

ORGANISM-SEDIMENT RELATIONSHIPS ON A MODERN TIDAL FLAT,
BODEGA HARBOR, CALIFORNIA

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ABSTRACT

Sandflats in the protected Bodega Harbor are inhabited by a diverse infaunal assemblage (over 200 species) consisting predominantly of molluscs, polychaetes and other worm-like animals, and crustaceans. Sediment generally is well sorted, fine to medium grained sand with small amounts of silt and clay. Although ripples are formed by wind-driven and tidal currents, micro-cross-lamination and other physical sedimentary structures are later obliterated by intense bioturbation. On the upper tidal flat the thalassinid shrimp *Callianassa californiensis* is an active deposit feeder. It produces predominantly staghorn-shaped burrow networks which extend 40 cm or more below the sediment-water-interface. The deposit-feeding tellinid bivalve *Macoma secta* inhabits the middle sandflat and is also an important bioturbator. On the lower flat the phoronid *Phoronopsis viridis* is abundant, producing dense clusters of vertical tubes. In general suspension feeders live more deeply within the sediment than do deposit feeders. Deposit feeders are abundant throughout the flat; they tend to burrow more deeply in sediment of the high flat than in that of the low flat.

Gradients in species abundances from mean lower lower water to higher areas on the flat suggest that physical factors such as exposure time are important controls of the species' distributions. However, experimental field studies in Bodega Harbor have shown that ecological interactions between species may also affect distributions (Ronan, 1975). Presence of phoronids in great abundance prohibits attainment of normal burrowing depths by *M. secta*, and in areas of overlap between phoronids and *Callianassa californiensis*, there is a high incidence of broken and disturbed phoronid tubes. Thus biological activity may affect, directly or indirectly, the distributions of infaunal animals. The same may also have been true in the past, and ichnocoenoses should be viewed as reflecting interactions between animals as well as between the animals and their physical environment.

INTRODUCTION

Purpose

The purpose of the Bodega Harbor portion of this guidebook is fivefold: 1) to briefly describe the physical and geological setting of Bodega Harbor, 2) to discuss sediment characteristics of the sandflat we will be visiting at the northern part of the harbor, 3) to describe the traces made by the dominant trace-makers and delineate their distributions, 4) to illustrate biological interactions on the Bodega sand flat and their implications regarding the structuring of modern and ancient communities, and 5) to discuss distributional controls of traces and possible paleoecologic implications.

Physical Setting

Bodega Harbor is a shallow coastal embayment located in southwest Sonoma County about 65 miles north of San Francisco (Fig. 1 on p. 1). The nearly landlocked embayment is sheltered from prevailing northwesterly winds by a rocky peninsula, Bodega Head, and a beach and dune-covered neck of land to the north that attaches it to the mainland (Fig. 1).

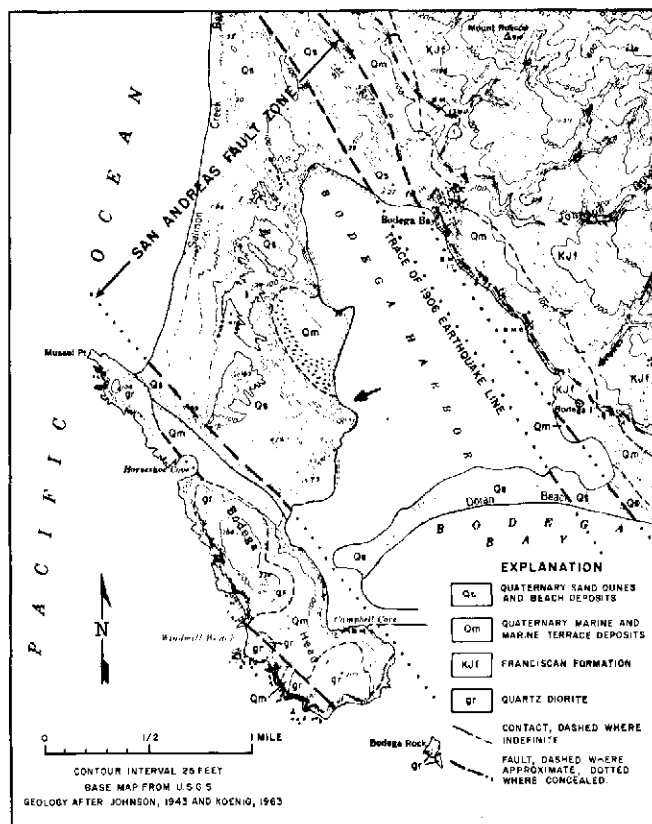


Figure 1. Geologic and location map of Bodega Harbor. Arrow points to sandflat locality. (from Koenig, 1963).

The harbor is bounded on the south by Donan Beach, a dune-covered sandspit that curves out from the mainland toward Bodega Head. On its west end, near Bodega Head, the sandspit is truncated by a narrow tidal inlet and a ship channel that is maintained by dredging. Maximum depths for the harbor (20 to 25 feet) are found in this channel. The harbor entrance is stabilized by two rock jetties that project into Bodega Bay, a broad bight of coastline that stretches south to Point Reyes peninsula. Tidal exchange

through the harbor channel exceeds 80% on the spring tide and 50% on the neap tide (Boyd, 1970); conditions within the harbor are fully marine with salinities from 32-34‰.

The Bodega Bay area includes a variety of exposed, semi-protected, and protected habitats. In the protected environment of the harbor, soft-bottom substrates are especially conspicuous. At low tide (0.0 ft, mean lower low water) some 500 acres of tidal sand and mud flats are exposed, which accounts for more than 60% of the total harbor area. The seemingly monotonous expanses of sand support a diverse marine community dominated by the tellinid bivalve *Macoma*, but consisting of more than 200 described infaunal species (Standing et al., 1975). The intertidal flats may be subdivided into several major subhabitats including high, mid, and low tidal flat, tidal channel and creeks, intertidal pond, and salt marsh; each subhabitat is characterized by particular substrate characteristics and species associations.

Geologic Setting

Bodega Harbor is traversed by the San Andreas fault zone which is locally expressed as a 2.5 km wide zone of intensely sheared bedrock covered by Recent marine and aeolian sediments (Fig. 1). Northeast of the fault zone the Franciscan Formation of Lake Jurassic to Late Cretaceous age (Bailey, Irwin and Jones, 1964, p. 115-123) is exposed. Locally it consists of thick and massively bedded sandstones interpreted as grain-flow deposits (Chipping, 1971, p. 50), whereas elsewhere it shows characteristics of turbidite deposition. To the north the Franciscan is a tectonic melange consisting of blocks of intensely deformed low-grade metagraywacke, shale, chert and greenstone in a sheared shaly matrix, with rare blocks of eclogite, glaucophane schist and other high pressure metamorphic rocks. The co-occurrence of high and low grade metamorphic assemblages is difficult to interpret in detail. In general the sequence appears to have formed by tectonic mixing of elastic wedges shed into a trench environment and high pressure metamorphic rocks formed at much deeper levels within the subduction zone.

The San Andreas fault zone separates Franciscan rocks on the mainland from Late Cretaceous granodiorite exposed on Bodega Head. Structurally the Bodega Head granodiorite is an extension of the Point Reyes granitic block and correlates in age and composition with granitic rocks on Pt. Reyes Peninsula, Tomales Point, the Farallon Islands, and Montara Mountain to the south of San Francisco (Koenig, 1963, p. 6). The Bodega Head granodiorite is significant as the northernmost outcrop of granitic rock west of the San Andreas fault zone.

Marine terraces and recent earthquake activity indicate that vertical and lateral movement has continued to the present. Late Pleistocene to Recent uplift resulted in the elevation of marine terraces, and higher terraces overlain by Upper Pliocene marine sediments occur farther inland. The most recent movement along the San Andreas Fault in the Bodega Bay area occurred during the San Francisco earthquake of 1906. Maximum right lateral displacement of 21 feet during that event was recorded near Olema in Marin County; vertical movement at Bodega Head was 18 inches, with the west side upthrown (Koenig, 1963, p. 7-9).

Submerged topography in estuaries around Bodega Bay indicates a sea level rise during the last 11,000 years since the last glacial advance. The dynamic interplay of vertical and lateral movement, changing sea-level, and nearshore sedimentation processes have undoubtedly been complex during the history of the Bodega Bay area. Bodega Head and smaller crustal blocks caught up within the fault zone probably have played an important role in the evolution of Bodega Harbor by creating obstructions to southward flowing sediment-laden longshore currents.

ECOLOGICAL STUDIES OF SOFT BOTTOM COMMUNITIES

AND THEIR IMPORTANCE TO ICNOCENOSES

The utility of trace fossils in paleoenvironmental interpretation has been demonstrated repeatedly (Crimes and Harper, 1970; 1975; Frey, 1975). It is based upon the correlation of changes in ichnocoenoses with changes in depth and related environmental factors such as wave and current activity and substrate characteristics. The assumption behind ichnological research has been that most marine communities, especially shallow-marine communities are "physically accommodated", i.e. controlled by physical environmental parameters (Sanders, 1969), and are maintained at low successional stages by physical environmental instability (Johnson, 1972).

As pointed out by Rhoads (1975), Osgood (1975) and Pickerill (1976), trace fossils also provide important information about the nature of soft-bottom communities. Estimates of the percentage of soft-bodied species in modern communities whose only record would be as trace fossils in paleocommunities range from 7% to 68% (Lawrence, 1968; Schopf, 1978). Clearly, soft-bodied organisms are important in the ecological structure of modern and presumably ancient communities. Knowledge of the traces made by various soft-bodied animals and of the interactions between these organisms may aid in the interpretation of paleocommunities. The use of x-radiography in observing and documenting the interactions of infaunal species with the substrate has been especially enlightening (see Howard, 1968; Howard and Elders, 1970; Howard and Dorjes, 1972), and this technique also has important applications to the study of ancient sediment-organism relationships (Howard, 1972).

The most important advances in the understanding of the ecology of modern soft bottom communities have come through the application of experimental field methods similar to those developed for rocky intertidal substrates by Connell (1961), Paine (1966), and Dayton (1971). Studies in soft-substrate shallow marine communities have revealed that biological interactions play an important role in structuring the community and in modifying the physical environment (e.g. Sanders, 1958; Rhoads and Young, 1970; Rhoads, 1973; Woodin, 1974, 1976; Kitchell (1979) has suggested that the same may be true in deep sea environments. Ancient communities may also have been structured in part by biological interactions which would have affected the distributions of trace-producing animals. Occurrences of trace fossils outside their typical ichnofacies may be a result of ecological interactions. Perhaps more information can be gained about the structure of paleocommunities if the trace-fossil assemblage, the only record of the soft bodied fauna, is viewed as potentially biologically accommodated rather than necessarily physically controlled.

SEDIMENT CHARACTERISTICS OF BODEGA HARBOR TIDAL FLATS

Sediment Source and Texture

The primary source of sediment is medium to fine grained sand from the Salmon Creek dunes which is carried by wind southward into Bodega Harbor. Although in the past, especially after overgrazing in the mid 19th century, this has provided enough sediment to partially fill the harbor, stabilization of the dunes by dune grass in the 1930's greatly reduced the amount of sediment entering the harbor so that now there is very little deposition. Of secondary importance is poorly sorted coarse-grained sand derived from the granite of Bodega Head and deposited near the harbor entrance.

There are several trends in grain size of sediment within the harbor. The first is a general decrease in grain size away from the inlet. Coarse granite-derived sand is present locally near the entrance, but passes laterally into moderately well to well sorted medium to fine grained quartz-rich sand which covers most of the harbor; at the northernmost corner fine sand, silt, and mud deposited during periods of quiet water at maximum flood tide is abundant. The second trend is a decrease in sand-grain size from high to low elevations across the tidal flat (Table 1). In part this trend is related to the dominance of algal cover at lower tidal levels or within bodies of standing water in higher areas of the flat. The algal cover in many places is dense enough to decrease current velocities sufficiently to allow deposition of fine grained sediment. The algal cover itself also contributes fine organic material. The trend toward fining toward lower elevation does not hold for tidal channels, which are floored with coarser sand and lag deposits of pebbles and shells.

Grain size parameter	<u>Callianassa</u> bed	<u>Macoma secta</u> bed	<u>Phoronopsis-Macoma secta</u> bed
coarse (%)	13.72	13.0	6.12
medium (%)	72.07	70.24	62.76
fine (%)	12.46	13.87	30.61
silt + clay (%)	1.75	2.89	.51
surface sand + mud	65.23	68.0	63.66
6 cm depth; sand: mud	56.14	36.0	65.33
sorting (graphic s.d.)	.490 well sorted	.563 moderately well sorted	.448 well sorted

Table 1. Textural characteristics of north sandflat sediment. The Callianassa bed is on the upper flat, the Phoronopsis-Macoma secta bed is on the lower flat, and the M. secta is on the lower flat. (From Ronan, 1975).

Physical Sedimentary Structures

The most common physical structures observed on the harbor sand flats are transverse ripples and drag or prod marks produced by floating algae or wood (Plate 1B,C). Bed forms usually preserved were produced by ebb tidal currents, although patches of interference ripples may be present where the ebb tide ripples have been superimposed over the flood tide forms without completely destroying them. As is typical for most tidal flats, the ebb and flood tide ripple sets are usually developed at a high angle to one another. Very small ripples, generated by wind induced bottom currents are often visible on the surfaces of the large tidal current ripples. Usual orientations of these small ripple forms reflect the northwesterly winds which dominate this area. Primary sedimentary structures are rarely observed in subsurface cores of the Bodega Harbor sand flats. Apparently, the intense reworking of the sediments by the burrowing infauna completely obliterates the primary fabric of the sandflat sediments in a very short time.

The presence of thin diatom mats which frequently cover large areas of the upper and mid flat may serve to stabilize the sediment and inhibit formation of ripple marks. Ronan (1973) observed that ripples are usually absent where the diatom mats are present.

Effects of Animals on the Sediment

Infaunal animals affect the compaction and water content of the sediment and the formation of physical sedimentary structures.

Compaction may be measured with a simple penetrometer consisting of a bar on which bar-bells of various weights are placed. Penetrometer data for approximately the middle, upper, and lower portions of the sandflat in the north part of the harbor are given in Table 2. The upper flat is covered with a crust 2 to 3 cm in thickness which resists penetration; this crust probably is related to long emergence time and dessication by the wind. Below this level the sediment is poorly compacted, as indicated by the deep penetration (33 cm) when sufficient weight was added to break through this crust.

	North Sandflat			South Sandflat	
Loadings	<u>Callianassa</u> bed	<u>Macoma secta</u> bed	<u>Phoronopsis-Macoma secta</u>	<u>Phoronopsis-Macoma Nasuta</u>	
5 lbs.	0.5 cm	1.0 cm	0.5 cm	1.0 cm	
74 lbs.	1.0 cm	2.5 cm	1.0 cm	1.0 cm	
12% lbs.	2.0 cm	5.5 cm	2.5 cm	1.5 cm	
22½ lbs.	33.0 cm	15.0 cm	7.5 cm	4.0 cm	

Table 2. Penetrometer data for localities on north and south sandflats (after Ronan, 1975, Table 3).

Callianassa californiensis is a thalassinid crustacean which constructs burrow networks to a depth of 40 cm. or more. Its burrowing activity serves to loosen the sand and reduce compaction. Similarly, in the mid flat Macoma secta bed, the maximum penetration depth correlates well with the common burrowing depth of this mobile tellinid bivalve. Near MLW, the maximum penetration depth (7.5 cm) corresponds roughly with the average depth of the tops of phoronid tubes. In

the south sandflat near the inlet where active burrowers are absent and only the sessile *M. nasuta* and *Phoronopsis* are abundant, the sediment is more highly compacted (Table 2). Apparently the burrowing of *Callianassa* and *Macoma* secta decrease compaction whereas the tubes of the sessile *Phoronopsis* either increase it or do not affect it.

In the *Callianassa* bed (upper sand flat) Water content increases with depth (Table 3); and where *M. secta* is present (middle and lower flat) it remains roughly constant or decreases slightly with depth. This contrasts with the south sandflat where *Callianassa* and *Macoma* secta are both absent, but where sessile forms are present (Table 3). Bioturbation by mobile forms probably loosens the sediment, allowing a greater interstitial volume for accumulation of water.

Core Increments	North Sandflat		South Sandflat	
	<i>Callianassa</i> bed	<i>Macoma</i> <i>Secta</i> bed	<i>Phoronopsis</i> - <i>Macoma</i> <i>secta</i> bed	<i>Phoronopsis</i> - <i>Macoma</i> <i>nasuta</i> bed
Top 10 cm	19.85%	19.53%	20.45%	32.03%
Middle (10-20 cm)	20.71%	18.61%	18.97%	19.15%
Bottom (20-30 cm)	41.40%	18.42%	18.05%	11.91%

Table 3. Averaged water content, in percent from replicate cores on the north and south sandflats in Bodega Harbor (after Ronan, 1975, Table 2).

Ronan (1973, 1975) suggested that the tubes of *Phoronopsis viridis* prevent the formation of ripple marks as well as increasing the sheer strength of the subsurface sediments. This is in accord with Featherstone and Risk (1977) who showed that dense stands of tube-building stabilize surface sediments and inhibit the formation of ripple marks on tidal flats in the Bay of Fundy.

THE SANDFLAT COMMUNITY OF BODEGA HARBOR

Distribution of the Animals on the Sandflat

Transect surveys across the north tidal flat of Bodega Harbor over a period of years have demonstrated a distinct pattern of zonation of infaunal species with respect to elevation above MLLW (mean lower low water). The vertical zonation for a few of the most abundant of the more than 200 infaunal species present on the flat is illustrated in Fig. 2.

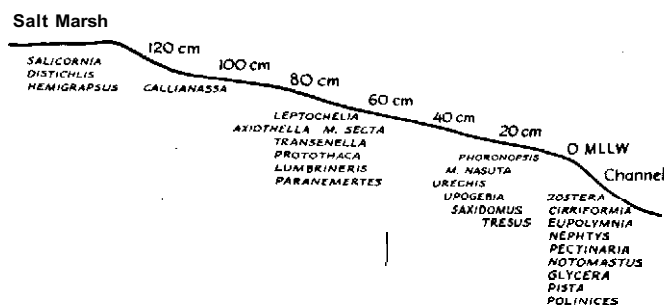


Figure 2. Distribution of major infaunal species relative to elevation above mean low tide, north sand flat, Bodega Harbor (after Ronan, 1973).

At MLLW and low tides of the eel grass (*Zostera*) are abundant and the common animals include one snail (*Polinices*) and several polychaete worms (*Cirriformia*, *Eupolyornia*, *Nephtys*, *Pectinaria*, *Notomastus*, *Glycera*, and *Pista*). Slightly higher a phoronid worm (Phylum Phoronida, *Phoronopsis*), an echiuroid worm (Phylum Echiurida, *Urechis*), a thalassinid crustacean (*Callianassa*), and the bivalves *Macoma nasuta*, *Tresus*, and *Saxidomus* are common. The fauna of the midflat consists of polychaetes (*Axiiothella*, *Lumbrineris*), a nemertean worm (Phylum Nemertinea, *Parameletes*), bivalves (*Macoma secta*, *Transenella*, *Protothaca*) and a canaid crustacean (*Leptochelia*). The thalassinid shrimp *Callianassa* is abundant in the high intertidal, and in the marsh the shore crab *Hemigrapsus* constructs burrow systems around the roots of the marsh plants *Salicornia* and *Distichlis*.

An illustration such as Fig. 2 gives the impression that faunal changes are quite abrupt. Actually, the sandflat is over .4 km wide, so that changes in elevation and substrate characteristics over the sandflat are gradual. The fairly continuous environmental gradients are reflected in broad ecotones where species intergrade.

Burrow Morphology and Feeding Type

Burrow morphology, maximum depth of burrowing, feeding type and habitat of the common trace producers on the sandflat at Bodega Harbor are given in Table 4. It should be noted that many animals produce traces which do not fit neatly into one category. For instance, *Glycera robusta* has a U-shaped burrow the arms of which are linked by a cross-burrow, and the thalassinid shrimp *Callianassa* produces a staghorn shaped burrow network. Surface traces and burrow openings of some of the trace producers as well as radiographs of burrowed sediment are illustrated in Plates 1, 2. This table and the plates may serve as a guide in identifying biogenic structures on the sandflat.

An abbreviated form of this table summarizing some of the information about the traces made by the common suspension and deposit feeders in high and low tidal flat areas is given in Table 5. Many of the worm-like animals listed as deposit feeders are actually omnivores feeding on a variety of food resources within the substrate including encrusted grains, fragments of eelgrass, metazoans, and fecal pellets; the relative importance of food items differs from species to species (Ronan, 1977). Other animals are trophic generalists, utilizing both deposit and suspension feeding, and the relative contributions of each are difficult to assess.

Discussion

Data given in Tables 4 and 5 about the animal-sediment relations of burrowers in Bodega Harbor reveal several interesting facts and trends. The first is that the sediment is highly reworked; rate of churning by animals clearly exceeds rate of sediment accumulation or reworking by wave and current activity. Physical sedimentary structures such as ripple marks are produced but would not be preserved in the sedimentary record.

A second notable fact is that deposit feeders are abundant throughout the sand flat, even in the highest areas where the sediment is very clean aeolian sand. This indicates that suspension feeders in vertical or U-shaped tubes are not the only or necessarily even the dominant infaunal elements in clean intertidal

Habitat/
Species

Subsurface Trace Characteristics (Diameters are for structures produced by adults)

LOWER SANDFLAT Phylum Phoronida <i>Phoronopsis viridis</i> (Plate 1GGI)	Vertical cylindrical tubes (rarely crooked) up to 3 cm in diameter.				
<i>Annelida</i> /Polychaeta <i>Girri-formia</i> <i>Spirambramcha</i>	Variable: Straight shafts to J-shaped burrows 5 mm in diameter; vertically oriented	Cone-shaped mounds of fecal pellets, 1 cm high. Density = 15-20/m ² , 1 opening/individual.	22 cm; tube top is flush with the surface.	Deposit-feeding omnivore (tentacle feeding at and just below SWI).	Produces mottled sediment by tentacular movement and lateral movement of entire worm. Abundant in eelgrass beds. Trace fossil: <i>Skolithos</i> , <i>Arenicolites</i> , <i>Chomatichnus</i> .
<i>Eupolymnia</i> <i>Crescentis</i> (Plate 2B)	Weakly agglutinated U-shaped tubes 3 mm in diameter.	Cone-shaped, mucous-rich mounds 1 cm high, 2 openings/individual; density (ind.) = 7/m ² .	13 cm	Deposit-feeding omnivore (tentacle feeding at surface)	<i>Amphipods</i> burrow in mound. Trace fossils: <i>Arenicolites</i> , <i>Chomatichnus</i> .
<i>Glycera</i> <i>robusta</i> (Plate 2D)	U-shaped burrow 5 mm in diameter, with gallery connecting arms of U. Abundant explanatory burrows make system complex and variable.	2 holes (1 cm in diameter)/individual; density (ind.) = 1/m ² .	18 cm	Deposit-feeding, raptorial, sub-surface omnivore.	Trace fossil: <i>Arenicolites</i> (irregular and modified).
<i>Pectinaria</i> <i>californiensis</i> (Plate 2B)	Cone-shaped agglutinated dwelling tube used as an exoskeleton; up to 1 cm in diameter.	Tapered end of tube projects just above SWI. Produces cone shaped depressions or mounds of finer sediment 1 cm high, 2 cm diameter. One tube/individual; density = 2.5/m ² .	10 cm	Subsurface deposit-feeding omnivore	Migrates laterally 1-2 cm/week; produces mottled sediment. Trace fossil: <i>Chomatichnus</i> .
<i>Pista</i> <i>Pacifica</i>	Agglutinated (fine sand, shell fragments) vertical cylindrical tubes, 1.5 cm in diameter.	Tube extends up to 5 cm above SWI, One tube/individual; density = 1/m ² .	65 cm	Deposit-feeders extends many tentacles over sediment surface.	Found where eelgrass not abundant. Trace fossil: <i>Skolithos</i> , <i>Phoebichnus</i> .
<i>Nephtys</i> <i>coecoides</i> (Plate 2B)	Weakly consolidated, recumbent Y-shaped tubes 1 cm in diameter; may be interconnected.	Openings commonly occluded by sediment, 2 openings/individual; density (ind.) = 6/m ² .	15 cm; rare below 12 cm, most common in top 5 cm.	Subsurface omnivore. Deposit feeder; predator.	Active burrower; can withstand burial by 30 cm of sediment. <i>N. coecoides</i> prefers muddy sand, <i>N. californiensis</i> prefers clean sand.
<i>Natomastus</i> <i>magnus</i> (Plate 2A)	Irregular burrows; 5 mm in diameter; many horizontally oriented. Burrow systems do not open to surface. Density (ind.) = 2/m ² .		25 cm; is deepest active burrowing polychaete on sand-flat.	Deposit feeder,	Reversible proboscis used in locomotion and feeding, produces localized expansions of burrow wall, Trace fossil: <i>Planolites</i> (burrow not back-filled).
Phylum Mollusca Class Gastropoda <i>Polyplacis lewisii</i>	Not well known; ? Irregular pathways through upper 10 cm of sediment! snail is buried to apex of shell,	May produce low mound on surface above shell. (East coast species produces ridged trails of varying morphology on surface).	15 cm	Carnivore; preys on shallow dwelling bivalves,	Common at channel margins or in intertidal ponds. Produces concave borings in umbo of prey, and also egg cases of mucous-bound sand.

	Surface Trace	Maximum Depth	Feeding Type	Comments
Class Bivalvia <i>Yacoma nasuta</i>	Irregular "burrows" through which siphons extend to surface.	10 cm	Primarily suspension feeder, but known to deposit feed at surface.	Common in muddy sands (south flat) near MLW. "Bent nose clam".
<i>Saxidomus nuttalli</i>	Vertical roughly cylindrical shafts, expanding downward. Elliptical in cross-section.	95 cm	Suspension feeder	
Phylum Arthropoda Class Crustacea <i>Upogebia ugettepsis</i>	Y-shaped to complex branching burrows up to 5 cm in diameter. Walls are smooth and mud-lined.	70 cm	Suspension feeder	Prefers muddier sediment than Callianassa. Same commensals as Callianassa. Trace fossil: ? <i>Ophiomorpha</i>
Phylum Echinurida <i>Eurechis caupo</i> (Plate 1CE)	U-shaped with constricted arms. Arms 2Q to 8Q cm apart near surface.	45 cm near MLW 60 cm on middle flat.	Mucous net suspension feeder	Able to turn around in burrow and switch incurrent-excurrent openings. Commensals include a scale worm, a pea crab, and a goby fish. Trace fossil: <i>Arenicolites</i> .
MIDDLE FLAT Phylum Annelida <i>Axothella</i> <i>Rubrocincta</i> (Plate 1CH) Phylum Nemertea <i>Paranemertes peragrina</i> (Plate 1B)	Subvertical to vertical cylindrical tubes 5 mm in diameter consisting of mucous. Found fine sand. Irregular	Tubes 1Q cm long, 15 cm to max burrow depth. Unknown	Deposit feeder	Trace fossil: <i>Skolithos</i>
Phylum Arthropoda Class Crustacea (tanaid) <i>Leptochelia dubia</i>	Weakly cemented, multi-branched tubes.	12 cm; concentrated near surface, 5Q cm	Deposit-suspension feeder	Extremely abundant in mud-dier areas; especially on south sandflat. Disturbs upper 4 cm.
Phylum Mollusca Class Bivalvia <i>Macoma secta</i> (Plate 1CG)	Irregular; lies on left valve and extends siphons to surface.	Commonly 10-30 cm	Deposit-feeder, primarily; periodically suspension feeds.	Most abundant deposit feeder; mid flat. Shows depth stratification by size, with longer deeper. Trace fossil: ? <i>Häntzschelina</i>
<i>Protothaca staminea</i> (Plate 1K) HIGH FLAT	Local bioturbation.	8 cm	Suspension feeder	Prefers clean sands of mid flat.
Phylum Arthropoda Class Crustacea (thalassid) <i>Callianassa californiensis</i> (Plate 1ADJ; 2C)	Unlined multibranched galleries 1-5 cm in diameter, connected to surface by vertical shafts. Bulbous swellings (turn arounds) at bifurcations.	60 cm	Deposit feeder	Prefers clean sands of high intertidal. Many commensals. (see section on natural history). Trace fossil: <i>Thalassinoides</i> .
<i>Hemigrapsus oregonensis</i> (brachyuran)	Shallow U-shaped excavations with lateral galleries.	1Q cm	Omnivore (Scavenger)	Usually 2 or more individuals per burrow. Forage on marsh at low tide. Trace fossil: Name named, similar to burrows described by Miller, 1977a.

Table 4. Biogenic structures produced by and feeding habits of common infaunal animals in the lower, middle and upper sandflat in Bodega Harbor. Data from Ronan (1973, 1977) and observations of Farmer, students at Bodega Marine Lab, and Miller.

sands. Encrusted grains and plant fragments, and fecal pellets apparently provide sufficient food resources even though the percent of silt and clay, which correlates with organic carbon content, is low.

Other points of interest involve the maximum depths to which suspension and deposit feeders burrow. Suspension feeders live much more deeply than deposit in both high and low tidal areas. Similarly, Rhoads (1967) found that suspension feeders on tidal flats live much more deeply (>30 cm) than do subtidal deposit feeders (<10 cm). The deeper burrowing of suspension feeders within the tidal flat may be related to mobility. Suspension feeders tend to be more sessile than deposit feeders (Schopf, 1978) and thus are less able to move to avoid environmental perturbations. (The suspension feeders also tend to be larger, which would also decrease mobility.) A deep burrowing habit provides a buffer as protection from changes affecting the sediment-water interface. The fact that Urechis burrows more deeply on the mid flat, where exposure would be greater than on the low flat, supports this hypothesis. Conversely, algal and bacteria encrusted sand grains, metazoans, and fecal pellets would all be most abundant in the upper part of the sediment column; thus, it is not surprising that most deposit feeders are relatively shallow burrowers.

A final observation is that on the average deposit feeders burrow more deeply on the upper flat than lower flat (Table 5); the deep burrowing Callianassa and Macoma secta are responsible for this trend. Possible reasons for this may be that the upper flat is exposed for longer periods of time during the tidal cycle and thus the animals must burrow deeper to avoid dessication or that bird predation is more intense on the upper flat.

MLLW to LOW FLAT	Deposit Feeders	Maximum Depth (in cm)
SUMMARY:	U-shaped:	13, 18
max depth:	<u>Eupolymnia</u> , <u>Glycera</u>	
\bar{x} =16.8 cm;	Y or J shaped:	22, 15
s.d.=5.2	<u>Cirriformia</u> , <u>Nephtys</u>	
range: 10-	Complex branching:	18
25 cm	<u>Glycera</u> Irregular:	10, 15, 25
	<u>Pectinaria</u> , <u>Nephtys</u> , <u>Notomastus</u>	
SUMMARY:	Suspension Feeders	
max depth:	U-shaped: <u>Urechis</u>	45
\bar{x} =61.4 cm;	Y or J-shaped: <u>Upogebia</u>	70
s.d.=38.5	Vertical: <u>Pista</u> , <u>Tresus</u>	65, 120
range: 10-	<u>Phoronopsis</u> , <u>Saxidomus</u>	25, 95
120 cm	Irregular: <u>Macoma nasuta</u>	10
	Predators	
	Irregular: <u>Polinices</u>	15
MID TO UPPER FLAT		
SUMMARY:	Deposit Feeders	
max depth:	Y or J-shaped: <u>Callianassa</u>	60
\bar{x} =34.3 cm;	Complexly branching:	
s.d.=24.3	<u>Leptochelia</u> , <u>Callianassa</u>	12, 60
range: 12-	Vertical: <u>Axiuthella</u>	15
60 cm	Irregular: <u>Macoma secta</u>	50
SUMMARY:	Suspension Feeders	
max depth:	U-shaped: <u>Urechis</u>	60
\bar{x} =42.5 cm;	Vertical: <u>Phoronopsis</u>	25
s.c.=24.7		
range: 25-		
60 cm		

NATURAL HISTORY AND ANIMAL SUBSTRATE RELATIONS OF DOMINANT INFAUNAL ANIMALS IN BODEGA HARBOR

Callianassa californiensis

One of the most abundant animals in the middle to high intertidal areas in Bodega Harbor and other west coast lagoons is the burrowing thalassinid ghost shrimp Callianassa californiensis (Plate 1D). Thalassinid shrimp are decapod crustaceans, of the Suborder Reptantia which includes crawlers such as lobsters, hermit crabs, and crabs. Because one thoracic appendage is reduced in thalassinids, they are included in the Section Anomura (hermit crabs) by some taxonomists; others put them in the Section Macura (lobsters). Thalassinids are widely distributed in marine and estuarine environments, where they are active burrowers. Burrows are highly variable, but most consist of deep networks with both horizontal and vertical components marked by expansions serving as turn-around areas. Trace fossils interpreted as thalassinid in origin include Thalassinoides and Ophiomorpha; the latter has been extensively reviewed by Frey et al, 1978.

Along the central coast of California there are 3 species of thalassinid shrimp: C. californiensis, C. gigas and Upogebia pugettensis. C. gigas is rare. Upogebia pugettensis builds from U- or Y-shaped burrows in mud or muddy sand (Smith and Carlton, 1975). MacGinitie (1934) generalized that C. californiensis preferred muddy sand substrates. However, in both Mugu Lagoon (located 50 miles NW of Los Angeles) and Bodega Harbor it is most abundant in clean sand, occurring in densities of 170/m² (Mugu Lagoon) and 35/m² (Bodega Harbor) (Ronan, 1975; Miller, 1977b). In some areas the surface is covered with mounds, craters and burrow openings which are the surface representations of the three dimensional burrow systems of C. californiensis (Plate 1A).

Burrows and burrowing: Ronan (1975) studied the morphology of burrows constructed by Callianassa californiensis in Bodega Harbor and determined that the burrows are basically staghorn shaped with horizontal branches (Plate 2C). In areas of Bodega Harbor where sediment is poorly oxygenated and black, C. californiensis burrows have rust-colored, oxygenated halos, indicating that they are often flushed with oxygenated water.

The number of burrow openings per burrow system is not known, nor is it readily determined by resin casting. Warne (1967) found that under laboratory conditions C. californiensis burrows have two or more openings. There are apparently many more burrow openings than shrimp in Mugu Lagoon. Numbers of burrow openings at the surface and number of shrimp present to a depth of 50 cm were determined for 48 cores from muddy and sandy sediments in Mugu Lagoon (Miller, 1977b); results are shown in Fig. 3.

C. californiensis unlined burrows collapse readily when excavated. This has lead several workers (Thompson and Pritchard, 1969; MacGinitie, 1934) to suggest that the burrows are impermanent. However, using radiography and laboratory observations Ronan found that only disturbed or abandoned parts of the burrow system were collapsed. The facts that C. californien-

Table 5. Common producers of biogenic structures on the lower sandflat and middle to upper sand flat and their burrow shapes and maximum depths. Data from Table 4.

sis continually removes fecal material from the burrow, that it constructs turn-around spots and side branches, and that its burrows are inhabited by commensals (e.g. *Cryptomya californica*) are evidence that burrows are permanent, for these are attributes characteristic of other shrimp inhabiting permanent burrows.

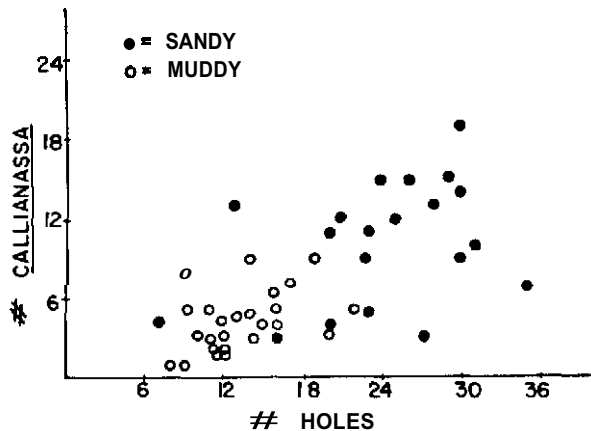


Figure 3. Number of burrow openings at surface vs. number of *Callianassa* recovered from .06 m² cores taken in sandy and muddy sediments of Mugu Lagoon (from Miller, 1977b, Fig. 19).

The depth to which *Callianassa californiensis* burrows is not certain. Although Thompson and Pritchard (1969, p. 116) did not find *Callianassa* in the upper 45 cm during low tide, and Wame (1971) indicated that its burrows extend 75 cm or more into the sediment, other evidence suggests that most of its activity occurs closer to the SWL. MacGinitie (1934) found that the burrowing mostly is confined to the upper 45 cm. Fig. 4 shows the depth distribution of *C. californiensis* recovered from hand excavated cores in sandy or muddy sediments in Mugu Lagoon during low tide. Most individuals occur from 15 to 30 cm deep, although some may extend beneath the 50 cm core depth. In muddy sediments *C. californiensis* rarely recovered from depths greater than 40 cm.

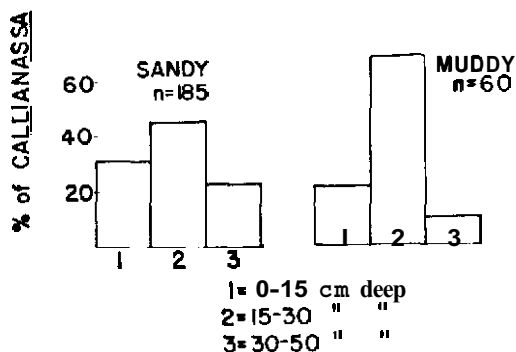


Figure 4. Vertical distribution of *Callianassa californiensis* within sediment column in sandy and muddy substrates, Mugu Lagoon (from Miller, 1977b, Fig. 17).

The burrowing of *C. californiensis* profoundly affects the sediment. Burrows provide conduits for well oxygenated water to penetrate to greater depths than would otherwise be possible. Reworking of sediment destroys primary sedimentary structures and re-

duces compaction, which, in conjunction with void space provided by the burrows themselves, results in a very loosely packed, water-rich substratum. Burrowing also alters the vertical grain size distribution of the sediment.

Ronan (1975) implanted laminae of fine-grained lead in the *Callianassa* beds in Bodega Harbor and documented subsequent lead movement with a series of radiographs of cores; there was significant lead dispersal after 7 days. MacGinitie and MacGinitie (1949, p. 287) estimated that 20 to 50 cc of sand are deposited around the entrance of a burrow of *C. californiensis* per day. Using observed densities of shrimp and burrow openings per .06 m² core in sandy and muddy sediments in Mugu Lagoon, and making the assumption that each individual deposits sediment around only one burrow opening in a 24-hour period, it is estimated that in a 24-hour period *C. californiensis* deposits on the surface a layer of sediment 3.4 to 8.5 mm thick in the sandy areas, and 1.5 to 3.8 mm thick in the muddy areas. This implies that populations of *C. californiensis* in Mugu Lagoon overturn the top 50 cm of sediment, in which most live, in a period of 117 to 330 days. As Wame (1967) pointed out, the rate of reworking greatly exceeds the sedimentation rate of approximately 1 m/100 yrs.

Mass properties of the sediment including water content and stability are strongly affected by *C. californiensis* burrowing. As shown in Table 2, Ronan found a two-fold increase with depth in the water content of cored sediment from the *C. californiensis* zone in Bodega Harbor. This contrasts with cores from other parts of Bodega Harbor, in which water content decreases with depth. Penetrometer data, which reflects sediment stability, is given in Table 2. In Mugu Lagoon where the sediment texture is similar to that of the north sandflat of Bodega Harbor but the density of *Callianassa* is higher, the penetrometer sank 6 cm with the maximum loading of 5 lb. This indicates that sediment stability is correlative with amount of burrowing activity.

Substrate preference and feeding habit:

Although MacGinitie (1934) reported that *C. californiensis* prefers muddy sediments, within Bodega Harbor and Mugu Lagoon it occurs in greatest densities in clean sands. In Bodega Harbor, however, it is present in impacted clay muds of the high intertidal flat at the southeast end of the harbor. Another thalassinid shrimp, *Upogebia pugettensis*, is more characteristic of muddy sediment than *C. californiensis*. Miller (1977b) quantitatively compared densities of *C. californiensis* in sandy (mean 2.9% silt and clay; mean 2.05 phi sand fraction) vs. muddy (mean 15.9% silt and clay; mean 1.99 phi sand fraction) sediments within Mugu Lagoon. For 24 samples each .06 m² in diameter excavated to a depth of 50 cm, there was a mean of 10.2 shrimp in the sandy sediments compared to 4.7 in the muddy sediment.

Feeding habit and substrate preference are closely related for many benthic marine invertebrates. As documented by many authors (e.g. Sanders, 1958; Purdy, 1964) deposit feeders dominate in fine grained sediments whereas suspension feeders are more abundant in sands deposited under higher energy conditions. In fine-grained sediments small particles of organic debris are included in the sediment, and the small sized grains provide a large surface area for attachment of micro-organisms. In contrast, food particles in higher energy environments tend to be kept in suspension, leading to a predominance of sus-

pension feeders.

Feeding habits of callianassid shrimp vary from species to species; there is also evidence that some species combine suspension and deposit feeding. *Callianassa filholi* primarily deposit feeds, although Devine (1967) observed a specimen in an aquarium flicking sediment into the water column and feeding on the material as it settled. *C. major* is considered to be a suspension feeder, but has also been found to sift sand for microscopic particles of organic matter (Pohl, 1946, p. 77, 80).

There is little agreement about the diet of *Callianassa californiensis* or about the method of feeding. According to MacGinitie (1934, p. 169) *C.iforniensis* is a deposit feeder, feeding on minute detrital particles in the sediment. He observed *C. californiensis* feeding on fine grained sediment and also cited the presence of chitinous structures within the gut as evidence of a deposit-feeding habit. Ricketts and Calvin (1968) and Warne (1971) concurred with this interpretation, and Peterson (1978) considered *C. californiensis* a deposit feeder in his study of the structure of the soft-bottom community in Mugu Lagoon. However, Powell (1974) suggested that *C.iforniensis* may obtain a significant portion of its nutrition from suspension feeding. He noted that *Callianassa californiensis* is most abundant in very clean sands in Bodega Harbor, where the supply of organic debris would be quickly depleted by a population of deposit feeders. Although he interpreted structures of the foregut as adaptations for dealing with inorganic grains, he did not see their presence as necessitating a deposit feeding habit; they would also handle grains inadvertently taken into the digestive system during burrowing activity. Powell (1974, p. 29) found that the mouth parts of *C. californiensis* closely resemble those of the suspension feeding *Upogebia pugettensis*.

In Bodega Harbor during much of the year the tides deposit large quantities of algae (*Ulva*) on the *C. californiensis* bed; the algae is subsequently buried by drifting sand and sand brought to the surface by *C. californiensis*. Ronan (1975, p. 139) found sizable pieces of *Ulva* in 29 of 40 samples excavated by hand in the *C. californiensis* bed; some even had ghost shrimp clinging to them. The presence of plant material in the gut contents of shrimp is further evidence that the detritus and its epiflora is an important food source.

In Mugu Lagoon there is not enough plant debris present in the clean sands to support the large population size of *C. californiensis*. Miller (1977b) suggested that the main food source may be epigranular flora. Rapid replenishment of bacterial films on grains would be enhanced by the diurnal movement of nutrient and oxygen-rich waters through the highly porous sediment honeycombed with burrows.

Conclusions about *C. californiensis* are difficult to draw, although it is likely that deposit feeding provides some or all of its nutritional needs.

Ability of *C. californiensis* to withstand sedimentation: There have been no systematic field studies in Bodega Harbor on the ability of *C. californiensis* to withstand rapid sedimentation. However, an extensive bed of *C. californiensis* is located near drifting blowing dunes so that clean sand is added to the sand flat by prevailing winds. Storm induced dune slumps

can result in as much as a foot of sediment being added to the flat. Apparently little mortality results from such mass deposition, for within 24 hours numerous mounds and crater-shaped burrow openings appear, indicating that shrimp have regained contact with the sediment-water-interface.

Studies in Mugu Lagoon have shown that *C.iforniensis* responds differently to disturbance and sedimentation in subtidal vs. intertidal areas. Peterson (1978, p. 345) effectively removed *C.iforniensis* from a large area (6 x 20 m) of the subtidal channel by walking over the surface and disturbing the top 5 to 10 cm of sediment; 24 hours later no burrow openings had reappeared. Based on rate of reappearance of burrow openings, intertidal ghost shrimp are more able to survive disturbance. Miller (1977b) trampled a 25 square foot area in the intertidal zone densely populated with *C. californiensis*. After a week it was impossible to distinguish between the trampled and undisturbed areas. Rate of appearance of burrow openings appeared to be uniform throughout the disturbed area. Although ghost shrimp bodies were not seen on the sediment surface, many *Callianassa* must have been killed by the vigorous stomping. Apparent recovery in the intertidal zone may occur by migration of *Callianassa* into disturbed areas rather than re-establishment of contact with the sediment-water interface by the original inhabitants. Average density of ghost shrimp in sand intertidal sediment is 170/m² (Miller, 1977b), whereas in the subtidal sand community it is 87/m² (Peterson, 1978). Space may be at a higher premium in the intertidal areas, resulting in more rapid reburrowing of disturbed areas.

A field method for determining the ability of *C. californiensis* to withstand rapid sedimentation was designed by Miller (1977b). Roughly circular rings of thin fiberglass were sunk several centimeters into the sediment; the resulting enclosures were approximately 1.5 m in diameter and .5 m high. Before emplacement, the number of burrow openings was determined. For each treatment a layer of sand of a predetermined thickness was added. Burrow openings at the surface of the sand were subsequently counted at intervals of hours to days.

This method has several inherent difficulties, of which the primary one is the lack of one-to-one correspondence between *C. californiensis* and burrow openings. Other investigations of anastrophic burial such as that by Kranz (1974) have been laboratory studies on animals which do not produce burrow systems. However, the advantages of adding sediment in the field where the ghost shrimp are undisturbed outweigh the difficulty of not knowing how many shrimp are present and actively burrowing before and after addition of sediment. Other unavoidable problems include the facts that it is difficult to accurately count the large number of burrow openings, and that the areas surrounding the enclosures are disrupted by the procedure.

Results of the burial experiments are shown in Fig. 5. Clearly *Callianassa* was capable of rapidly re-establishing contact with the SWI after burial by sediment, and its rate of recovery tended to be faster when thinner layers of sediment were added. The discrepancies between the replicate experiments reflect the large experimental error caused by the procedural difficulties discussed above. The difference between values for the 10 cm trials was partly due to the fact that no count of one of the burrow openings was

taken after 25 hours; the recovery paths of other experiments show that the recovery rate is usually greater during the first day, and levels off in the second and third days. The recovery path for the 14 cm experiment was clearly in error; this can be attributed to difficulty or error in counting holes, either initially or, more likely, after 75 hours.

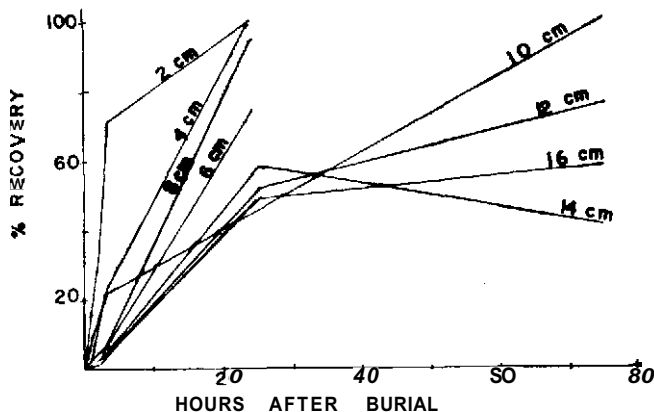


Figure 5. Re-establishment of *Callianassa* burrow opening at surface after burial with various thicknesses of sediment (from Miller, 1977b, Fig. 21).

To test whether or not burial was fatal to *Callianassa*, buckets containing 8 individuals were filled with 10 and 15 cm of sediment and buried so that the top of the bucket was level with the sediment surface. None of the ghost shrimp had died after two days, indicating that the weight of the sediment alone does not harm *Callianassa*.

Although the experimental difficulties prohibit drawing firm conclusions, *Callianassa* apparently is capable of surviving burial by sediment, and the rate of recovery is inversely proportional to the thickness of sedimentary overburden. The rate of reburrowing when thicker layers were added may well have been as fast or faster than when thinner layers were added, but less of the burrowing activity may have resulted in burrow openings at the surface. The rapid rate of recovery shown in both burial and trampling experiments probably reflects the pressure to use all available space caused by the high population density of *Callianassa* in this high intertidal area of Mugu Lagoon.

Commensal relationships: Several species live with *C. californiensis*, including a polychaete worm, two species of crabs, a clam, and a goby fish. The relationships have been discussed in detail by MacGinitie (1934, p. 171-173). The polyoid polychaete and the crabs, both of which are small and laterally elongated, subsist largely on organic debris uncovered by burrowing of *C. californiensis*; the crabs may also be facultive suspension feeders. *Cryptomya californica* is a small suspension feeding clam with short siphons. It accrues the benefits of a deep burrowing lifestyle by living adjacent to the burrows of *C. californiensis* which provide it with a supply of oxygen and food-rich water. The goby fish feeds off debris within the burrow (MacGinitie, 1934, p. 173); these fish commonly flop out on the sediment-water interface during excavation of *Callianassa*.

Macoma

General: The cosmopolitan bivalve genus *Macoma* is a highly successful component of many soft sediment marine communities of intertidal and shallow subtidal nearshore environments (Thorson, 1957). *Macoma* is typically most abundant in muddy substrates of silt or fine sand (Stanley, 1970). Species of this genus have long, flexible siphons that can be extended to many times the shell length, and most are active burrowers. Depth of burrowing is in the range of 4 to 40 cm; most species show depth stratification by size. The usual life orientation is horizontal on the left valve with the siphons projecting upward to the sediment-water interface (SWI) (Plate I).

The feeding biology of the Tellinacea is poorly understood (see reviews by Yonge, 1949; Pohlo, 1969). *Macoma balthica* is a trophic generalist (Brafield and Newell, 1961). Tunnicliffe and Risk (1977) concluded that in the Bay of Fundy *M. balthica* obtains much of its nutritional requirements from bacteria attached to sand grains, but that suspension feeding is also important.

Macoma secta: Although 5 species of *Macoma* have been reported from the sand flats at Bodega Harbor only two species, *M. secta* and *M. nasuta* are abundant at mid to high tidal levels. These two species live sympatrically in the harbor, but their relative abundances change both with regard to elevation above MLW (increased elevation results in increased exposure time) and substrate character. *Macoma secta* is primarily a deposit feeder that burrows to depths of 10 to 30 cm, and is most common in the better sorted looser sands at intermediate elevations. Maximum densities on the north sand flat are 20/m² between 60 and 80 cm above MLW (Fig. 2; Ronan, 1973). *M. secta* is uncommon at elevations above 100 cm, probably due to the intense bioturbation of the sediment by *Callianassa californiensis* at these elevations and the significant change in mass properties that result from its burrowing activities.

When deposit feeding, *Macoma secta* extends its incurrent siphon to the surface and vacuums detritus from the upper 3-5 mm of surface sediment. It typically produces surface mounds of sediment and fecal pellets up to 1 cm high. Often a siphon hole, 5 mm or less in diameter, is found at the center of this mound. Most surface traces produced by *Macoma secta* during feeding are stellate or arcuate rills of lighter-colored, coarser material that were left as a lag deposit by the incurrent siphon (Plate 1C, 1G). This contrasts with the typical surface traces reported for *M. balthica* in the Bay of Fundy which are shallow depressions 5 cm in diameter (Tunnicliffe and Risk, 1977). However, densities of similar sized *M. balthica* in the Bay of Fundy averaged 832/m², many times greater than *M. secta* in Bodega Harbor.

Macoma nasuta: Below an elevation of 40 cm, and along the margins of standing ponds at higher elevations, *Macoma secta* numbers decline and the density of *M. nasuta* reaches a maximum. *M. nasuta* is a shallower burrower than *M. secta*, being found at depths of 10 to 12 cm. Maximum densities of 70/m² are reached below 40 cm on the south sandflat where the substrate is muddier, firmer, and dryer (Ronan, 1975). The surface traces produced by *M. nasuta* are not distinguishable from those of *M. secta* although stellate deposit feeding traces are produced infrequently. This species is primarily a suspension feeder on planktonic diatoms and flagellates.

Polychaetes

Polychaete worms are abundant in the lower portions of the sand flat at Bodega Head. The burrow morphology and feeding habits of 5 common species have been studied extensively by Ronan (1975, 1977) and will only be briefly summarized here.

Radiographs of some polychaete burrows are shown in Plate 2, and surface traces are illustrated in Plate 1C, H. Ronan (1977) found that one species could produce a variety of biogenic structures; even *Cirriformia branchiata* which lives in a vertical burrow could move laterally. Burrow morphology does not clearly reflect feeding habit; all the species studied were detritivores or omnivores, yet two produced U-shaped burrows. Gut contents of all species included a variety of food items although some had food preferences. Although some of the burrows were meandering and similar to traces attributed to the activity of deposit feeders, none were filled with fecal material.

Phoronopsis viridis

The Phylum Phoronida consists of a small group of worm-like, vertical tube-dwelling lophophorate suspension feeders. They occur in patches in densities up to 150,000/m² in the sand flats of Bodega Harbor (Ronan, 1978).

The tubes of *P. viridis* are about 3 mm in diameter and up to 25 cm long, and are composed of agglutinated sand grains in a chitinous matrix. Oriented vertically, the top of the tube is about 8 cm below the sediment-water interface (Plate 1I); the top of the tube is connected to the SWI by a well formed burrow. During low tide the phoronids retract into their tubes, leaving a small hole in the substrate (Plate 1C, G).

Ronan (1975, 1978) studied the natural history of *Phoronopsis viridis* including its feeding habits and ability to withstand rapid sedimentation. During high tide *P. viridis* extends its lophophore and collects food items resuspended from the sediment-water interface; gut analysis indicate that it prefers small (< 100 μ) encrusted grains flocculent material, and fecal pellets (Ronan, 1978, p. 483). In dense patches lophophores are stratified, allowing each to be fully extended.

In laboratory and field experiments Ronan (1975) found *P. viridis* able to withstand anastrophic burial. Under laboratory conditions, 100% (n=25) had re-established contact with the sediment-water interface within 45 minutes of burial by 2 cm of sand. Thirty-six hours after burial by 16 cm of sand, 92% (n=25) had burrowed to the SWI.

Ronan (1975) added sediment to field enclosures 2 cm at a time, and the number of lophophores present observed at the next high tide. After 15 cm had been added, 90% of the specimens were above the SWI. Careful dissection of the container indicated that many of the phoronids had abandoned their tubes, and some were in the process of tube rebuilding.

Phoronopsis has been suggested as a modern producer of the ichnogenus *Skolithos*. Certainly the size, morphology and orientation of the two traces are very similar. *Skolithos* also often occurs in dense patches, as does *Phoronopsis*. However, whether or not this is a behavioral characteristic and there-

fore taxonomically significant, is open to question.

COMMUNITY STRUCTURE

Community Concepts and the *Macoma* Community

The *Macoma* community of Bodega Harbor is widely recognized as one of Thorson's (1957, 1958) now classic parallel communities which he defined as recurring associations of characteristic genera or species that are found in similar environments throughout the world. The wide recurrence and high fidelity of this association leads to the question of whether the *Macoma* community is a biological entity that through co-evolution has become integrated at a higher level, or whether it is a group of species brought together because of similar physiological tolerances, but little evolutionary interaction. If the species merely live together because of congruent tolerances, the boundaries of the assemblage may represent environmental discontinuities that exceed the tolerances of the component species. On the other hand, if the boundaries are interfaces of biological interaction, the group may represent an interacting, biologically accommodated community. These two possibilities represent the end-points in the classical debate concerning the nature of communities (see Whittaker, 1962, for review).

The question of the importance of biological interactions in soft-bottom benthic communities has been of recent interest. Several studies have shown that a range of biologic interactions probably are important. Rhoads and Young (1970) found that deposit-feeding activity may alter substrate characteristics at the sediment-water interface so that the sediment is easily resuspended; this effectively excludes suspension feeders. Sanders et al. (1962) documented the deleterious effect of massive populations of a shallow burrowing mud snail on a tube-building amphipod on tidal flats in Barnstable Harbor (Mass.) and Peterson (1978) provided evidence that competition for space is important in structuring the infaunal tidal channel community of Mugu Lagoon. Studies by Woodin (1974, 1976) also using field experimental techniques demonstrated the importance of adult-larval interactions in determining boundaries of clusters of animals, and the effects of interactions between species in determining the abundance of polychaetes within a community; she also reviewed the subject.

Biological Interactions in Bodega Harbor

To determine the importance of biological interactions in controlling the distributions of some dominant species in the intertidal sand flats of Bodega Harbor, Ronan (1975) conducted several manipulative field experiments. The experiments focused on *Callinassa californiensis*, *Macoma secta*, and *Phoronopsis viridis*; each is abundant in the high, middle or lower portions, respectively, of the north sand flat in Bodega Harbor. Details regarding the experimental techniques and methods of data processing are given in Ronan (1975).

Phoronopsis viridis - Macoma secta

In Bodega Harbor, *Macoma secta* is rare or absent where dense stands of *Phoronopsis viridis* occur near or on the southern sand flat MLW where individuals of *M. secta* found in phoronid beds on the north sand flat are recovered from uncharacteristic depths and in abnormal orientations. Ronan's (1975) experimental field methods tested the hypothesis that tubes of *Phoronopsis viridis* prevent the lateral and vertical

migration of Macoma secta, thereby largely excluding it from the lower sandflat.

To test the effect of P. viridis on lateral migration of M. secta, Ronan transplanted large clams (>3 cm) into plots densely ($710,000/m^2$), sparsely ($<6,000/m^2$) or unpopulated by phoronids. Careful excavation showed that the mean depth of burrowing (11 cm) of M. secta was significantly less in the densely populated plot than in the sparsely and unpopulated plots (15 cm, 17 cm, respectively); the burrowing depth correlated with the tops of the phoronid tubes, which terminate at about 8 cm below the SWL. Although in the low density and phoronid-free treatments there was a strong correlation between depth of burrowing and size of M. secta, this relationship did not hold in dense stands of P. viridis.

The south sandflat in Bodega Harbor consists of less well sorted and more compacted sand than the north sandflat, with a greater proportion of fine grained sediment. M. secta burrowed to shallower depths in phoronid-free plots on the south plot, presumably because of the greater degree of compaction. The burrow depths were shallower than sediments transplanted from the north to south sandflat or from the south to north sandflat, or in phoronid-free sediment in the north flat. Lateral migration of Macoma secta was not significantly altered by presence of phoronid tubes.

The results of the vertical burrowing experiments suggest that although dense stands ($>10,000/m^2$) do prevent deep burrowing by Macoma secta, the mass properties of the sediment, particularly water content and degree of compaction, also greatly affects mobility of this bivalve. The effects of the phoronid tubes are two fold: they provide obstacles to burrowing and they also serve as sediment stabilizers which further inhibits burrowing.

Callianassa californiensis - Phoronopsis viridis

Although P. viridis tends to live in lower elevations on the tidal flat than C. californiensis, P. viridis extends higher onto the flat and into contact with Callianassa on the margins of several drainage channels. Zones of overlap 1 to 5 m wide between the species are sparsely populated; these areas provide opportunities for studying interactions between these two animals.

Ronan (1975) assessed the impact of C. californiensis on P. viridis by planting P. viridis in plots within Callianassa bed and in a caged plot within the Callianassa bed from which the shrimp had been excluded. Excavation and radiography of box cores from the plots revealed that when Callianassa is present, the phoronid tubes were commonly at unnatural depths or orientations (20% of tubes; Plate 2C), or actually broken (about 10%). This contrasts with the plot from which Callianassa was excluded, where only about 1% of the phoronid tubes were broken and 2% were disoriented.

Ronan (1975) found former occupants of the disturbed tubes free in the sediment, constructing new tubes. Ronan suggested that the problem of maintaining contact with the sediment-water interface and repair of damaged tubes is energetically expensive and that this may result in P. viridis being abundant only when Callianassa is rare. He generalized (1975, p. 156) that extensive sediment disruption by Callianassa may prohibit development of large populations

of any animal dependent upon constant contact with the sediment-water interface.

Importance of Biological Interactions In Determining Community Structure

The work of Ronan (1975) on ecological and animal-substrate interactions in Bodega Harbor in addition to other recent studies (e.g. Woodin 1974, 1976) reveals that biological interactions play an important role in structuring the communities of soft substrate intertidal habitats. Some animals within these communities profoundly affect the physical environment through burrowing activity which can affect the mass properties, water content, grain size and distribution and organic content of the sediment. This effect on the sediment in addition to spatial competition, commensal relationships (commensals are abundant on the sand flats in Bodega Harbor; see discussion of Callianassa) and predator-prey interactions is an important component in the integration and structure of these communities.

Is the Macoma community integrated in the evolutionary sense, or is it a group of species with no real interactive structure? Although the evidence is preliminary, recent studies do suggest that biological interactions are important in producing ecotonal boundaries between species groups that are as important as those associated with tidal height or substrate characteristics. Both physical and biological factors enter into the determination of structure in the Macoma community in Bodega Harbor. The fact that this association (one of Thorson's parallel communities) recurs in similar environments throughout the world hints at the importance that biological integration may have played during its evolution.

GERMAN RANCHO AND BODEGA HARBOR

ICHOENOCENOSES: A COMPARISON

It is difficult to compare individual traces in Bodega Harbor with those of the German Rancho Formation. Ophiomorpha and Thalassinoides in the German Rancho probably were produced by thalassinid crustaceans related to Callianassa californiensis and Upopugettensis. Upogebia is a suspension feeder whose burrow is mucous lined and permanent, whereas C. californiensis probably is a deposit feeder whose burrow is unlined and impermanent. A lined burrow would be advantageous for a suspension feeder. Perhaps Ophiomorpha was produced by a suspension feeder and Thalassinoides by a deposit feeder; however, the gradations between the two ichnogenera at Stump Beach are not compatible with this interpretation. Results of experiments on the escape potential of Callianassa californiensis suggest that the producers of Ophiomorpha and Thalassinoides may have been able to withstand deposition of thick sands.

More generally, the rocks at Stump Beach were deposited in deep sea fan environments with abundant evidence of environmental perturbation (debris flow, turbidites). This environmental instability would have led to the establishment of "physically controlled community" (Sanders, 1969) in which physical stress and unpredictability would inhibit various ecological processes and subsequent development of a diverse community with complex interactions between species. In contrast, Bodega Harbor sediments are highly bioturbated and contain a diverse fauna. Here physical environmental perturbations appear to be much less intense. This has led to the apparent development of

a "biologically accommodated" community (Sanders, 1969) in which diverse ecological interactions are well developed; the existence of these interactions has been demonstrated by Ronan (1975) but more work is needed to evaluate their importance.

PALEOECOLOGIC IMPLICATIONS

The degree to which information about modern traces and their producers is applicable in the interpretation of ancient biogenic structures is not clear. As indicated by Seilacher (1964) and Frey (1970, 1971) and by the paucity of trace fossil analogs for Bodega Harbor traces, there are severe limitations to the uniformitarian approach to palaeoichnology. Of the 20 animals listed in Table 4, only about half (11) produce traces that can be assigned confidently to an ichnogenus. There is no evidence that back filled burrows and traces with spreite, both common in the fossil record, are being produced on the Bodega Harbor sandflat; as Ronan (1975, 1977) noted, the polychaetes discard fecal material outside of their burrow. Lack of direct correlation between modern and ancient traces may well be due, in part, to preservational enhancement of biogenic structures by diagenesis (Seilacher, 1964; Frey, 1971).

Although ichnologists cannot rely on direct comparison with modern traces to interpret the ethology of most trace fossils, they can use knowledge of the relations between anatomy, behavior and trace morphology to develop internally consistent interpretations of the behavior represented by ichnofossils. The large amount of information compiled about behavior of animals living on and in sediment and their effects on the sediment by many workers (e.g. many papers by Rudolf Richter, Schaefer, 1972; Frey and Howard, 1969; Frey, 1970; Howard and Dorjes, 1972; Dorjes and Hertweck, 1975; Basan and Frey, 1977) provides a solid data base for broadly uniformitarian interpretations of ancient lebensspuren. In addition, distributional patterns of bioturbation and biogenic structures within rock sequences have been compared with those in modern nearshore sediments; the results have aided in the interpretation of the ancient environments (e.g. Howard, 1972).

Data about the natural history, distribution and structures produced by Bodega Harbor trace producers give new information regarding ethological interpretations of individual trace fossils and factors controlling the distributions of their producers. First, the relationship between burrow morphology and feeding mode is not clear cut. Both deposit feeders and suspension feeders inhabit vertical (trace fossil=Skolithos) and U-shaped burrows (trace fossil=Arenicolites). Inhabitants of these burrow types may tend to be less mobile than other burrowers, and suspension feeders may tend to be sessile (Schopf, 1978), but there are many deposit feeders and some carnivores, especially polychaetes, which live in vertical burrows (Barnes, 1974). Secondly, a consistent relationship between grain size of the sediment and feeding mode of the infauna is lacking. The relatively clean sands of the Bodega Harbor sandflat support a diverse deposit-feeding as well as suspension-feeding infauna. Some of the most common suspension feeders (Upogebia, Macoma nasuta) are most abundant in the muddiest areas. Thirdly, the feeding mode of most animals is not well understood and many combine feeding methods. Macoma secta and M. nasuta feed both by ingesting sediment and by sucking water and suspended materials through their siphons. Callianassa californiensis and Upo-

gebia pugettensis feed differently, although they are closely related and morphologically similar. This behooves paleoecologists to be careful in assigning feeding habits for analysis of trophic structure.

Finally, study of the infauna in Bodega Harbor has indicated that the structure of soft-bottom marine communities is dependent upon biological interactions as well as on physical environmental parameters. Thus, the distributions of trace fossils in some cases reflect ecological as well as physical controls. Although the biological interactions are difficult or impossible to deduce from the rock record this does not negate either the importance of these interactions or the utility of trace fossils in paleo-environmental and paleoecological reconstructions. Paleoecologists and sedimentologists should be aware of these interactions, should look for evidence of them in the rock record, and use knowledge of their importance in modern communities to develop more realistic models of the structure of ancient marine communities and of the distributional controls of ancient traces.

ACKNOWLEDGMENTS

We thank Mary Graziose and Peggy Wrenne for preparing the photographs and Kelly Boyte for typing the manuscript. G.A. Polis critically read the paper and made helpful suggestions. We appreciate the help and support of Jana Ronan. Financial support was provided by the Vanderbilt University Research Council.

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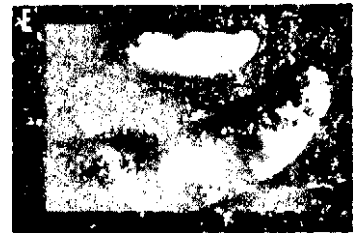
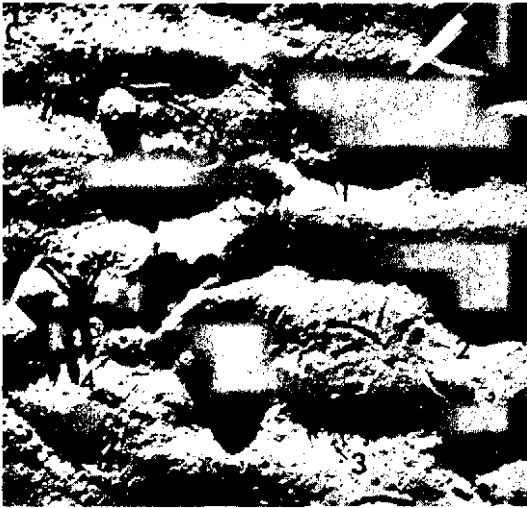
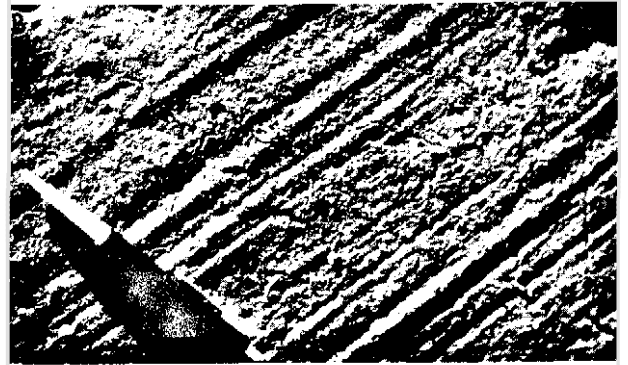
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Plate 1.

- A. Microtopography produced on sediment surface by the burrowing of *Callianassa californiensis* on the upper sandflat.
- B. Drag marks and fine dendritic trace of *Paranemertes peregrina* on the sediment surface.
- C. Ripple marks and biogenic structures on sediment surface. 1. Burrow opening of *Urechis caupo*; note surrounding mound of sediment. 2. Stellate siphon mark of *Macoma secta*. 3. Opening of *Phoronopsis viridis* burrow. 4. *Axiothella rubrocincta* burrow opening surrounded by material ejected by worm.
- D. Specimen of *Callianassa californiensis* about $\frac{1}{2}$ of natural size.
- E. Two specimens of the echinurid *Urechis caupo*; larger is approximately 8 inches long.
- F. Specimen of the polychaete *Glycera robusta*.
- G. Occurrence of *Macoma secta*, as indicated by siphon mark to the left of the penny in bed of *Phoronopsis viridis*. Holes are openings at the surface of the phoronid burrows.
- H. 1. *Callianassa californiensis* burrow openings. 2. Tubes of *Axiothella rubrocincta* and surrounding ejecta.
- I. Radiograph of box core taken in phoronid bed after introduction of *Macoma secta*. Note that *Macoma secta* is either vertically oriented (not its normal position) or horizontal at a shallow depth above the tops of the phoronid tubes. (Approximately $\frac{1}{4}$ of actual size; from Ronan, 1975, Plate 8).
- J. Fecal pellets of *C. californiensis*; key at left for scale.
- K. Re-entry trace of *Protothaca staminea*. A shallow burrowing bivalve, *P. staminea* is easily exhumed, thus these traces are fairly common.

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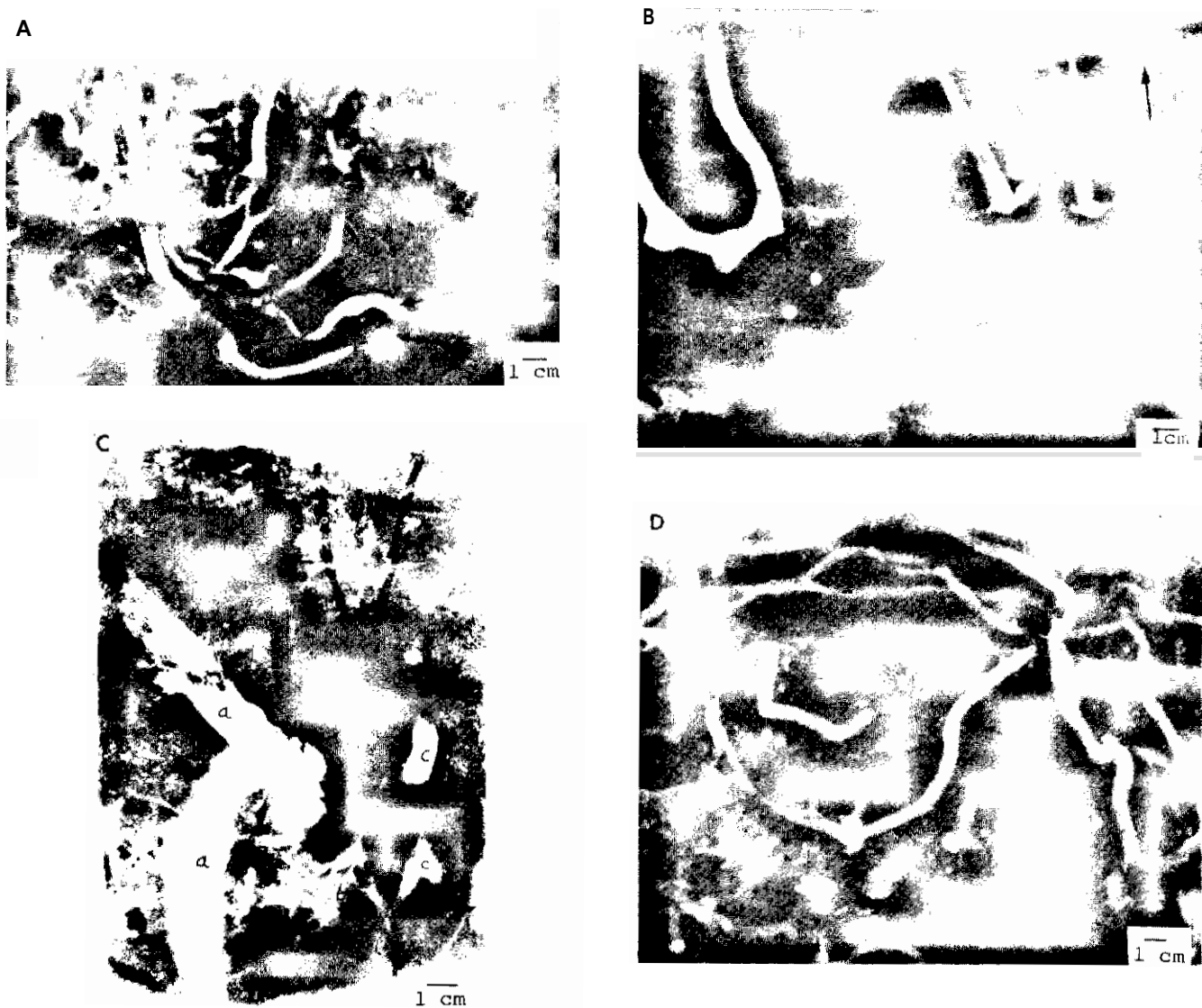


Plate 2

- A. Radiograph of a field collected box core containing the biogenic structures produced by *Notomastus magnus* (Polychaeta; Capitellidae). Arrows point to *N. magnus* proboscis strike mark. (From Ronan, 1977, Fig. 5).
- B. Biogenic structures produced by the polychaetes *Eupolyornia crescentis* (left), *Pectinaria californiensis* (right center) and *Nephtys caecodes* (arrow at extreme right). Sediment within the digestive tract of *Pectinaria* shows up as narrow darker zone. Fine grained sediment at top of radiograph appears lighter than underlying sediment; it was transported to the sediment surface by the feeding of *Pectinaria californiensis*. (Radiograph of field collected box core; from Ronan, 1977, Fig. 4).
- C. Radiograph of box core collected from *Callianassa* bed into which phoronids were transplanted. Note broken phoronid tubes at points "b". *Callianassa* burrows such as "a" and burrow galleries (c) have disrupted the phoronid tubes (from Ronan, 1975, Plate 12).
- D. Radiograph of biogenic structures produced by the polychaete *Glycera robusta*. Note broadly U-shaped burrow with cross-connecting galleries and abruptly terminating exploratory burrows (from Ronan, 1977, Fig. 3).

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