRENI).
- 44. Eugyra glutinans, (Pista alata), Acteocina carinata, Acuminodeutopus heteruropus, Ampelisca compressa, Amphideutopus oculatus, Axiothella rubrocincta, Corophium baconi, Lembos macromanus, Listriella melanica, Lumbrineris minima, Microdeutopus schmitti, Orchomene magdalenensis, Paraphoxus obtusidens, Rudilemboides stenopropodus, Tellina buttoni, Uristes entalladurus, COSSURA CANDIDA.
- Acuminodeutopus heteruropus, Brania clavata, Cossura candida, Megalomma pigmentum. PRIONOSPIO MALMGRENI.
- 46. Acuminodeutopus heteruropus, Paraphoxus obtusidens, EUGYRA GLUTINANS, (COSSURA CANDIDA), (PRIONOSPIO MALMGRENI).
- 47. Onuphis microcephala, Prionospio malmgreni, (Scoloplos acmeceps), Paraphoxus obtusidens.
- Amphideutopus oculatus, Lumbrineris minima, Paraphoxus obtusidens, Uristes entalladurus, EUGYRA GLUTINANS.

- Prionospio malmgreni, Acuminodeutopus heteruropus, Brania clavata, Chone mollis.
- 50. (PRIONOSPIO MALMGRENI), EUGYRA GLUTINANS.
- Eugyra glutinans, (Cirriformia luxuriosa), (Prionospio malmgreni), Acuminodeutopus heteruropus, Axiothella rubrocincta, Megalomma pigmentum, Neanthes caudata, Paraphoxus obtusidens, Scyphoproctus oculatus.
- 52. (Chone mollis), (Lumbrineris minima), EU-GYRA GLUTINANS).
- Capitita ambiseta, (Prionospio malmgreni), Hyale frequens, Listriella melanica, Platynereis bicanaliculata, Pontogeneia quinsana, (EXOGONE VE-RUGERA).
- (Cossura candida), Chone mollis, Exogone verugera, Listriella melanica, Pista alata, Scoloplos ohlini, (FABRICIA LIMNICOLA), (PRIONOSPIO MALMGRENI), EUGYRA GLUTINANS.
- 55. Scoloplos acmeceps.
- 56. (EUGYRA GLUTINANS).
- 57. None.
- Prionospio malmgreni, Brania clavata, Scoloplos ohlini, COSSURA CANDIDA.
- 59. Acteocina carinata.
- 60. Chone mollis, Eugyra glutinans, (Pista alata), Acuminodeutopus heteruropus, Amphideutopus oculatus, Axiothella rubrocincta, Listriella melanica, Megalomma pigmentum, Microdeutopus schmitti, Prionospio malmgreni, Rudilemboides stenopropodus, Scoloplos acmeceps.
- 61. Capitita ambiseta, Pista alata, Prionospio malmgreni, Corophium baconi, Cossura candida, Elasmopus rapax, Ericthonius brasiliensis, Exogone verugera, Hyale frequens, Lembos macromanus, Listriella melanica, Lumbrineris minima, Orchomene magdalenensis, Platynereis bicanaliculata, Pontogeneia quinsana, Scoloplos acmeceps.
- 62. Capitita ambiseta, (Prionospio malmgreni), Cossura candida, Elasmopus rapax, Ericthonius brasiliensis, Exogone verugera, Hyale frequens, Lembos macromanus, Listriella melanica, Orchomene magdalenensis, Pista alata, Platynereis bicanaliculata, Pontogeneia quinsana, Rudilemboides stenopropodus, Scoloplos ohlini.
- 63. Scoloplos acmeceps.
- 64. Eugyra glutinans, Pista alata, Prionospio malmgreni, Scoloplos acmeceps, Acuminodeutopus

- heteruropus, Brania clavata, Chone mollis, Exogone verugera, Listriella melanica, Megalomma pigmentum, Microdeutopus schmitti, Neanthes caudata, Rudilemboides stenopropodus.
- 65. Eugyra glutinans, (Capitata ambiseta), (Chone mollis), Acuminodeutopus heteruropus, Ampelisca compressa, Amphideutopus oculatus, Megalomma pigmentum, Microdeutopus schmitti, Paraphoxus obtusidens, Rudilemboides stenopropodus, Uristes entalladurus.
- 66. Chone mollis, Cossura candida, Megalomma pigmentum, Prionospio malmgreni, Acuminodeutopus heteruropus, Capitata ambiseta, Corophium baconi, Ericthonius brasiliensis, Hyale frequens, Lembos macromanus, Listriella melanica, Neanthes caudata, Onuphis microcephala, Pista alata, Pontogeneia quinsana, Rudilemboides stenopropodus, Scoloplos acmeceps.
- Eugyra glutinans, Acteocina carinata, Acuminodeutopus heteruropus, Axiothella rubrocincta, Microdeutopus schmitti, Rudilemboides stenopropodus, PRIONOSPIO MALMGRENI, (SCOLOPLOS ACMECEPS).
- (Scoloplos acmeceps), Acteocina carinata, Paraphoxus obtusidens.
- 69. Eugyra glutinans, (Chone mollis), (Lumbrineris minima), Ampelisca compressa, Axiothella rubrocincta, Brania clavata, Capitita ambiseta, Corophium baconi, Lysianassa holmesi, Orchomene magdalenensis, Paranthura elegans, Paraphoxus obtusidens, Rudilemboides stenopropodus, Uristes entalladurus.
- Capitita ambiseta, (Cossura candida), Elasmopus rapax, Ericthonius brasiliensis, Hyale frequens, Lembos macromanus, Listriella melanica, Orchomene magdalenensis.
- 71. Prionospio malmgreni, (Scoloplos acmeceps).
- 72. None.
- 73. Eugyra glutinans, Ampelisca compressa.
- Neanthes caudata, Acuminodeutopus heteruropus, Axiothella rubrocincta, Corophium baconi, Elasmopus rapax, Hyale frequens, Scoloplos acmeceps, Scoloplos ohlini.
- 75. None.
- 76. Eugyra glutinans, (Neanthes caudata), Scoloplos acmeceps, Acuminodeutopus heteruropus, Axio-

- thella rubrocincta, Brania clavata, Cossura candida, Onuphis microcephala.
- 77. Eugyra glutinans, (Capitita ambiseta), (Megalomma pigmentum), Amphideutopus oculatus, Lembos macromanus, Pista alata, Rudilemboides stenopropodus.
- Ampelisca compressa, Corophium baconi, Microdeutopus schmitti, Orchomene magdalenensis, Rudilemboides stenopropodus.
- Platynereis bicanaliculata, Capitita ambiseta, Elasmopus rapax, Ericthonius brasiliensis, Exogone verugera, Hyale frequens, Lembos macromanus.
- 80. (Exogone verugera), Acteocina carinata.
- 81. Pista alata, (Capitita ambiseta), Corophium baconi, Cossura candida, Elasmopus rapax, Ericthonius brasiliensis, Exogone verugera, Hyale frequens, Listriella melanica, Neanthes caudata, Onuphis microcephala, Platynereis bicanaliculata, Pontogeneia quinsana, Scoloplos ohlini.
- 82. No sample.
- 83. Platynereis bicanaliculata, Rudilemboides stenopropodus, Tellina buttoni.
- 84. (Scoloplos acmeceps), Acteocina carinata.
- 85. (Chone mollis), (Neanthes caudata), Axiothella rubrocincta, Megalomma pigmentum, Pontogeneia quinsana, Scoloplos ohlini, Scyphoproctus oculatus.
- 86. None.
- 87. Pista alata, (Cossura candida), Capitita ambiseta, Elasmopus rapax, Hyale frequens, Lembos macromanus, Lumbrineris minima, Neanthes caudata, Megalomma pigmentum, Orchomene magdalenensis, Pontogeneia quinsana.
- 88. (Scoloplos acmeceps), Acteocina carinata, Megalomma pigmentum.
- 89. (Capitita ambiseta), (Cossura candida), Corophium baconi, Hyale frequens, Lembos macromanus, PRIONOSPIO MALMGRENI.
- Scoloplos acmeceps, (Fabricia limnicola), (Neanthes caudata), Acuminodeutopus heteruropus, Axiothella rubrocincta, Chone mollis, Lembos macromanus, Onuphis microcephala, Scoloplos ohlini.
- 91. Scoloplos ohlini, (Neanthes caudata), (FABRI-CIA LIMNICOLA).

## Appendix II

List of miscellaneous species and phyla identified from San Quintin samples. Names of Amphipoda (Barnard, 1964), Polychaeta (Reish, 1963), Mollusca (Keen, 1962), and Isopoda (Menzies, 1962) are listed in Appendix III for convenience of readers unfamiliar with names mentioned in text. Ophiuroids have been identified by Capt. F. C. Ziesenhenne, Cumacea by Mr. R. R. Given, and various worm phyla sorted by Dr. D. J. Reish. The ascidian, Eugyra glutinans has been identified by Dr. D. P. Abbott.

Turbellaria: SQ 12 (1), 25 (1), 34 (1), 38 (6), 43 (2), 51 (1), 53 (1), 64 (+), 66 (1), 67 (4), 69 (10), 76 (1), 77 (1), 81 (4).

Sipunculida: SQ 13 (20), 28 (83), 30 (10).

Phoronidea: SQ 26 (21).

Nemertea: SQ 1 (1), 2 (1), 4 (5), 5 (3), 7 (2), 9 (3), 10 (1), 12 (1), 13 (63), 14 (5), 15 (20), 17 (2), 20 (2), 23 (7), 24 (2), 25 (8), 26 (4), 27 (4), 30 (2), 31 (40), 34 (12), 35 (11), 36 (11), 37 (7), 38 (27), 39 (9), 40 (4), 43 (9), 44 (30), 47 (4), 48 (5), 51 (9), 52 (2), 53 (11), 58 (4), 59 (4), 60 (17), 62 (12), 64 (13), 65 (9), 66 (4), 67 (67) sic, 69 (10), 71 (2), 72 (1), 73 (4), 74 (5), 76 (25), 77 (12), 79 (12), 81 (4), 84 (3), 85 (1), 88 (1), 89 (8), 90 (13), 91 (10).

Oligochaeta: R= rare (1-10), S= sparse (10-20), G= significant (20-50), A= abundant (50-100), V= very abundant (100+), individuals often fragmented and counted mainly by estimate: SQ 0 (R), 1 (A), 2 (S), 3 (S), 5 (V), 6 (A), 7 (G), 8 (A), 9 (A), 10 (A), 11 (G), 12 (R), 13 (V), 14 (G), 15 (G), 16 (G), 17 (G), 18 (R), 19 (A), 20 (G), 22 (R), 23 (V), 24 (R), 25 (R), 26 (V), 27 (R), 30 (G), 31 (S), 32 (S), 35 (G), 36 (G), 37 (G), 38 (G), 39 (A), 40 (R), 41 (G), 42 (G), 43 (V), 44 (R), 45 (R), 46 (S), 47 (A), 49 (A), 50 (G), 51 (G), 53 (R), 54 (G), 58 (G), 60 (G), 63 (R), 64 (A), 66 (R), 68 (R), 72 (R), 74 (R), 75 (R), 76 (G), 79 (R), 81 (R), 84 (R), 85 (R), 88 (S), 90 (R).

Crustacea:

Tanaidacea:

Kalliapseudes crassus: SQ 10 (68), 12 (71), 13 (8580), 15 (25), 18 (4), 22 (2), 24 (2), 25 (1), 28 (1632), 30 (4), 43 (1), 65 (1).

Other tanaids: SQ 1 (2), 2 (8), 4 (82), 5 (640), 6 (13), 7 (17), 8 (3), 12 (19), 13 (40), 15 (1), 25 (2), 38 (3), 55 (1), 60 (3), 65 (1), 67 (3), 74 (8), 87 (5).

Decapoda, shrimp, Callianassa spp.: SQ 14 (1), 16 (1), 19 (2 + 60 larvae), 23 (1), 27 (1), 28 (1), 29 (9), 30 (1), 41 (1), 51 (1), 52 (1), 64 (1), 65 (1). Other shrimp: SQ 65 (1), 77 (1), 79 (21), 81 (1).

Mysidacea: SQ 60 (1). Brachyura: SQ 61 (1), 70 (2), 72 (2).

Cumacea:

Oxyurostylis tertia: SQ 10 (1), 14 (1), 17 (2), 18 (57), 20 (10), 25 (10), 33 (20), 35 (29), 36 (1), 37 (3), 38 (3), 40 (1), 43 (7), 44 (21), 45 (3), 46 (14), 47 (12), 48 (1), 51 (28), 53 (1), 60 (14), 61 (3), 64 (24), 65 (25), 66 (1), 67 (1), 69 (10), 74 (1), 76 (7), 77 (13), 88 (1).

Oxyurostylis pacifica: SQ 12 (1), 17 (1), 20 (1), 33 (10), 55 (3), 65 (3), 68 (7), 71 (2), 76 (1), 80 (2), 84 (8), 91 (4).

Oxyurostylis sp.: SQ 12 (1), 61 (3), 67 (1).

Cumella sp.: SQ 9 (1), 35 (1), 51 (1), 64 (1), 65 (1), 74 (1), 76 (4), 85 (4), 87 (1).

Other Cumacea: SQ 15 (5), 25 (1), 38 (3), 48 (1), 51 (2), 60 (2), 64 (1), 65 (1), 76 (1), 77 (1), 90 (1).

Ostracoda: SQ 1 (80), 2 (16), 3 (30), 4 (35), 5 (171), 6 (43), 7 (23), 8 (10), 9 (46), 10 (55), 11 (1), 12 (422), 13 (600), 14 (20), 16 (7), 17 (40), 18 (105), 19 (42), 20 (83), 23 (55), 24 (23), 25 (107), 26 (9), 27 (2), 28 (43), 29 (78), 30 (10), 31 (40), 32 (3), 33 (290), 34 (89), 35 (601), 36 (285), 37 (57), 38 (471), 39 (214), 40 (11), 41 (52), 43 (322), 44 (438), 45 (108), 46 (244), 47 (255), 48 (162), 51 (697), 52 (35), 53 (139), 55 (116), 58 (98), 59 (60), 60 (399), 61 (135), 62 (546), 63 (15), 64 (733), 65 (195), 66 (771), 67 (149), 68 (3), 69

(1470), 70 (45), 71 (112), 72 (2), 73 (12), 74 (396), 76 (443), 77 (210), 79 (40), 80 (2), 81 (199), 84 (110), 85 (261), 87 (285), 88 (6), 89 (96), 90 (228), 91 (148).

Caprellidea: SQ 1 (1), 2 (1), 7 (1), 12 (4), 15 (456), 17 (3), 18 (13), 20 (2), 22 (1), 24 (1), 25 (56), 28 (2), 33 (170), 34 (18), 35 (205), 36 (4), 38 (84), 39 (8), 43 (50), 44 (3), 45 (2), 51 (13), 53 (21), 55 (7), 60 (93), 61 (123), 62 (78), 64 (106), 65 (102), 66 (98), 67 (65), 70 (51), 71 (12), 74 (5), 76 (5), 79 (12), 81 (62), 85 (14), 87 (18), 89 (9), 90 (15), 91 (40).

Nebaliacea: SQ 43 (7), 44 (9), 51 (3), 53 (1), 60 (4), 61 (18), 62 (36), 64 (2), 65 (15), 66 (8), 69 (600), 70 (99), 73 (1), 77 (6), 81 (9), 85 (6), 87 (2), 89 (1), 90 (2).

Chironimid larvae: SQ 1 (26), 2 (1), 4 (1), 5 (15), 6 (1).

#### Echinodermata:

#### Ophiuroidea:

Amphipholis squamata: SQ 25 (1), 28 (3), 30 (1), 34 (3), 35 (1), 38 (6), 43 (1), 53 (2), 64 (3),

65 (1), 66 (2), 67 (3), 69 (10), 70 (6), 71 (1), 73 (1), 74 (1), 76 (1), 77 (1), 81 (4), 87 (1).

Amphiodia occidentalis: SQ 52 (4).

Holothurian, brown, 5-12 mm long: SQ 24 (4), 27 (8), 29 (27), 34 (2), 35 (43), 37 (1), 38 (6), 39 (7), 48 (49), 51 (10), 60 (19), 67 (7), 69 (10), 74 (19), 85 (7), 90 (3).

Holothurian, black: SQ 53 (14), 62 (21), 66 (8). Enteropneusta: SQ 8 (5), 9 (6), 19 (2), 26 (3), 36 (10), 37 (11), 38 (21), 41 (14), 43 (226), 46 (7), 47 (1), 51 (13), 53 (2), 58 (7), 59 (1), 63 (1), 64 (7), 66 (5), 67 (2), 69 (1420), 71 (1), 74 (1), 77 (3), 85 (1), 89 (3), 90 (1), 91 (2).

Ascidiacea, Eugyra glutinans: SQ 12 (72), 14 (1), 15 (25), 18 (82), 20 (15), 31 (10), 34 (1), 35 (465), 38 (39), 39 (5), 42 (5), 43 (153), 44 (519), 45 (2), 46 (71), 47 (9), 48 (57), 50 (55), 51 (143), 52 (15), 54 (43), 56 (43), 58 (2), 60 (616), 62 (3), 64 (198), 65 (479), 66 (4), 67 (705). 69 (1420), 73 (280), 76 (835), 77 (781), 88 (2), 91 (2).

### Appendix III

Nomenclatural List of Amphipoda, Polychaeta, Isopoda, and Mollusca from Bahia de San Quintin

References: Barnard (1964), Reish (1963), Menzies (1962), Keen (1962).

Amphipoda, Gammaridea: Acuminodeutopus heteruropus, Ampelisca compressa, Amphideutopus oculatus, Amphilochus neapolitanus, Ampithoe longi-Ampithoe plumulosa, Ampithoe pollex, mana, Aoroides columbiae, Colomastix pusilla, Corophium acherusicum, Corophium baconi, Corophium uenoi, Elasmopus antennatus, Elasmopus rapax, Ensayara ramonella, Ericthonius brasiliensis, Heterophoxus oculatus, Hippomedon denticulatus, Hyale rubra frequens (=H. "nigra"), Jassa falcata, Lembos macromanus, Leucothoe alata, Leucothoides pacifica, Listriella diffusa, Listriella melanica, Lysianassa holmesi (= Aruga h.), Maera danae, Maera sp., Metaphoxus fultoni, Microdeutopus schmitti, Microjassa macrocoxa, Monoculodes hartmanae, Orchomene magdalenensis, Orchestia traskiana, Orchestoidea benedicti, Orchestoidea californiana, Paraphoxus bicuspidatus, Paraphoxus heterocuspidatus, Paraphoxus obtusidens, Paraphoxus spinosus, Parallorchestes ochotensis, Pontogeneia "minuta," Pontogeneia quinsana, Pontogeneia rostrata, Pseudokoroga rima, Rudilemboides stenopropodus, Stenothoe valida, Uristes entalladurus.

Polychaeta: Anaitides williamsi, Anaitides nr. multiseriata, Arabella iricolor, Arenicola cristata, Armandia bioculata, Axiothella rubrocincta, Brania clavata, Capitella capitata, Capitita ambiseta, Chone mollis, Chrysopetalum occidentale, Cirriformia luxuriosa, Cossura candida, Dorvillea articulata, Eteone dilatae, Eteone pacifica, Exogone verugera, Fabricia limnicola, Glycera americana, Goniada brunnea, Haploscoloplos elongatus, Hypoeulalia bilineata, Lepidonotus caelorum, Lumbrineris erecta, Lumbrineris minima, Marphysa disjuncta, Megalomma pigmentum, Neanthes caudata, Nephtys caecoides, Nerinides maculata, Notomastus magnus, Onuphis microcephala, Ophiodromus pugettensis, Pherusa capulata, Pista alata, Platynereis bicanaliculata, Polydora uncata, Polyophthalmus pictus, Prionospio malmgreni, Prionospio pygmaeus, Scoloplos acmeceps, Scoloplos ohlini, Scyphoproctus oculatus, Sphaerodorum minutum, Spiophanes missionensis, Trypanosyllis gemmipara, Typosyllis variegata.

Isopoda: anthurid, Cirolana diminuta, Dynamenopsis dianae, Erichsonella crenulata, Exocorollana kathyae, Gnathia steveni, Haliophasma geminata, Jaeropsis dubia, Lironeca sp., Munna ubiquita, Paranthura elegans, Paracerceis sculpta, Rocinela aries, Serolis carinata, Sphaeroma pentodon.

Mollusca: Acmaea depicta, Acteocina carinata, Aequipecten circularis aequisulcatus, Assiminea compacta, Bittium quadrifilatum, Brachidontes sp., Chaetopleura gemmea, Cooperella subdiaphana, Crucibulum spinosum, Cryptoma californica, Haminoea sp., Hiatella arctica, Lasaea subviridus, Leptopecten latiauratus, Lyonsia californica, Macoma yoldiformis, Marginella californica, Marginella pyriformis, Marginella regularis, Mitrella carinata, Modiolus sp., Odostomia fetella, Odostomia sp., Orobitella singularis, Ostrea lurida, Parvilucina tenuisculpta, Protothaca staminea, Solen rosaceus, Tellina buttoni, Terebra pedroana, Trachycardium quadragenarium, Transennella tantilla, ?Tricolia sp., Turbonilla sp., Nudibranchiata (various spp.).

# Appendix IV

# Data Decks and Methods Data Decks

- Alphabetical list of species and specimens for each sample.
- 2. Chronological list of all samples and specimens for each species.
- 3. A recast of deck 2 with samples arranged in order according to number of specimens in each sample, from low to high.
- 4. Master list of all species (like Table 1) arranged alphabetically with the following columns: (1) number of samples in which species occurs; (2) total number of specimens in all samples; (3) mean number of specimens per sample; (4) median number of specimens in positive samples; (5) straight-line numerical median between columns 3 and 4 to indicate minimal frequency of contagion for each species; see deck 5 for option.
- 5. (optional) Plots on arithmetic graph paper for each species occurring in 10 percent or more of the samples (found in deck 4, column 1); data from deck 3 are graphed with number of specimens per sample plotted on abscissa and samples plotted by even increments on ordinate. Line connecting dots is drawn and dot selected where significant curve commences near high end of plots. Dot level read as number of specimens and entered in deck 4, column 5 as optional substitute for minimum level of contagion.

#### Method 1

Test of association between pairs of species to produce Figures 1-3. Formula adapted from Cole (1949). Represents rudimentary elucidation of community foci. Pairs of species are selected from deck 2 to include only those occurring in more than 10 percent of the samples or those with very high specimen frequencies in a few samples.

Formula:

$$C = \frac{hn}{ab}$$

C = coefficient of association; a = number of samples with first species of the pair; b = number of samples with second species of the pair; h = number of samples containing both species of the pair; n = number of samples (90).

Results of C are tabulated in a matrix like Figure 4. C-values for pairs of species are separately listed in order from high to low. Arbitrarily high values of C arranged in polygons like Figures 1-3 so that each species permitted in a corner has a selected minimum value with all other species in the corner. Minimum values may be selected by drawing on field experience if one biotope has been observed to contain two or more species strongly associated together. Various polygons are constructed to utilize several arbitrary levels of C; final presentation of association polygon based on best fit; polygons made from San Quintin data show best fit when all species with 99 percent of their specimens confined to Zostera community are incorporated in one corner; good fit assumed because another corner contains obvious members of a second assemblage recognized in the field (Eugyra-Ampelisca); third corner thus contains associates not otherwise determinable in the field. Lines in Figures 1-3 connecting species outside of corners present associative pairs with C-values higher than stated minimum.

#### Alternatives of n in Method 1

- A. All positive samples for each species of the pair are utilized.
  - 1. n = 90 (total samples in survey) (Figure 3).
  - 2. n = a + b h.
- B. Only positive samples contagious for each species of the pair are utilized.
  - 1. n = 90 (Figure 1).
  - n= a + b h (superior method) (Figure 2).

#### Method 2

RESIDUALS.—Samples assigned to assemblages by means of Method 1 are removed from deck 1. If each

corner of the polygon represents an Assemblage, then all samples containing any of those species in contagious frequencies are removed from deck 1. Residual samples contain associations based on one pair of species or one species alone. Recast of Method 1 on residual samples of deck 1 will select any further samples with pairs of species as dominants. Residual samples are arranged according to their dominant species (by highest frequency of specimens).

#### Method 3

MINIMUM FAUNAL PERCENTAGES (MFP) (Sanders, 1960).—The total number of specimens of all species in one sample is summed (from deck 1). The percentage composition of each species in a sample is found by dividing the number of specimens of each species by the total number of specimens of all species. Data sheets are completed for all samples. Samples are now compared by pairs. If a species is found in both samples of a pair the lesser percentage factor of that species in either sample is extracted to a new data card, identified by the joint numbers of the samples. The lesser percentage factors of all species common to both samples are extracted and summed on the data card. This sum is the MFP; it is found for all possible pairs of samples. The new data deck is arranged with MFP values from highest to lowest. The highest sum is chosen as a focus and the deck searched for the next highest sum having one of its conjoint sample numbers identical to one of the sample numbers on the focal card. Two cards now set together have three sample numbers between them. The deck is searched again for the next highest sum having any of the three sample numbers; three cards now have four sample numbers; this procedure is repeated through the half of the deck having the highest MFP values; after the first cluster of cards is removed, the next highest card is chosen as a focus and a second cluster of cards is generated. All clusters in the first half of the deck are found; samples in these clusters represent the majority of samples that can be utilized as foci for the description of communities but a few samples will remain in the deck that are highly dominated by one species but have low MFP values. The MFP system delegates high conjoint indices to samples with internal homogeneity but delegates low values to the odd samples with low diversity of species and high specimen frequencies of only one of the species. Unless

two or more of these samples occur in the data deck they fail to form clusters. The San Quintin data contain no similar pairs of these samples (like sample 78 in Figures 9-10), but presumably a higher sampling frequency would produce clusters of these.

Clusters of samples may be arranged in trellises (Figure 4) and the MFP values for each sample summed so as to determine weak samples with low sums that should not be included in the descriptions of community foci.

Cards in the second half of the deck may be joined to the initial clusters in the same procedure and a tree of relationships formed by spreading the cards on a table top in the form of clusters as they are removed from the deck and matched.

To clarify anomalous samples in the tree of relationships, a master visual card for each sample is formed. A symbol for each species in the samples is devised and printed by replication on the sample card, one symbol for each specimen of the species in the sample. To reduce the sizes of the cards generated from the San Quintin data, one symbol was printed for each ten specimens in the sample. This reduced the positive reports in a sample to less than ten species. Symbols can be formed from the alphabet and the most frequently occurring species can be assigned colors to assist visual correlations of cards. The master cards are distributed throughout the tree of relationships at the positions marked by conjoint occurrences of the samples. One may now readily detect anomalous samples, especially those that are heavily dominated by one main species and that have been displaced in the MFP system.

#### Method 4

Morisita-ono index of faunal affinity (Morisita, 1959, b; rewritten by Ono, 1961).—An index of affinity is found for a pair of samples by this method; coefficients (C $\lambda$ ) are stored on cards or in matrices and may be evolved into trees of relationships as in Method 3.

Formula:

$$C\lambda = 2\sum_{i=1}^{\infty} \frac{n! i \, n! i \, n! i}{(\lambda 1 + \lambda 2) \, N! \, N!}$$
 in which n1i and n2i

are the number of specimens of conjoint species (i-th) in the two samples and N1, N2 are the total numbers

of specimens in the two samples. The  $\lambda$  coefficients are determined for each sample by

$$\lambda = \sum_{i=1}^{\infty} \frac{ni(ni-1)}{N(N-1)}$$

The arithmetic is elaborated in a sample problem below:

Lambda-values (formula 2) are first determined for each sample; the values for samples 44 and 89 are found as follows:

$$\lambda 44 = \frac{9(8)}{20(19)} + \frac{6(5)}{20(19)} + \frac{3(2)}{20(19)} + \frac{0(0)}{20(19)} + \frac{2(1)}{20(19)} = \frac{111}{380} = 0.29 \text{ (rounded)}$$

$$\lambda 89 = \frac{34}{132} = 0.26$$
 (rounded) (same procedure).

The coefficient of affinity (formula 1) is computed utilizing values (SD=same denominator as first expression)

$$\begin{split} C\lambda = & 2\sum \frac{(9)(2)}{(.29 + .26)(20)(12)} \\ & + \frac{(6)(4)}{SD} + \frac{(3)(0)}{SD} + \frac{(0)(1)}{SD} + \frac{(2)(5)}{SD} = 2\sum \frac{18}{132} + \frac{24}{132} \\ & + \frac{0}{132} + \frac{0}{132} + \frac{10}{132} = (2) \frac{52}{132} = 0.79 \text{ (Rounded)}. \end{split}$$

#### Method 5

Dendrograms.—The scores of the C $\lambda$  or MFP coefficients are arranged in a half-matrix (trellis). Dendrograms are formed in a weighted pair-group method (Mountford, 1962), by evolving a series of matrices calculated in succession from the prime matrix. The pair of samples in the first matrix with the highest joint coefficient is coalesced as if it were a single

sample and a new matrix is developed by comparing the conjoint sample with all others. The second matrix also includes all of the prime-matrix coefficients less the first pair. From the second matrix the pair of samples with the highest joint coefficient is again selected, joined together as one sample and compared with all others to form the third matrix. This procedure is carried to its conclusion when all samples have been joined together by their highest successive coefficients. In comparing à conjoint sample with a single sample one must average the joint coefficient of the two numbers of the conjoint sample with the coefficient of the single member in the immediately previous matrix without returning to the first matrix, except in the first increment. The conjoint coefficients are recorded and utilized to make dendrograms as in Figures 7-10, by joining together samples and groups of samples according to the coefficient arranged along the ordinal axis. The spread of the dendrites on the abscissa is simply a matter of convenience in dispersing sample pairs that overlap.

These techniques are extraordinarily time-consuming; intercomparison of more than 24 samples requires a computer; a desk-calculator is necessary for any number of samples between 10 and 24. A group of 24 samples requires about 40 hours of calculating time (if samples have a maximum number of 120 species and an average of 1,000 specimens per sample).

#### Method 6

MAZE-GRIDS.—A maze-grid as herein defined is a compression into 2 dimensions of a 3-dimensional tree of relationships evolved in Method 3 or a dendrogram evolved in Method 5. A tree of relationships may be formed without computing either Cλ or MFP values by making a card for each sample on which are printed symbolically the number of specimens of each species; a symbol for each species is replicated on the card for each specimen (or a consistent fraction of the specimens). In the San Quintin samples, N=90, total species about 120, mean number of specimens per sample of 1006, it was possible to divide by 10 the number of specimens of each species and put one symbol per ten specimens of each species on each card. If color symbols or blocks of color in proportion to frequencies of species are used the landscape effect on the card can be readily classified by eye and the samples arranged

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into a tree. The maze-grid is found by arranging the cards into several best fits on a rectangular or square grid (Figure 11). Lines of close interrelationship between samples may be plotted; walls between boxes of the grid may be thickened or windows may be opened according to the degree of relationships among con-

tiguous samples found in MFP or  $C\lambda$  values. The ease in classifying samples from San Quintin by this method did not warrant calculation of window widths in the grids printed herein and they are simply left closed where no obvious relationships between samples occurred.

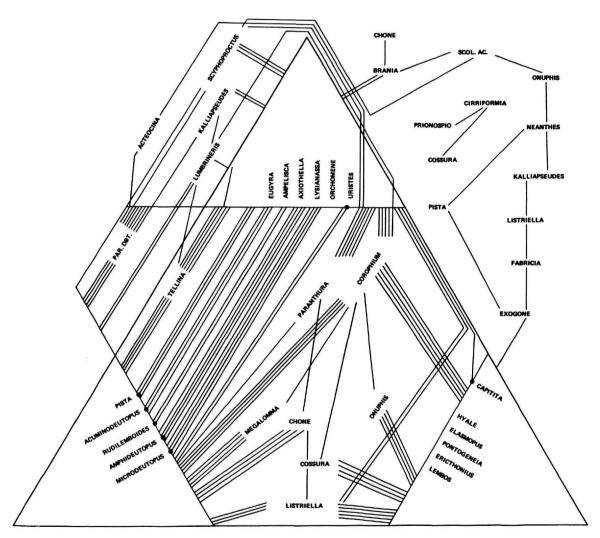


FIGURE 1.—Relationships of three groups of species in Bahia de San Quintin, Each corner holds species with coefficients of association exceeding 3.37 to all other species in the group. Lines connect other species with similarly high coefficients of association. For example, Listriella would be included in the Ericthonius corner, but it has a strong association with only 5 of the 6 species in the Ericthonius group. Diagram based on standard formula with n=90 and utilizing only "contagious" samples for each species (method B-1).

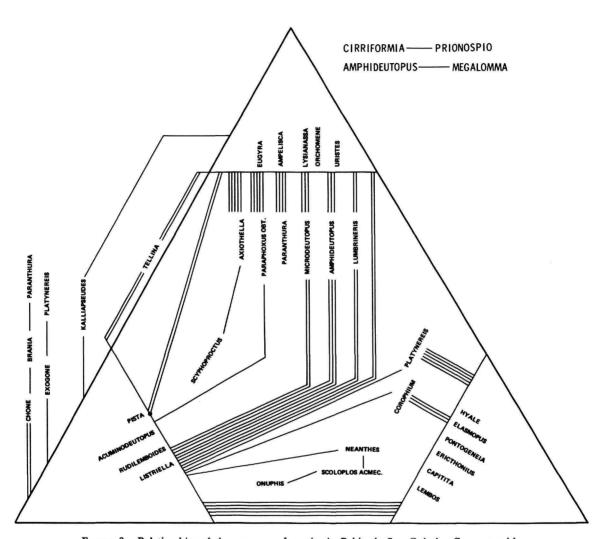


FIGURE 2.—Relationships of three groups of species in Bahia de San Quintin. Compare with Figure 1. Diagram based on standard formula utilizing "contagious" samples for each species with n=a+b-h (method B-2).

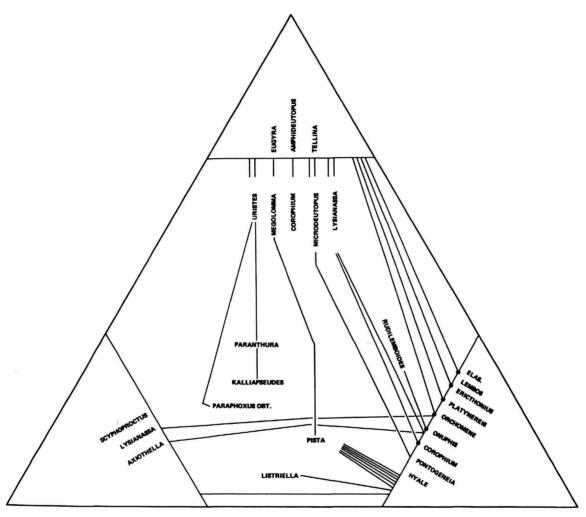


FIGURE 3.—Relationships of three groups of species in Bahia de San Quintin. Compare with Figures 1 and 2. Diagrams based on standard formula utilizing all samples, including "non-contagious" members with n=90 (method A-1).

	90	89	87	85	81	79	74	70	66	62	61	53	34	STA.	TOTAL	.S		
12	$\times$	37	38	50	33	30	56	28	43	35	33	28	27	90	438			
15	65	$\times$	61	34	61	47	40	63	58	54	62	57	37	89	611			
18	50	40	$\times$	37	61	52	43	62	68	56	56	39	46	87	619			
35	26	21	46	$\times$	33	29	57	23	44	32	29	28	23	85	419			
43	17	9	24	33	$\times$	64	40	71	64	76	79	57	63	81	702			
44	39	46	27	30	28	$\times$	40	58	57	59	60.	48	56	79	600			ITA
46	37	27	55	57	32	20	X	33	46	40	39	39	40	74	513			CAPII
48	28	20	32	49	30	30	40	X	59	76	78	44	54	70	649			ZOSTERA-ERICTHONIUS-CAPITITA
51	43	31	57	64	29	22	71	43	$\times$	57	58	39	52	66	645			THON
60	29	17	46	65	42	33	52	46	54	X	84	50	61	62	680			-ER I(
64	34	29	44	50	52	28	52	27	47	53	$\times$	54	63	61	695			STERA
65	48	42	44	46	37	59	37	43	39	51	38	$\times$	57	53	540			70
67	22	19	35	52	39	27	43	39	46	66	37	46	X	34	579			
69	39	44	27	12	13	70	14	14	16	14	11	44	16	X				
73	37	43	34	26	13	54	27	24	27	40	12	48	44	56				
76	19	15	30	36	16	11	35	28	41	47	24	22	49	11	46	$\setminus$		
77	18	10	30	40	28	25	38	37	37	57	25	42	54	16	50	53		
78	29	40	15	3	6	67	5	3	6	6	6	37	8	66	44	1	8	
STA.	12	15	18	35	43	44	46	48	51	60	64	65	67	69	73	76	77	78
TOTALS	579	518	989	929	448	616	642	533	673	718	569	723	642	483	625	484	268	350

# EUGYRA-AMPELISCA

FIGURE 4.—Strength of association among samples of two communities; lower left of graph = Eugyra-Ampelisca, upper right=Zostera, Method=minimum faunal percentages (see text).

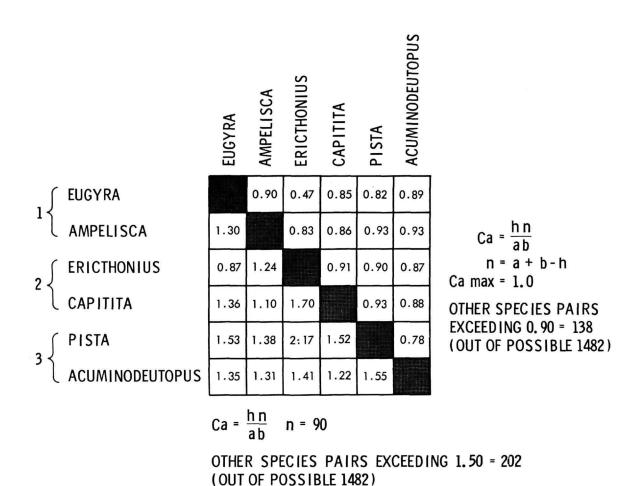


FIGURE 5—Associative indices of pairs of species obviously dominating three associations utilizing two methods as shown. Graph demonstrates low information content of these methods as opposed to utilizing samples in "contagious" condition for each species.

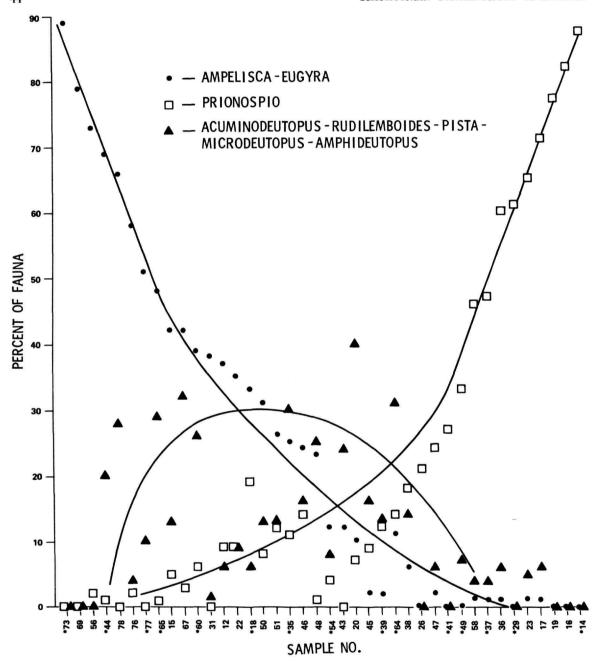


FIGURE 6.—Continuum of samples from center of Eugyra-Ampelisca community on left, through Acuminodeutopus-Rudilemboides ecotone in middle to center of Prionospio community on right. Samples marked with asterisks are arranged in a dendrogram of Figure 8.

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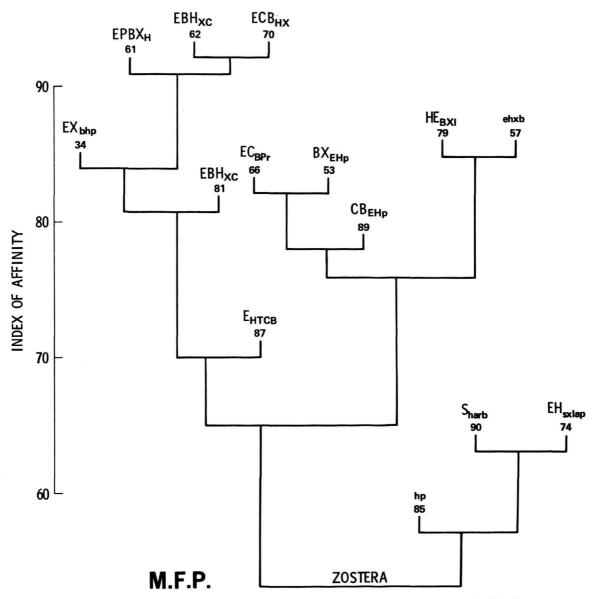


FIGURE 7.—Dendrogram showing association among all samples of Zostera community. Based on minimum faunal percentages. Each dendrite bears sample number and letter abbreviations denoting major species in sample. Letters occur in four sizes, largest denoting occurrence of 200+specimens in sample, next 101-199 specimens, next 51-99, smallest 11-50. Abbreviations: A=Acuminodeutopus, B=Capitita ambiseta, D=Amphideutopus, E=Ericthonius, H=Hyale, L=Elasmopus, M=Microdeutopus, P=Prionospio, R=Rudilemboides, S=Scoloplos acmeceps, T=Pista, X=Exogone.

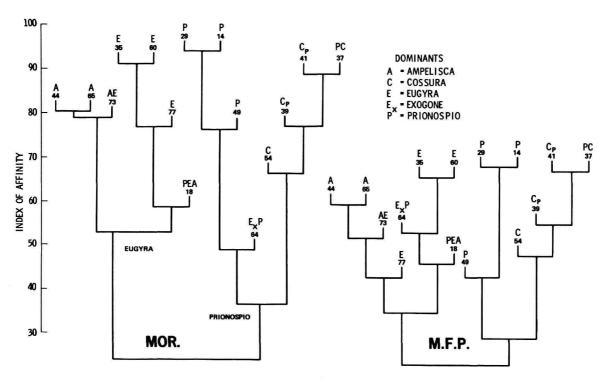


FIGURE 8.—Dendrograms representing relationships among samples of Eugyra-Prionospio continuum of Figure 6. Based on two methods, Morisita and Minimum Faunal Percentages.

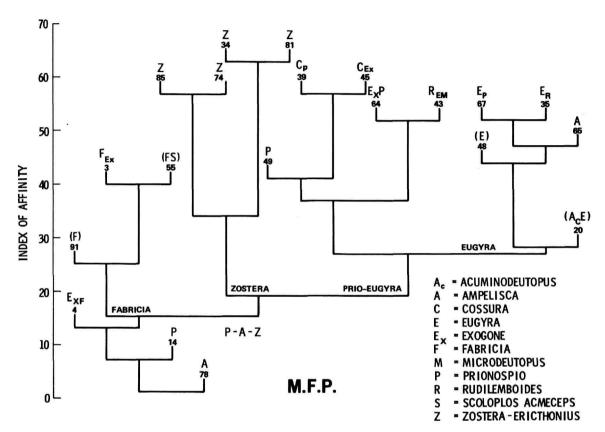


FIGURE 9.—Dendrogram of strong, medium, and weak samples of 4 communities and one ecotone in Bahia de San Quintin. Based on minimum faunal percentages. A strong sample (heavy dominance by one species), a weak sample (small numbers of individuals), and two medium samples (diversity of species with numerous individuals) are plotted for each of the five assemblages. Four strong clusters representing good communities occur; two strong samples remain with their communities but two others (14 and 78) are cast out of their clusters because of heavy dominance by one species.

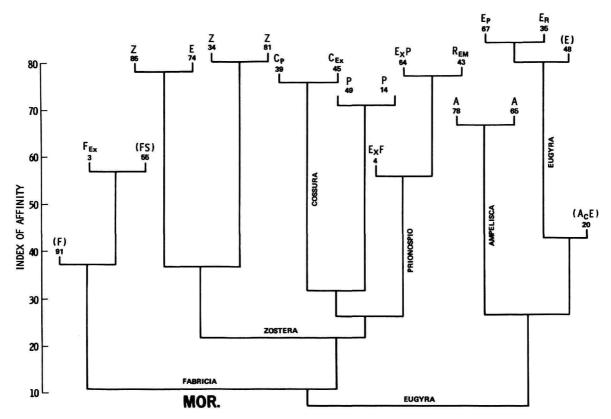
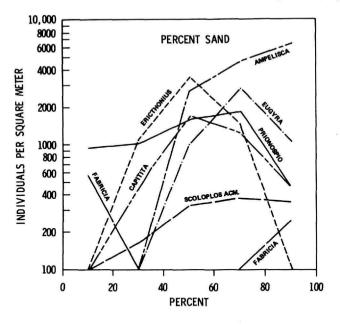


FIGURE 10.—Recasting of data plotted in Figure 9, utilizing Morisita index of affinity.

NUMBER 44

Г		31		44		65		15		20		56	46		48		43
ı			: A		: A		Α									R	
AC			REDMT		ERIDA <sub>c</sub>	M	A <sub>c</sub> PS		A <sub>c</sub> (E)		E		ECPA <sub>c</sub> E <sub>x</sub> R	EDR		EM	
		22	••	78		69		73	,	51		76	60		77		80
(A)			: A		AE LUIR		AE		E		. E		. E	_ E		L	
(A)	_	13	W(R)	10	LUIN	12		50	PA <sub>c</sub> C	35	SCA <sub>c</sub>	67	RA <sub>e</sub> DTC	IR	~=	E <sub>x</sub>	
••	••••					12		50		30		67	64		25	••	5
	<b>KA</b>		KH		Α				E		. E		E <sub>x</sub> PA <sub>c</sub>			E×	
Ex		28	(SE)	44	PEHA <sub>c</sub>	-	EA	40	PA <sub>c</sub> RDFC		RA <sub>c</sub> M		RTE	E <sub>x</sub> A <sub>ç</sub> S	R	F	
•	•••	28	h-in-	14		19		18		45		54	38		1	News	4
E	×Κ		Р		Р		PEA		C E <sub>x</sub> A <sub>c</sub> (P)		C e <sub>x</sub> fea		E <sub>x</sub> PC	(E <sub>x</sub> F)		E <sub>x</sub>	
		11		16		29		32		47		88	33		2		3
l			Р		Р		С		Р				A <sub>c</sub> F			F	
(P)			-						s		s		PR	(E <sub>x</sub> F)		E <sub>x</sub>	
		21		37	12.2	26		36	;	71		63	40		42		6
			PC		C		Р				S			F		F	
(P)					P		(CS)		PS				(S)	P		(E <sub>x</sub> )	
	•	17		9		27		39		74		84	. 34		91		55
	Р		CP				С		Z		l		Z				
С			•		(CSP)		PIS		s		(SR)		E <sub>x</sub>	μ̈́F		(FS)	
		23		41		49		62	,	90		83	79		85		57
	Р	ı	C		Р		z		Z				Z	z			
С	•		Р		IE <sub>x</sub> A <sub>c</sub>		E <sub>x</sub> PC		SRAc		RZ		E <sub>x</sub>	_		z	
		58		24		66		53		61		81	87		70		89
					Z		Z		Ž		ż		Z	· Z		. Z	
PC			СР		CP Z		E <sub>x</sub> P		PE <sub>x</sub> C		E <sub>x</sub> C		ст	ċ Z		ċ Z	

FIGURE 11.—Association grid of 81 samples from Bahia de San Quintin. Two-dimensional presentation represents one of several possible "best-fits." Heavy lines separate communities, but windows denote relationships contributing to appearance of continuum among communities of lagoonal habitat. See Figure 18 for condensation. Sample numbers in upper right corners of squares. Dots indicate extreme abundance of certain species. Letter symbols in middle of boxes indicate primary domination (numerical) and symbols on lower margins of boxes denote secondary dominants. Parentheses indicate weak domination (low numerical abundance). A=Ampelisca, Ac=Acuminodeutopus, C=Cossura, Cap=Capitella, D=Amphideutopus, E=Eugyra, Ex=Exogone, F=Fabricia, I=Capitita, K=Kalliapseudes, L=Lysianassa, M=Microdeutopus, P=Prionospio, S=Scoloplos acmeceps, T=Pista, U=Uristes, Z= (Zostera aggregates), combined frequencies of Ericthonius, Hyale, Elasmopus, Pontogeneia.



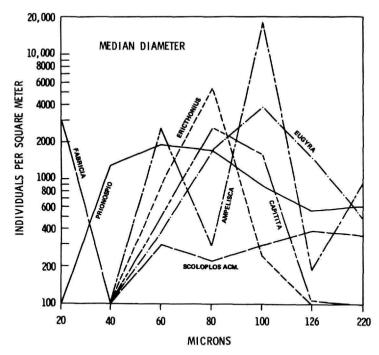


FIGURE 12.—Relationships of important benthic species to sedimentary parameters. Upper graph represents abundance in relation to percentage of sand in substrate and lower graph represents abundance in relation to median diameter of particles in substrate. Partition of Fabricia into two sections in upper graph demonstrates stratification of silt over sand.

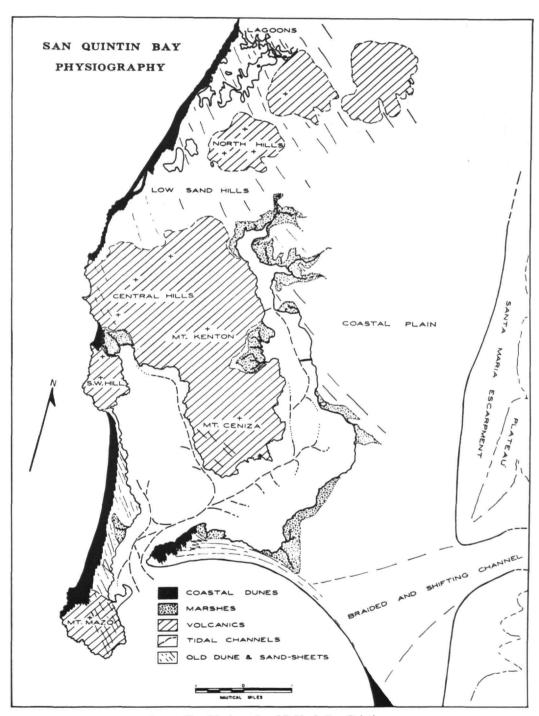


FIGURE 13.—Physiography of Bahia de San Quintin.

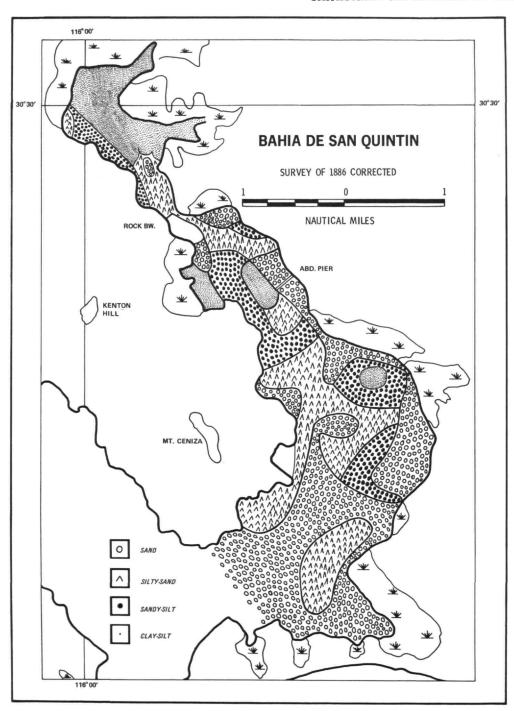


FIGURE 14.—Distribution of sediments in east arm of Bahia de San Quintin.

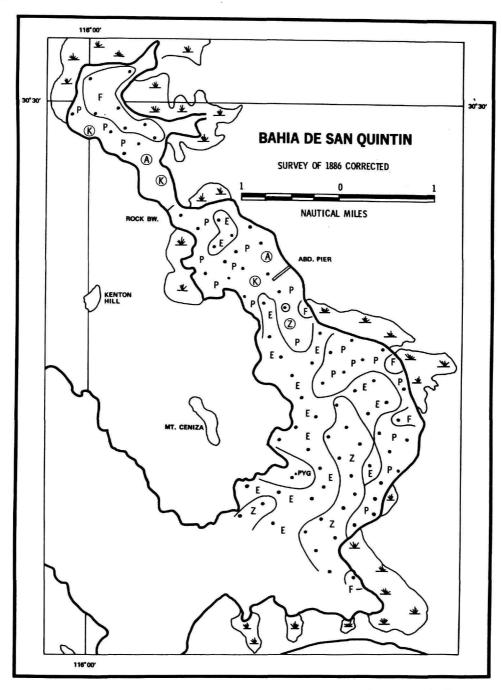


FIGURE 15.—Distribution of biotic communities in east arm of Bahia de San Quintin. Dots indicate samples. A=Ampelisca, E=Eugyra, F=Fabricia, K=Kalliapseudes, P=Prionospio, Z=Zostera, pyg=Megalomma pigmentum.

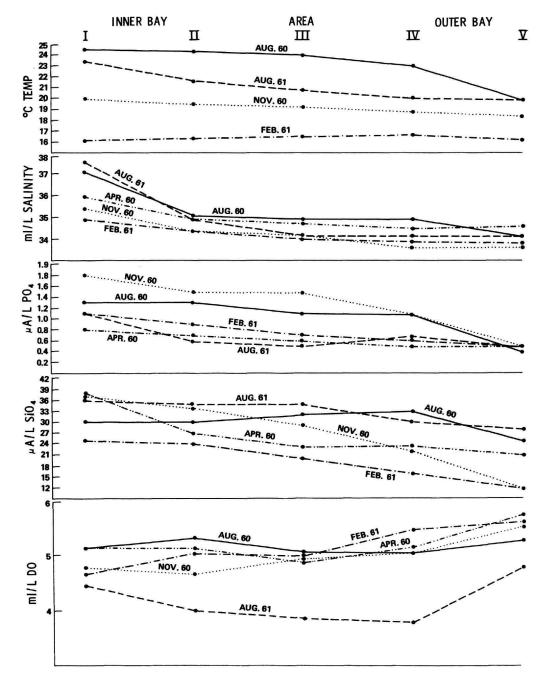


FIGURE 16.—Water quality of 5 zones in east arm of Bahia de San Quintin, extending from I=innermost to V=outermost portion of arm. Temperature, salinity, phosphates, silicates, and dissolved oxygen are plotted in either 4 or 5 surveys. Considerable differences are noted in the August 1960 and August 1961 surveys.

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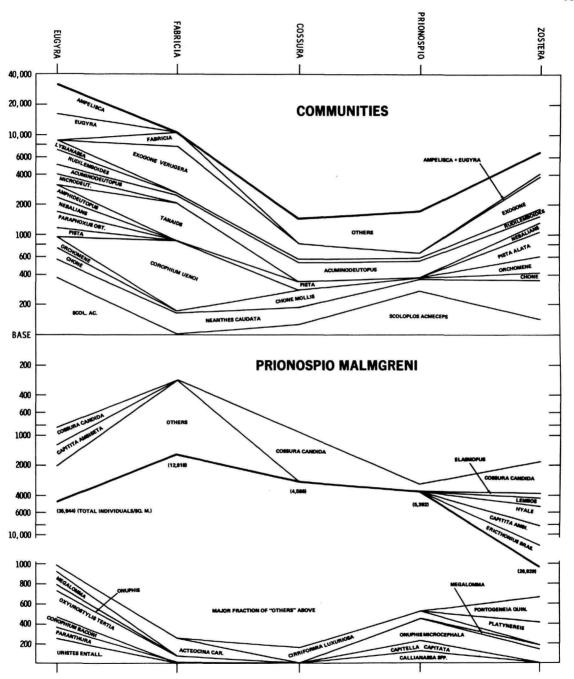


FIGURE 17.—Cross section of numerical frequency of major species in 5 biotic assemblages of Bahia de San Quintin. Plotted on semilog scale from base line in middle with overemphasis on frequency of species in middle of graph. Species situated toward base line commonly occur in all communities. Species plotted above base line dominate Eugyra-Ampelisca and Fabricia communities, those below base line dominate Ericthonius and Prionospio communities. Cross-sectional limits occur between outermost heavy lines in upper graph, with total individuals per square meter summed below for each community. Lower graph plotted on arithmetic scale, representing important species of "others" fraction in main graph. For purposes of clarity this figure has been condensed.

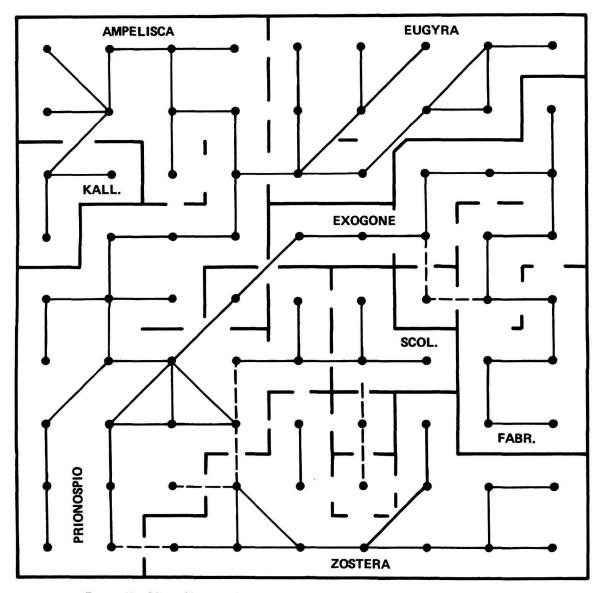


FIGURE 18.—Maze-grid summarizing Figure 11. Lines connecting centers of sample boxes represent imaginary expansion of 2-dimensional presentation to 3-dimensions.

#### Index

Citations of species in tables and appendices omitted unless species is cited only in those places; but minor species generally cited only once, either in a table or in one appendix. Names of genera and communities in text are cited as binominals in index. a=appendix; t=table.

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