TUBE HOOD ORIENTATIONS OF <u>Pista</u> <u>Pacifica</u>

(POLYCHAETA: TEREBELLIDAE)

by

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A THESIS

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The tube hood orientation of Pista pacifica is non-random and related to current direction. Results from field measurements and from one flow tank experiment suggest that Pista pacifica build their tube hoods at right angles to local currents, and perhaps away from the direction of any sediment transport which may occur normal to the prevalent current direction. By orienting their tube hoods perpendicular to water currents, the animals may be making use of the kinetic energy of the water motion around them to generate a tube ventilation current. This current may in turn lessen the energetic needs of the worms by providing internal ventilation and sediment flushing currents at little energetic cost to the organism.

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INTRODUCTION

Many organisms harness the energy of wind or water currents in their environment to perform or support tasks which would otherwise be dependent upon the metabolism of the organism (Barnes, 1960; Wainwright, 1969; Vogel and Bretz, 1972; Barling, 1975; LaBarbera, 1975; Murdock and Vogel, 1978; Vogel, 1978; and Brenchly and Tidball, 1980). Often the structure or a behavior of the organism causes external air or water currents to drive internal currents. These internal currents circulate air or water through the body or domicile of the organism. For example, black tailed prairie dogs of the Great Plains of North America construct low, rounded "dome" mounds at one end of their burrows, and higher, sharper edged "crater" mounds at the other end. Even a gentle breeze across the prairie generates an air current inside the burrow which flows from the lower mound to the higher mound, and which ventilates the burrow. The conservation of energy in a constantly moving fluid, described by Bernoulli's principle, is the basis of this process (Prandtl, 1934; Vogel, 1978). Prairie dogs tap the kinetic energy of the external medium to drive a burrow ventilation system. Other organisms use similar internal currents for filter-feeding, gamete dispersal, humidification, respiration, CO_2 exchange (in the case of plant leaves), and other purposes (Vogel, 1978). By harnessing the plentiful external mechanical energy in their environment, certain organisms gain a selective advantage over those which do not (LaBarbera, 1975; Vogel, 1978). The movement of wind and water is such a pervasive element of our biosphere, Vogel (1978) argues,

that adaptations to utilize them are extremely common. As he
eloquently implores, "Animals care about currents, biologists should
too."

Organisms adapt behaviorally and structurally to make use of the
fluid motions around them. Orientation to the direction of external
currents, either by the animal itself or by some structure which it
builds, is a special form of behavioral adaptation. In order to
demonstrate that this behavior occurs, and that it increases an
organism's fitness, four conditions must be met.

First, it must be shown that air or water movement through the
organism or its abode is altered by its orientation to the external
current. This can be evaluated theoretically using the geometry of
the structure and the principles of hydrodynamics, or experimentally
with dye studies performed with models in a flow tank. Both of these
methods were effectively demonstrated by LaBarbera (1975) in his studies
on the orientation of brachiopods, and in studies of the water move-
ment through and around sponges, keyhole limpets, and other organisms
(Wainwright, 1969; Vogel and Bretz, 1972; Murdock and Vogel, 1978;
Vogel and Bretz, 1978). The information gained from these experiments,
along with what is already known about how an organism utilizes
internal air or water currents, can be used to predict a preferred
orientation for the animal (Wainwright, 1969; LaBarbera, 1975).

Secondly, the organism must be shown to exhibit orientation
behavior. The animal may twist or turn or move so that it consis-
tently faces the prevailing current with a particular orientation.
This structure will then supply evidence of previous orientation

behavior. Orientation behavior may be tested in vivo (if current directions are known) by field sampling (Barnes, 1960; Brenchly and Tidball, 1980; Myers, 1972). It may be tested in vitro with flow tank experiments with living animals (LaBarbera, 1977; Murdock and Vogel, 1978; Brenchly and Tidball, 1980).

Third, it must be shown that, when the oraganism or some structure which the organism builds is in its preferred orientation, the energy needs of the organism are reduced. For example, LaBarbera (1977) has used models to show that, for certain orientations to a water current, filter feeding currents in living brachiopods would be enhanced. In other orientations, external currents generate pressures which would oppose the ciliary driven feeding currents of the animal. In order to prove that the energy economy of the animal is actually improved, it would be necessary to show that the amount of food removed from a water current per unit time increases with an increasing flow rate.

Finally, it should be shown that this enhancement of energy effi-ciency confers a selective advantage to the organism. This last assump-tion is often accepted without proof.

Currents and Annelid Tube Building

Lanice conchilega is tubicolous terebellid which has often been studied since at least the late 1800's (Watson, 1890). The worm is widespread and common in the North Sea and parts of the eastern Atlantic Ocean, and occurs in depths to 50 meters. Its population density ranges from isolated individuals to, in extreme cases, over 20,000 m^2 (Buhr and Winter, 1976). Lanice conchilega is a tentaculate, surface-deposit

feeding animal which builds a "fringed crown" on the top of its tube. The crown stands upright like a small fan or fringed sail (Seilacher, 1951; Ziegelmeir, 1952, 1959; Schafer, 1972). Seilacher (1951) and Zeigelmeir (1952, 1959) have shown that this fan-shaped crown faces against the direction of a constant current. The frilly projections of the fan trap phytoplankton and zooplankton, and the turbulence that it creates causes material transported by the current to drop out of suspension. The tentacles then harvest particles off of the fan and the surrounding sediment. L. conchilega may also be a suspension feeder and harvest particles which adhere to mucus secreted by the tentacles, as, supported by the tube-crown's fringes, they stream out into the current (Buhr, 1976; Buhr and Winter, 1976; Fauchauld and Jumars, 1979). Lanice and other terebellids may absorb dissolved organic material from the water as well. (See Fauchauld and Jumars, 1979, for references.)

The tube building behavior of Lanice conchilega is described in great detail by Arnold Watson (1890, 1916), who also wrote the classic description of tube building by Pectinaria koreni (Watson, 1928). The existence of intelligence in lower life forms apparently was a hotly debated topic in the early 1900's, and Watson (1916) had his say on the subject in a paper entitled, "A Case of Apparent Intelligence Exhibited by a Marine Tube Building Worm, Terebella (=Lanice) conchilega." The paper noted that the worm, while attempting to cement a relatively large shell fragment to its tube, applied cement and sand grains first to one side of the shell fragment, and then to the other. At the same time, it held the shell fragment in place with

several cooperating tentacles. It was particularly interesting to read Watson's description of how L. conchilega constructed the frilly extensions on the end of its tube crown since it is hard to imagine how such delicate structures could be formed. Quoting from the 1890 paper:

> ...the observation of how the sandy fringe is built is a most difficult matter, and was only obtained after about fourteen days of almost constant watching.... A moderately large grain of sand is first laid as a foundation stone; then the creature usually retires into its tube, and the tentacles collect and carry down to it a large supply of grains of sand, which is all received by the lips and no doubt duly coated with the secreted cement. The animal now slowly emerges, and lays first one grain upon the foundation stone; then whilst still holding this with the lower portion of its lip, it forces a second grain, out of the supply of its mouth, above the first, through the upper portion of its lip. It then slides the whole lip up to the second grain, which it holds as before, passing forward above it a third grain, and so on until the whole supply is exhausted, the worm keeping hold with its lip all the time, and withdrawing at lightning speed as soon as the last grain is attached, the whole operation occupying, in the cases I observed, from 5 to 10 seconds only. The straightness of the filament is secured by the above means combined with a very steady and gradual advance of the body of the worm as each grain is added. When the top grain has been added the creature has often emerged so far that the whole three pairs of branchiae are outside the tube.

Tube structure can be an excellent record of past animal behavior, and if environmental conditions can be shown to influence tube building behavior, then tube structure may be used to infer past environmental conditions. For example, Schäfer (1912) shows how the sub-sediment tube structure of a Lanice conchilega colony can illustrate the local depositional history of a mudflat. In particular, "undergrown" tube crowns indicate a past period of slow or no sedimentation followed by a period of rapid sedimentation. When sediment begins to accrete over the tube of a worm, the worm responds by building its tube upwards

through the accumulating sediment. Remnants of old hoods can be found beneath the new surface.

Amphitrite ornata is another sedentary, tube building, surface-deposit feeding terebellid. In their comprehensive study of the tube dwellings of this worm in Barnstable Harbor, Cape Cod Bay, Aller and Yingst (1978) found only burrows which had two openings to the surface. Neither of these openings is elaborated into a hood or cap. Since the Amphitrite, like other terebellids, is able to turn end for end in its tube, it is capable of feeding out of either end of its tube. The worm generally uses its U-shaped tube as two, separate, vertical burrows. It feeds and defecates out of only one side of its tube at a time, and even actively irrigates only one side at a time (Aller and Yingst, 1978).

Diopatra cuprea is an onuphid polychaete which captures and feeds on small organisms which pass near the entrance to its tube. The worm builds a long, sand grain reinforced tube which is approximately vertical in the sediment, and which has only one opening to the surface. This opening is elaborated into a cap, or hood, with a definite front and back; the hood is directional. Myers (1972) described the hood of D. cuprea as an "inverted 'J'". He found that, in the field, Diopatra cuprea tended to orient their tube caps at right angles to the prevalent current direction. Myers felt that this tendency was in accord with the worm's raptorial feeding habit — that perhaps the worm sampled water passing by its tube opening and only needed to poke the tips of its tentacles out of its tube to do so. Subsequent laboratory flow tank and field studies by Brenchly and Tidball (1980) showed

that isolated Diopatra cuprea did indeed build their tube caps perpendicular to the current. In one flow tank experiment, 138 worms housed in glass tubes and subject to a unidirectional water current constructed tube caps with a bimodal orientation distribution, generally perpendicular to the current. The angle of the resultant vector of the orientation was 175° (or 5°). The vector magnitude was 0.639 (see the procedure section of this paper for a definition of these statistics). Based on a chi-square test, the likelihood of non-random orientation was greater than 99.5%. Specimens in a control experiment (standing water), and specimens subject to a point source of food in standing water, both exhibited random tube cap orientation. Field sampling indicated that at densities above $3/0.01m^2$ (=300/m^2), however, tube cap orientation became random with respect to current direction. The authors attempted to show that at the high densities worms oriented their tube hoods in order to maximize their ability to forage off neighboring hoods.

In another flow tank experiment, Brenchly and Tidball (1980) measured the time necessary for worms housed in glass tubes to build tube caps. They were subject to a current of constant velocity and direction. Two cases were tested. In one, the tops of the glass tubes were 0.2 cm below the level of the substrate, in the other, 0.5 cm above. The difference in the average time taken by each group to build their tube caps was quite significant. The group with the top of their tubes below the surface built their caps in $1.8^{\pm} 0.4$ days (n=95). Those with their tube openings above the surface took $8.4^{\pm} 2.1$ days (n=50). Flow tank experimentation on a glass model of

a Diopatra tube demonstrated that when the cap is oriented at right angles to a current, water is drawn out of the tube. Water is also drawn out of the tube when the cap points down stream, but not as rapidly. Thus, if an animal orients its tube cap at right angles to the current, sediment influx into the tube would be minimized due to water movement out of the tube. In addition, tube ventilation would be maximized. Brenchly and Tidball (1980) felt that tube cap orientation in Diopatra cuprea was a compromise between "physiology" at low worm densities, and foraging efficiency at high worm densities.

Research Objective

The research presented here examines the relationship between tube hood orientation and current direction in the tubicolous terebellid polychaete, Pista pacifica (Berkeley and Berkeley, 1942). The research deals with whether or not an organism exhibits orientation behavior. Since the hydrodynamic interaction of the tube and its hood with surrounding water currents has not been examined, no a priori prediction of a preferred tube hood orientation will be made.

The objective of this research is to answer the following questions:

1) In selected groups of Pista pacifica, is the distribution of tube hood orientations random or non-random?

2) If the tube hood orientation distribution is non-random, is it related to external current directions?

3) Do individual Pista pacifica construct tube hoods with a specific and consistant orientation to current direction?

The first two questions are addressed through field studies and are the basis of most of the research in this paper. The third question is addressed briefly with a flow tank experiment.

MATERIALS AND METHODS

The Study Organism

Pista pacifica, (Annelida; Polycheata: Terebellidae) was first described by Berkeley and Berkeley, 1942 (for other descriptions, see also Hartman, 1969; Smith and Carlton, 1975; and Fauchauld, 1977). Field specimens were identified only by their characteristic hoods which project a few centimeters above the sediment surface (Figure 2). The animals can be up to 39 cm long (Rudy, 1981), and their tubes may be up to a meter long (pers. obsv.). It appears to prefer a rather sandy mud (Berkeley and Berkeley, 1942, and personal observations). The body of the tube is parchment-like and situated more or less vertically in the sediment. Hartman (1969) notes that Pista pacifica occur in sandy intertidal mudflats in California and in western Canada. There is no detailed record of their regional distribution. In the Charleston, Oregon area, Pista pacifica occur in the mudflat areas of South Slough and in the southern-most portion of Coos Bay (Coos Bay Estuary Report, 1970). They also occur in the protected North Cove of Cape Arago, a headland approximately 5 miles south of Charleston. Their sub-tidal distribution has not been investigated.

Study Sites

The compass orientation of Pista pacifica tube hoods were measured at five sites in the vicinity of Charleston, Oregon (Appendix I).

Three of these sites were in estuarine mudflat areas and two were in a protected cove. Mudflat Sites A and B were on opposite sides of the channel which leads from Coos Bay into South Slough, between the Charleston Boat Basin and the Charleston Bridge. The third mudflat site was farther south along the same channel, between the Charleston Bridge and the Metcalf salt marsh property (Figure 3). All of the animals at Site A were within 6 m of the water's edge at a lower-low tide. At Sites B and C they were within 10 m and 20 m respectively. Site A was sampled on two occasions (A1 and A2). At Site B, two distinct sub-areas, B1 and B2 were sampled. B1 occupied a large portion of the mudflat and was free of eel grass (Zostera sp.). B2 was a smaller area which was densely covered with eel grass. Sites D and E were in the protected North Cove of Cape Arago (Figure 4). Waves were refracted as they entered the cove and generally broke parallel with the beach. The main force of the waves are absorbed by Simpson's reef before they enter the cove. Since the whole area is rather shallow, the wave generated water movement in the cove is in the form of extended swash and backwash currents. Site D was a large, sandy tide pool which held about 1/2-3/4 of a meter of water even at the lowest low tide (see photograph, Figure 5). It was bounded on the seaward side by a large boulder field and on the landward side by a sandy beach. The wave generated currents entered the pool at right angles to its long axis. There was a ripple pattern on the sand in the pool and on the sandy area behind it. Site E was a sandy area covered with small patches of eel grass. It was surrounded by eel grass on three sides and by a shallow pool on the seaward side (see

photograph, Figure 6). This site also had a strong ripple pattern
in the sand. The ripples at both Sites C and D appeared to be
symmetric; neither slope was built up steeper than the other. This
indicated that they were caused by back and forth currents of approxi-
mately equal force and duration (Johnson, 1919).

Orientation Measurements and Graphs

For each of the groups of _Pista pacifica_ examined, the hood
direction of each individual sampled was measured with a magnetic
compass. Figure 1 indicates the assigned directions of the hood. A
compass reading of 0° indicated a hood direction of due magnetic north.
Orientation readings increased in a clockwise direction. Hoods were
sometimes able to twist somewhat freely for about ± 10°, but the pre-
ferred orientation was always evident. Accuracy of the direction
measurements is estimated at ± 5°. The set of hood direction measure-
ments for each sample was sorted into thirty-six 10° orientation
classes. The number of hoods falling into each orientation class was
then plotted as a circular histogram. Thus, for each 10° orientation
class there is a vector on the histogram whose length corresponds to
the number of worms with tube hoods in that class. A solid line was
drawn on the histograms from Sites A1, A2, B1, B2, and C which repre-
sents the direction of the beach. A dashed line was drawn at an
angle perpendicular to the beach. On the histograms from Sites D and
E, a solid line was drawn at right angles to the sand ripples to
indicate the wave direction. A dashed line was drawn at an angle
parallel to the ripple pattern (Figure 7).

Statistical Analysis of the Field Data

Seven samples were obtained from five sites. Site A was sampled on two occasions (A1 and A2). In Site B, two separate samples in the same general area (B1 and B2) were taken (see Appendix I). For each of the seven hood orientation samples, the likelihood that the observed orientation distribution differed significantly from a theoretical distribution was evaluated using a chi-square goodness-of-fit test, as described by Batschelet (1965). In each case, the theoretical distribution was based on the assumption that no orientation class was preferred over any other, and thus that each class would contain an equal number of individuals. Chi-square is a measure of the deviation of the sample from the population of theoretical distributions. If the chi-square value for a sample exceeded a critical value, then the null hypothesis was rejected. It showed a statistically significant tendency to prefer certain orientation classes over others and the tube hood orientation distribution was probably not random. The significance level for this study was chosen as 0.005. The numbers of orientation classes for each sample were chosen in order to provide continuity between the samples where possible, and to meet the following criteria: 1) In each class the expected frequency was at least 5; and 2) The number of classes was between n/15 and n/5 (n=sample size). Thus the orientation distributions of samples A1, A2, B1, B2 and C were divided into eight 45° classes, and the orientation distributions of samples D and E were divided into four 90° classes.

Each empirical circular distribution is described by its median angle, ϕ, and confidence limits for the median angle as described by the confidence coefficient, Q. These statistics were calculated using the sign test as described by Batschelet (1965). This non-parametric test requires only that the distribution be continuous and that it exhibit some concentration around a certain direction. It does not require that the distribution be either unimodal or symmetric. The median, ϕ, is the measure of the angle of a line which halves the probability of the circular distribution. The line is drawn through the center of the circle and its angle is measured on that side of the distribution where the concentration is located. The medians of each distribution were calculated and are indicated on each of the circular histograms. The Q=90% confidence intervals for each of the median directions were also calculated and are likewise shown on the histograms. The meaning of the confidence interval is as follows. The median of the sample, ϕ, is an estimate of the median direction for the population being sampled. The confidence interval reveals how accurate that estimate is. A narrow confidence interval indicates an accurate estimate. Any angle which falls inside the 90% confidence interval for the median has at least a 90% chance of being the actual median direction of the entire population. Since at Sites B1, D and E, all of the worms in a given area were sampled, the interpretation of the confidence interval differs at these sites, (see the Discussion section). The calculation of the confidence intervals was based on methods described in Batschelet (1965, pp. 31-33) and Siegel (1956, pp. 36-42).

An empirical circular distribution can also be described by the polar angle, α, and the length, r, of the mean vector of the distribution. The mean vector is obtained by vector addition. The angle of each hood was resolved into its x and y coordinates. These were summed and divided by the total number of individuals. These mean X and Y coordinates were then converted back into polar coordinates, yielding the mean vector, $\bar{m}$. The angle of the mean vector, α, is a measure of the preferred direction for the distribution. The magnitude of the vector, r, is a measure of concentration around the preferred direction. An r value of 1.0 indicates that all of the hoods point in the same direction. An r value of 0 indicates a completely random, or uniform, distribution:

$$X = \frac{1}{n} \sum_{i=1}^{n} \cos \alpha_i \qquad\qquad Y = \frac{1}{n} \sum_{i=1}^{n} \sin \alpha$$

n=number of individuals

$$r = \sqrt{X^2 + Y^2}$$

α_i = the angle of the i-th tube hood

$$\alpha = \cos^{-1} X/r \;;\; \sin^{-1} Y/r$$

The data for each sample were also analyzed using Morisita's index of dispersion, I_d (Morisita, 1962; Brenchly and Tidball, 1980):

$$I_d = q \; \frac{\sum_{i=1}^{q} x_i (x_i - 1)}{n(n-1)}$$

where, q = the number of orientation classes (36)

x_i = the number of individuals in the i-th orientation class

n = the total number of individuals in the sample

If the distribution is contagious (clumped), I_d will be greater than 1. If the distribution is uniform, I_d will be less than 1. An I_d value close to 1 indicates a random distribution, that is, random tube hood orientation. The data from Sites D and E, because they exhibited a bimodal distribution, were divided into double angle groups before analysis (Brenchly and Tidball, 1980; Batschelet, 1965). In those cases, q=18.

In vitro Observations

Observations were made on a worm collected from Site A and maintained in a flow chamber from 1/31/79 to 4/28/79. The flow chamber was constructed from three 5-gallon plastic buckets which were cemented together end-to-end. The center bucket had had its bottom removed. The worm, in its original sand tube, was supported by mudflat sediment inside a 5 cm wide, 1 m long PVC pipe. This pipe was suspended in the center of the flow chamber from a hole in the center of a circular piece of plywood in the uppermost bucket. The top of the PVC pipe was flush with the surface of the plywood, which in turn was covered with 2.5 cm of mudflat sediment. A more or less steady, unidirectional current flowed across this false mudflat surface. On three occasions the worm constructed a new tube hood some time after a previously built one had been cut off. The new hoods' orientations to the water current were noted.

All of the observations made on the worm in this flow chamber were qualitative. Appendix II shows plans for a flow chamber which would provide a uniform and laminar current for eight worms, and which would facilitate quantitative measurements of tube hood orientation.

RESULTS

Hood Orientation Distributions

Table I summarizes the statistics for each of the seven samples. Figure 7 contains the circular histograms. Each histogram indicates the median and mean tube hood orientation of the sample as well as the 90% confidence interval for the median.

The chi-square values calculated for each of the seven sites all exceeded the tabled chi-square values corresponding to probability levels of 0.005. This indicated that, at all of the sites tested, the probability of tube hood orientation being non-random was greater than 99.5%.

The sites on the east and west sides of the entrance channel to South Slough both exhibited unimodal hood orientation distributions. The median hood orientation on the west side of the channel was almost directly towards the channel, perpendicular to the beach. In November, 1978 (A1), the median direction on the west side of the channel was 90°; at the same site in July, 1981 (A2) it was 70°. Both of these parameter estimates fell within the other's confidence interval (65°-119° for A1; 50°-90° for A2). A line drawn perpendicular to the beach falls within the 90% confidence interval for both samples. On the east side of the channel the median hood direction was obliquely towards the channel and up-river. The median direction at Site B1 was 205°; at Site B2 it was 195°. The confidence interval was wider

at eel grass covered Site B2 (168°-218°) than at Site B1 (194°-216°).
Neither of the confidence intervals encompassed a line drawn perpen-
dicular, or parallel, to the beach. It was not possible to find an
unambiguous median direction for Site C. However, the mean vector
may still be calculated. The angle of the mean vector (α) was 43.8°.
Its magnitude (r) was 0.43.

Sites D and E, the North Cove sites, both showed a bimodal
hood orientation distribution. In each case the median orientations
were 180° apart and parallel to the ridges of the sand ripples at
the site. The confidence intervals at both sites were very narrow.
The median orientations at Site D were 160° and 340°, with a Q=90%
confidence interval of 5° (155°-160°). At Site E the median hood
orientations were 50° and 230°, with a Q=90% confidence interval of
18° (220°-238°).

The median and mean tube hood orientations differed significantly
only at Sites B1 and B2. The orientation distributions at these sites
were very asymmetric. At Site B1 the median and mean directions were
205° and 155.5° respectively; at Site B2 they were 195° and 168.6°.

The Index of Dispersion, I_d, was highest at the two North Cove
sites, Sites D (I_d=3.44) and E (I_d=2.90). Of the mudflat sites, B1
(I_d=2.93), the site on the east side of the South Slough entrance
channel, had the largest I_d value. Site C (I_d=1.20), in South Slough
proper, had the lowest I_d value. As seen from Table II, "r" values
exhibit a pattern similar to the I_d values.

In vitro Observations

A specimen was inserted into the flow chamber on January 31, 1979. The hood of the worm, was cut off soon after the water flow started, pointed down-current. A new hood was built on February 4, 1979, in less than 12 hours, three days after the original hood had been cut off. The new hood was at right angles to the current, 90° counter-clockwise from the initial orientation. The hood was built during a period of no flow, as the marine station's salt water system had been inoperative for about 16 hours.

The first rebuilt hood was cut off even with the sediment on March 8, 1979, 32 days after it was constructed — it had never developed frilly extensions. By the next day, March 9, the worm had constructed a new hood, this time complete with frilly extensions. This tube hood was also built at right angles to the current, in the same orientation as the previous hood. The entire worm was then rotated 90° to face into the current and its hood was again cut off on March 9, 1979. By March 10 the worm had again constructed a new incomplete, hood without any frilly extensions. This hood was also oriented at right angles to the current, this time 90° clockwise from its previous orientation. Thus, on three occasions the worm built a new hood after an old one had been experimentally removed and the tube trimmed even with the sediment surface. In all cases the new hood was oriented at right angles to the current, although in one case it was built during a period of no flow.

DISCUSSION

The most important finding of this study is that the terebellid polychaete Pista pacifica tends to build its tube hood perpendicular to water currents. The median (ϕ) together with its confidence interval describes this tendency for a sample of worms even when the distribution is asymmetric. This can be seen clearly on the histogram for samples B1 and B2 (Fig. 7). Here, the approximate preferred direction can easily be judged, and ϕ appears to be a good measure of overall orientation. Other workers have used the mean vector to analyze similar data. For this asymmetric distribution, however, the angle of the mean vector (α) is clearly not a good indicator of the overall orientation. The angle and length of the mean vector have been calculated for each sample so that comparisons can be made with other studies on animal orientation, particularly the flow tank experiments of Brenchly and Tidball (1980). I do not consider these the best statistics for this study, however, because their use for a distribution which is either bimodal or asymmetric may lead to erroneous results (Batschelet, 1965). In addition, it is not possible to calculate confidence limits for the mean direction unless it is assumed that the theoretical distribution is circular normal. I do not believe that this assumption is valid for the data at hand. Batschelet (1965) does offer a method, angle doubling, which allows one to use the mean vector in analyzing a bimodal distribution. But again additional requirements must be met; the

distribution should be both radially and axially symmetric. These requirements might not be met by a bimodal orientation of tube hoods when, as in this study, the hoods are subject to currents from essentially unknown directions and the worms' responses are unknown. The Index of Dispersion, I_d, has also been calculated and presented for comparative purposes. The median direction, ϕ, together with its confidence interval, give the best description of the circular distributions encountered in this study.

The flow tank observations and the results from field sites D and E all indicate that Pista pacifica orient their tube hoods at right angles to water currents. The direction of wave generated water movement at Sites D and E is clearly shown by the ripple pattern in the sand at those sites (Figures 5, 6). Typically, waves are refracted as they enter the cove, and in any area break roughly parallel to the beach (see Figure 4). The wave driven water movement at these sites produces sand ripples whose long axes are perpendicular to the water motion (see Johnson, 1919). Histograms D and E (Fig. 7) indicate that Pista pacifica at those sites have a strong tendency to build tube hoods which are perpendicular to the ripples, and thus also perpendicular to the water movement generated by the waves. The distribution at Site E is clearly bimodal, indicating no preference of one perpendicular orientation over the other. At Site D the distribution was also bimodal, but more hoods pointed south than north.

Pista pacifica orients its tube hood by actively building it

with a particular orientation, and not by its being passively turned by currents. If the hoods were passively turned, their long axes would be parallel with the current, not perpendicular to it as at Sites D and E. The hoods would be turned in much the same way in which a weather vane is turned by the wind. The Pista pacifica which was kept in the flow chamber, starting from two different initial orientations, built three tube hoods at right angles to the water current. This also is evidence that the worms exhibit orientation behavior. Thus, the hood orientation patterns recorded on the histograms are probably a reflection of this behavior, and not of differential mortality based hood orientation. In other words the hoods point the way they do because the worms build them that way.

It could be argued, however, that the Pista pacifica at Sites D and E indeed had their hoods passively turned by the currents, but that the back-and-forth motion of the water at those sites left the hoods oriented, on the average, perpendicular to the flow. It should be remembered, though, that all of the measurements were made at low tide when the worms were experiencing no currents at all. If it were true that the hoods were turned by the currents, then the hoods on each side of the distribution should be at least partially turned in the direction of the last backwash current which swept over the area as the tide receded. There is no evidence for this at Site E, although this may have occurred to a small degree at Site D (Figure 7). Personal observations of Pista pacifica tubes reveal that the hoods resist being turned and this, together with the results from Sites D and E, lead me to reject the argument that P. pacifica tube

hoods can be passively turned by currents. In order to rule out this possibility completely, it would be necessary to conduct more flow tank experiments with unidirectional current flow, as was done with Diopatra cuprea by Brenchly and Tidball (1980). Observations of Pista pacifica subject to different current directions would also be very useful.

The hood orientations of Pista pacifica probably reflect local current direction. The variability of the worms' orientation behavior appears to be low. This is indicated by the Q=90% confidence interval which is presumably determined at each site by three factors:

a) Variation in the worm's response to unidirectional water movement.

b) Variation in the overall current direction at a site. At Sites D and E this would be caused by a variation in wave direction.

c) Variation in the direction of the local currents seen by the worms.

When any of these three factors is reduced, the confidence interval for ϕ becomes smaller. At Sites D and E, all of the worms in a defined area were sampled, and the variation in current direction from worm to worm was small because the sample areas were relatively small and free of eel grass, rocks, or other obstructions. At Sites D and E, then, the Q=90% confidence intervals can be interpreted as a measure of the variability of the worms' responses added to the variability caused by changes in wave direction. Therefore, the

confidence interval, when used as an estimate of worm variability alone, is a conservative estimate. It assumes that current direction is constant, and so overestimates the variability in hood orientation behavior. These confidence intervals were narrow at Sites D and E, 5° and 18° respectively. At Site D, the entire orientation distribution fell within a 50° range.

At Site B, the confidence interval was larger for sample B2 than for B1 (50° and 22°), but the median orientation at each was very similar (195° and 205° — the median directions differ by only 4° if the histograms are rotated so that the beach directions align). This suggests that the variability in current direction from worm to worm was higher at B2 than at B1, but that the overall, or average, current direction at each site was similar. This suggestion is reasonable since Sample B2 was covered with a dense stand of eel grass, which could be expected to alter the current direction experienced by individual worms, while Sample B1 was free of such surface obstructions. By the same reasoning, the local variability in current direction at Site C appears very high. This is in accord with the beach being irregular at this site, and with the sampling area being comparatively large (an alternate explanation is that current velocities were low).

The results from samples A1 and A2 indicate that even where Pista pacifica must rebuild their tube hoods often, the orientation distribution of these hoods remains essentially unchanged (Figure 7). Samples A1 and A2 were taken at the same site, 2½ years apart. Site A is probably the most popular clam digging area in Coos Bay — on

some days well over 30 people were digging there (personal observation). During weekend low tides and daylight hours, it was often impossible to sample this area because the tops of nearly all the Pista tubes had been chopped off by clam diggers. Thus, most of these Pista pacifica had rebuilt their tube hoods between the two sample dates, and yet the orientation distribution of each sample was nearly unchanged. The worms exhibited consistent orientation behavior, apparently in response to a consistent stimulus — current direction. An alternative explanation is that the worms maintained a consistent hood orientation with respect to the rest of their tubes. The portion of the tide cycle during which the worm might respond to current direction is not known and deserves further investigation.

Besides rebuilding severed hoods, Pista pacifica may also actively excise and then rebuild tube hoods. Worms with complete hoods, each of which had a more weathered hood lying beside it, were found in the field. In all cases the hood attached to the tube was lighter colored, thinner, and less weathered than the unattached hood. New hoods were occasionally seen on other tubes as well and were always in marked contrast to the thicker and older tubes below. This suggests that the worms may be able to change their hood direction if the current direction changes. The environmental conditions for such a change are not known, and may also deserve investigation.

At Sites A, B and C the current directions were now known. Assuming that Pista pacifica orient their hoods at right angles to the direction of water movement, it is possible to predict these directions. The median hood orientation at A1 and A2 is nearly perpendicular to

the strike of the beach, although there is a lot of variation in individual tube hood orientation (for A1, the Q-90% confidence interval = 44°; for A2, 40°). The distribution is unimodal, with the number of hoods pointing towards the water far outnumbering those pointing landward. Thus I suggest that the tidal current on the west side of the channel flows parallel to the beach. At Sites B1 and B2, however, the median hood direction is obliquely towards the channel and up-river at an angle of about 180° (200° magnetic). What is causing this particular orientation? Either a water current travels across the mudflat at an oblique angle, or some other external force, such as wave energy, generates water movement in a direction perpendicular to the preferred hood orientation. As seen by reference to the map in Figure 3, Site B is exposed to northwesterlies blowing in over the entrance range to Coos Bay and the low sand dunes of North Spit, and is protected from southwesterlies by forested hills southwest of the site. These winds could cause water movement perpendicular to the median hood orientation at the site by generating either wind-waves or wind driven water circulation. Along the Oregon coast summer winds from the north and northwest are common and have a seasonal average velocity of 14 miles per hour. I suggest that at Site B the worms are orienting their hoods at right angles to wind or wave generated water currents flowing at approximately 45° to the mudflat. Site A, because it is on the west side of the channel, is protected from these northwesterly wind effects. The exact current directions on the mudflats would have to be known in order to evaluate these hypotheses.

Pista pacifica build their tube hoods at right angles to the direction of water movement around them and by so doing control the way in which their tubes interact with water currents. In some cases the distribution of tube hood orientations is bimodal — one particular hood direction is not favored over another, opposite, hood direction. In other cases the distribution is essentially uni-modal. A comparison of situations differing in this respect may help to elucidate possible functions of tube hood orientation behavior in Pista pacifica. Tube hood orientation is unimodal at Sites A and B (Figure 7). At each of these sites, which are on opposite sides of the South Slough channel, the median hood orientation is generally towards the channel and away from the land. Worms appear to avoid certain hood orientation at these sites. At Site A, the avoided direction is approximately 180° away from the preferred orientation, perpendicular to the channel and up the beach. At Site B, the avoid-ed orientation makes an angle of about 135° with the preferred orientation, and points approximately parallel with the beach, towards Coos Bay (Figure 7, histograms A1, A2, B1, B2). Some influence must prevent these worms from displaying a bimodal distribution. Perhaps Pista pacifica build tube hoods which are perpendicular to local water currents, but which also face away from any one-way sediment transport which may occur normal or sub-normal to these currents during some phase of the tide cycle. In this way the animals could avoid acting as sediment traps. At Site B the direction of this hypothetical sediment may be deflected to the south by longshore currents generated by northwesterly wind-waves breaking on the beach. Thus, the hood

orientations which Pista pacifica avoid would indicate the direction from which most sediment moves. The tube hood orientations of animals at North Cove Sites D and E, unlike those at the mudflat sites, were bimodal. For each site there were two, approximately opposed, median hood directions (Figure 7). Sites D and E were in sandy, non-sloping areas in a protected ocean cove. As judged by sand ripple patterns, ocean waves refracted into the cove were the major source of water motion in the worms' environment. If Pista pacifica are inclined to point their hoods away from the direction of sediment transport, then perhaps these bimodal distributions indicate that no significant transport is occurring normal to wave generated currents in the area. It may be possible to test these assumptions in the field with models of Pista tubes. A series of such tubes could be inserted into the sediment, each having a different hood orientation. At the end of a tide cycle the tubes could be checked for sediment accumulation.

North Sea Lanice conchilega tube crowns were directed against the direction of a constant current (Seilacher, 1951, Schafer, 1972). This lends support to the notion that terebellids are capable of sensing current direction and of altering their tube building behavior in response to this stimulus. That L. conchilega show a different preferred orientation to current direction than Pista pacifica suggests that the tube crown of this worm functions in a different manner from Pista pacifica's tube hood. It has been argued that the major function of Lanice conchilega's tube crown is to trap suspended food particles, and that the worm orients its tube crown in such a way as to maximize the catch (Seilacher, 1951; Ziegelmeier, 1952,

1959; Schafer, 1972). The terebellid <u>Amphitrite ornata</u> builds a U-shaped tube of similar materials to the one built by <u>Pista pacifica</u>, but without any hoods, caps, or crowns. Perhaps the tube hood in <u>P</u>. <u>pacifica</u> serves a similar function to the U-shaped tube of <u>A</u>. <u>ornata</u>.

Orientation in <u>Pista pacifica</u> and in the onuphid polychaete, <u>Diopatra cuprea</u> show some striking similarities. Both worms build long, sand grain reinforced tubes which are approximately vertical in the sediment and possess only one opening to the surface. In both, this opening is elaborated into a cap or hood with a definite front and back (Meyers, 1972, and personal observation). Meyers (1972) sampled 46 worms at a site in Narragansett Bay. Tube cap orientations were generally perpendicular to the beach strike and to observed surface currents, and were directed towards the bay (unimodal distribution). At another site, 94 tubes were sampled. The strongest orientation component was perpendicular to the beach, but a weaker orientation component was roughly normal to the dominant wave approach direction. Brenchly and Tidball (1980) obtained similar field results. In a flow tank experiment, 138 worms built tube caps with a bimodal orientation distribution, approximately perpendicular to the current. For that distribution the angle of the mean vector (α) was 78° (and 267°), its magnitude (r) was 0.639. By way of comparison, the r value at Sites D and E of this study were 0.90 and 0.79, indicating that these worms showed an even stronger tendency to orient their tube hoods. Given the similarities in tube structure and in hood orientation behavior, it is reasonable to suggest that <u>Pista pacifica</u>

and _Diopatra_ _cuprea_ orient their tube hoods at right angles to the
currents for the same reasons. As suggested by Brenchly and Tidball
(1980), the worms may, in this way, minimize sediment influx into
the tubes and maximize tube water circulation.

FIGURE 1. Schematic drawing of <u>Pista pacifica</u> tube hood.
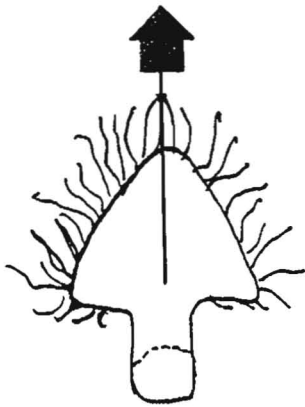The orientation of the hood is indicated by the
arrow.

FIGURE 2a .

Photograph of a typical _Pista pacifica_ hood taken at North Cove Site E. The orientation of the hood is indicated by the black arrow.

FIGURE 2b .

2b is a photograph of another hood which has been flipped back to expose the undersurface. The orientation of the hood, when in its normal position, is indicated by the black arrow.

a

b
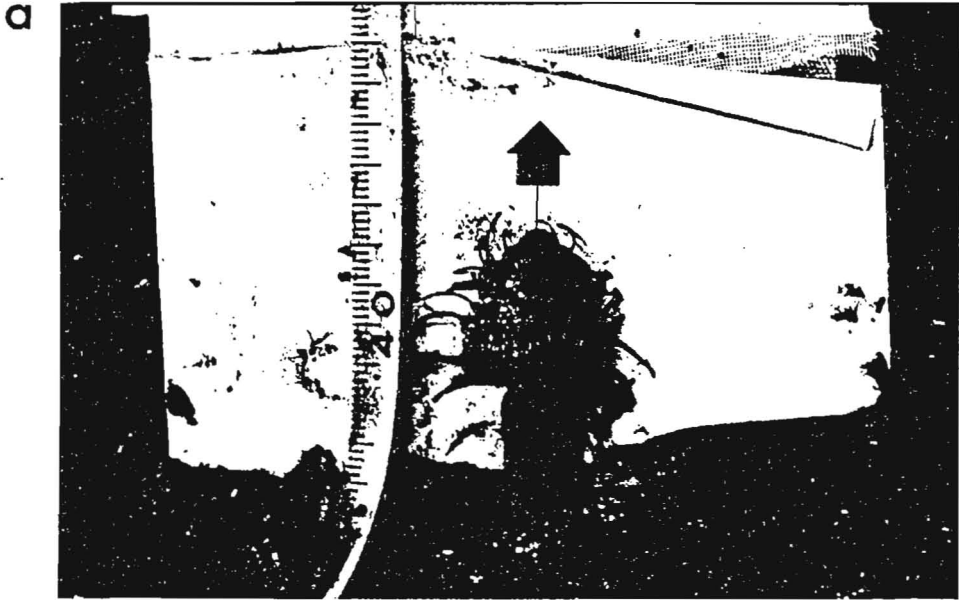
FIGURE 3. Map of South Slough Sites A, B, and C. Magnetic north

is indicated by the lower case "n".

43°22'

North Spit

N

Coos
Bay

A B

C

South
Slough

43°20'

0   FEET   3000

124°20'

124°18'
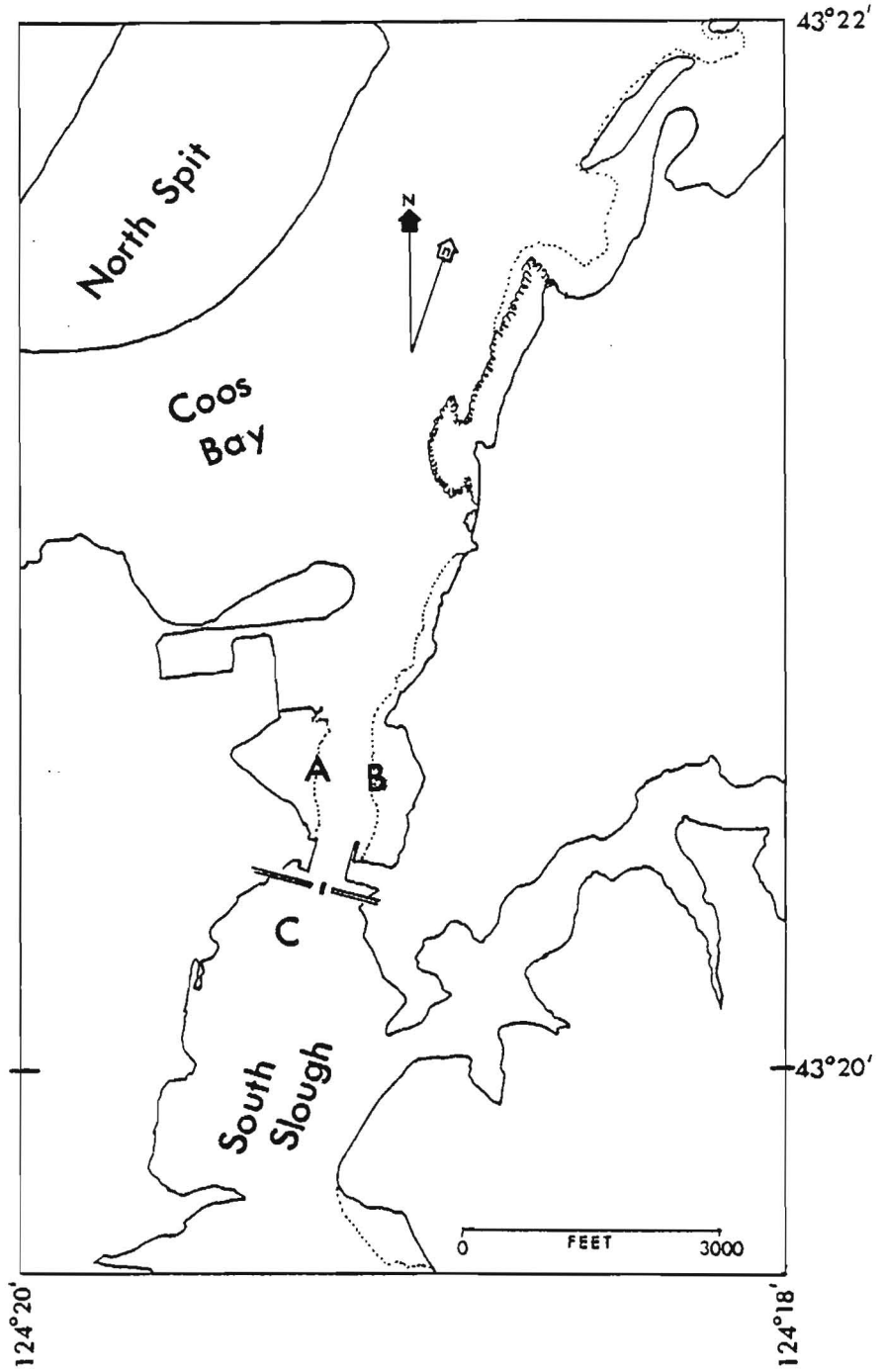
FIGURE 4. Map of North Cove Sites D and E. Magnetic north is
indicated by the lower case "n".

43°20'

N

Pacific Ocean

reef

D
E

Cape

Arago

OREGON

43°18'

0   FEET   3000

124°25'

124°22'
30"
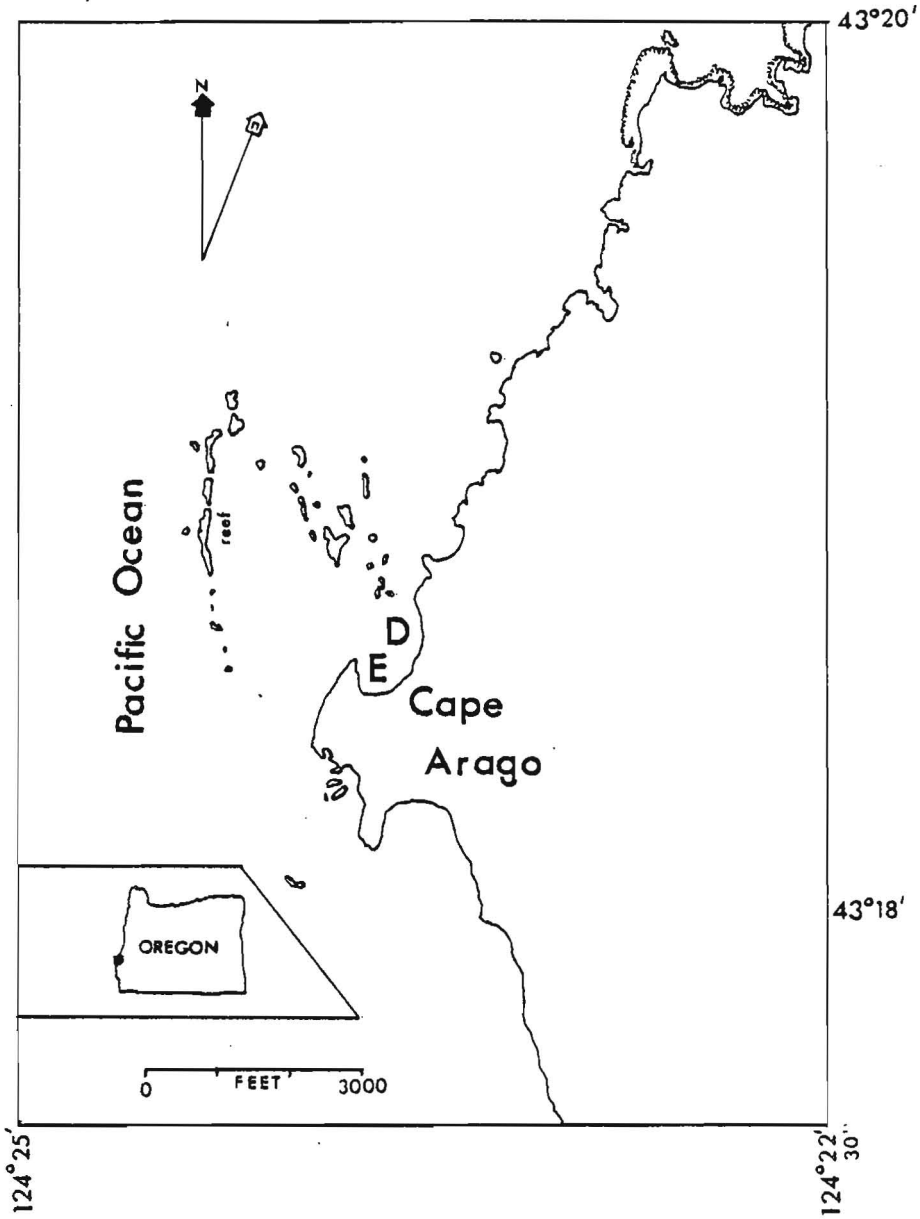
FIGURE 5. Photograph of North Cove Site D. The sample area was in
            the large pool. The ripples seen on the sandy area in
            the foreground continue into the pool. The long axis of
            the pool points approximately, from left to right, to
            the north.
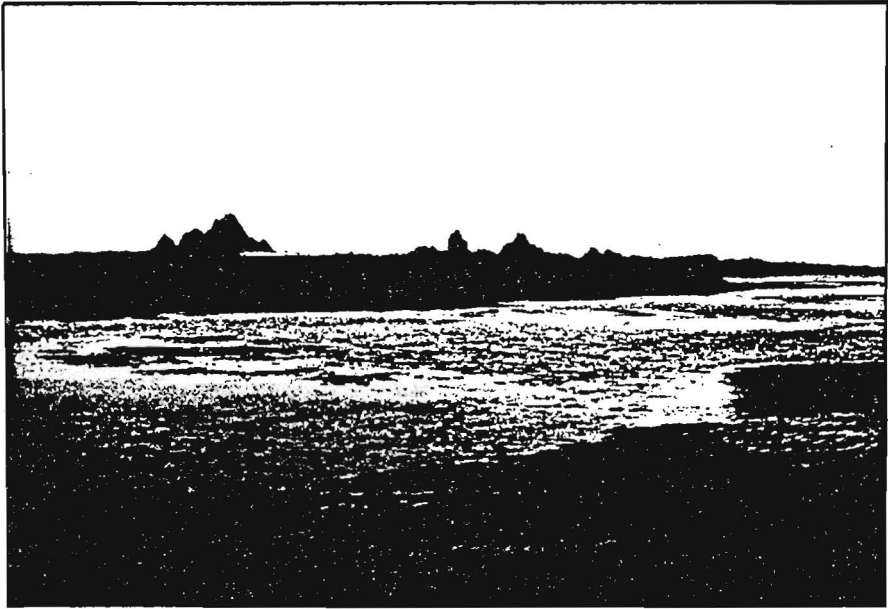
FIGURE 6. Photographs of North Cove Site E. The sample area is
the sandy area in the center of 6a. Figure 6b is a
close-up of sediment surface — note the marked sand
ripples.

a
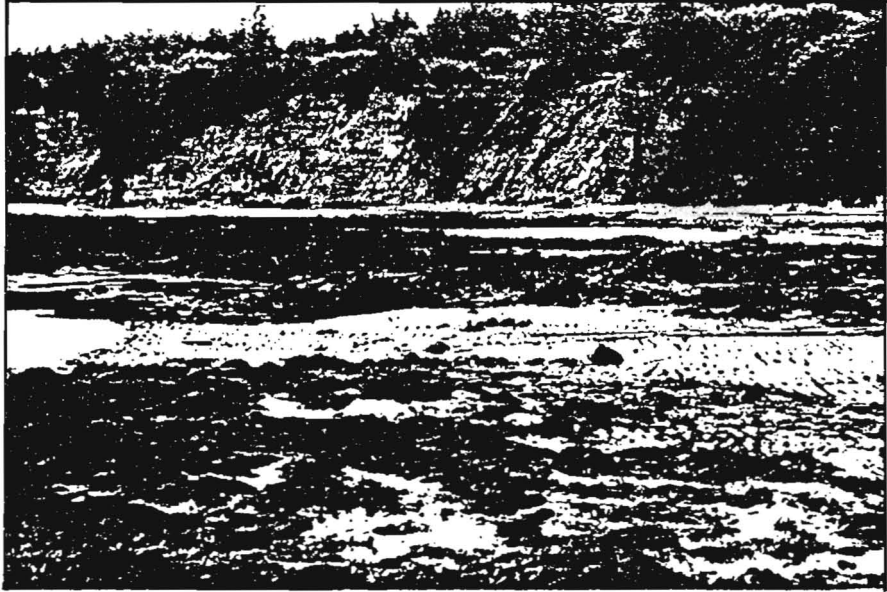
b

TABLE I. STATISTICS OF THE ORIENTATION DISTRIBUTIONS

SITE	MEDIAN ANGLE	90% CONFIDENCE INTERVAL	ANGLE OF MEAN VECTOR	MAGNITUDE OF MEAN VECTOR	INDEX OF DISPERSION	CHI-SQUARE (d.f.)	SAMPLE SIZE
	ϕ degrees	Q degrees (Range)	α degrees	r	I_d		n
A1	90	65—119 (44)	87.7	0.43	1.92	71.8 (7)	102
A2	70	65—90 (40)	69.5	0.55	1.61	64.9 (7)	104
B1	205	194—216 (22)	155.5	0.66	2.93	110.57 (7)	56
B2	195	168—218 (50)	168.6	0.51	1.48	43.12 (7)	69
C	--	---	43.8	0.36	1.20	21.23 (7)	52
D	160;218 (bimodal)	155—160 (5)	160;340	0.90	3.44	41.0 (3)	27
E	230;50 (bimodal)	220—238 (18)	47;227	0.79	2.90	31.32 (3)	31

FIGURE 7.

Circular histograms of tube hood orientation distributions.

A1--west side of South Slough entrance channel   11/78

A2--west side of South Slough entrance channel   7/81

B1--east side of South Slough entrance channel   7/81

B2--eel grass area on east side of South Slough
    entrance channel   7/81

C--west side of South Slough proper-Metcalf area   4/79

D--North Cove tide pool   4/79

E--North Cove sandy area   7/81

    The median direction of each distribution is indicated by the large, solid arrow, and the 90% confidence interval for the median is indicated by the zig-zag lines on each side of the arrow. The small solid arrow shows the mean direction. The hollow arrow on the top of each histogram indicates magnetic north. The units of the radial axis are in the number of Pista tube hoods per 10° orientation class.
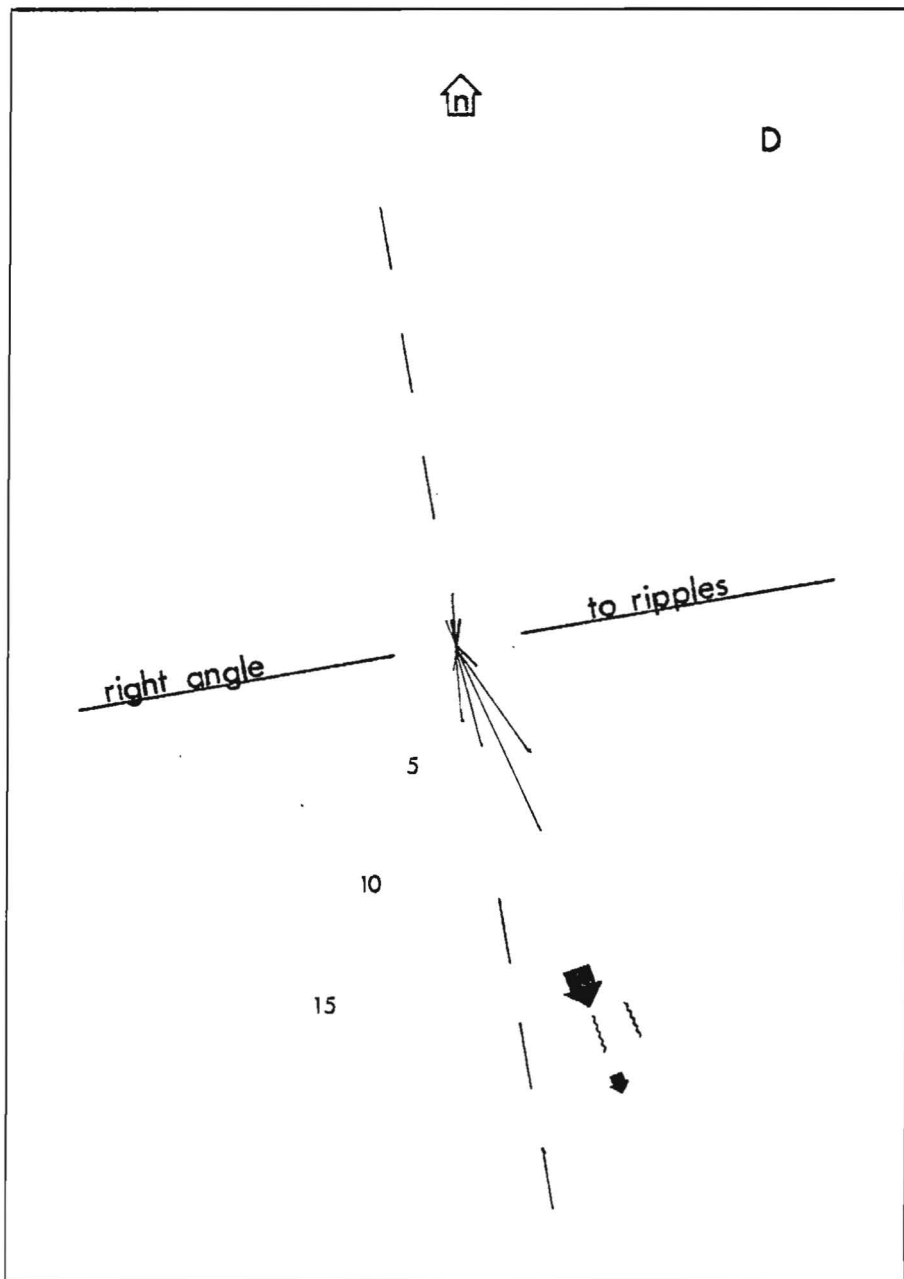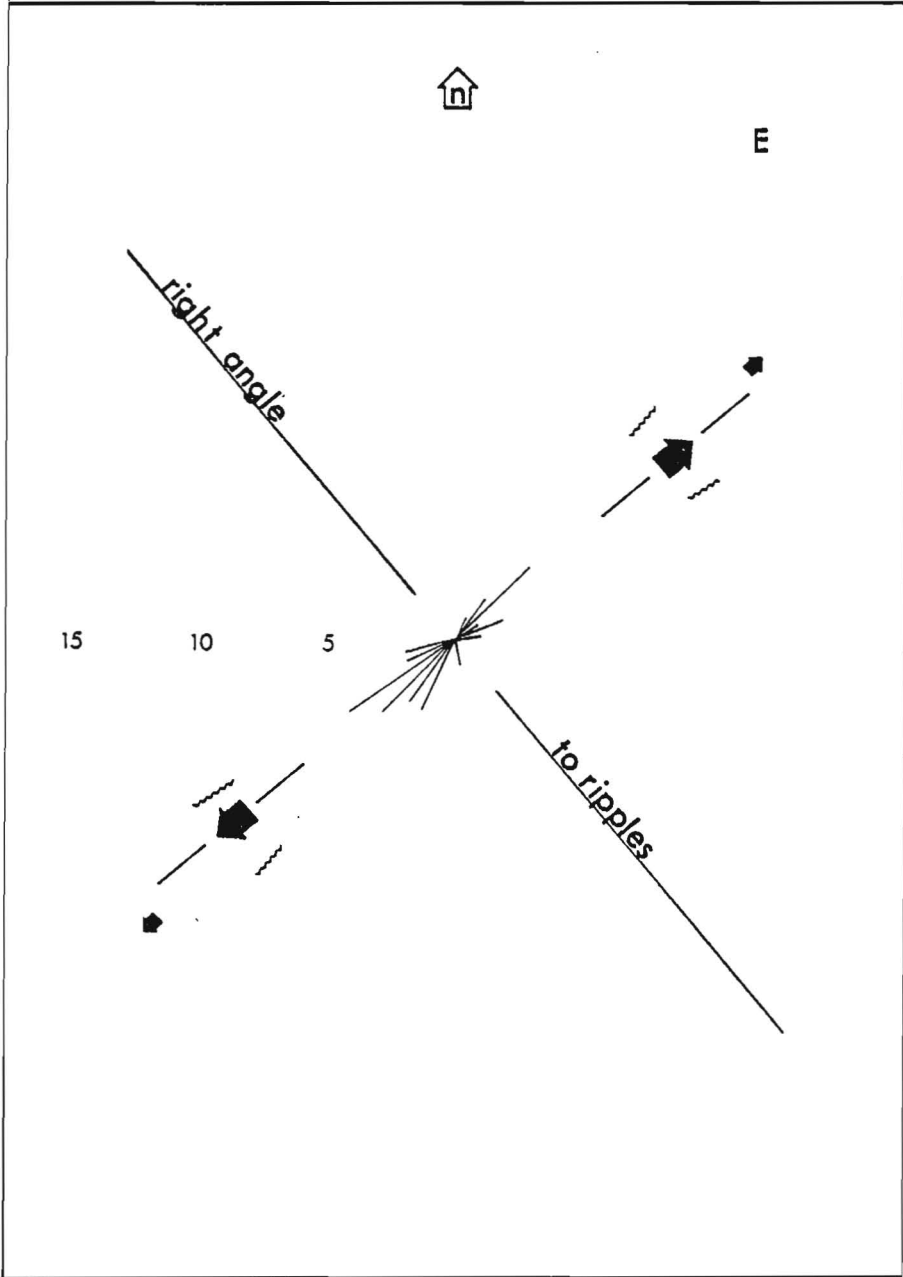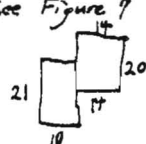
mud water

A1

15 10 5

B1

water

mud

15   10   5

B2

mud   water

C

5

10

15
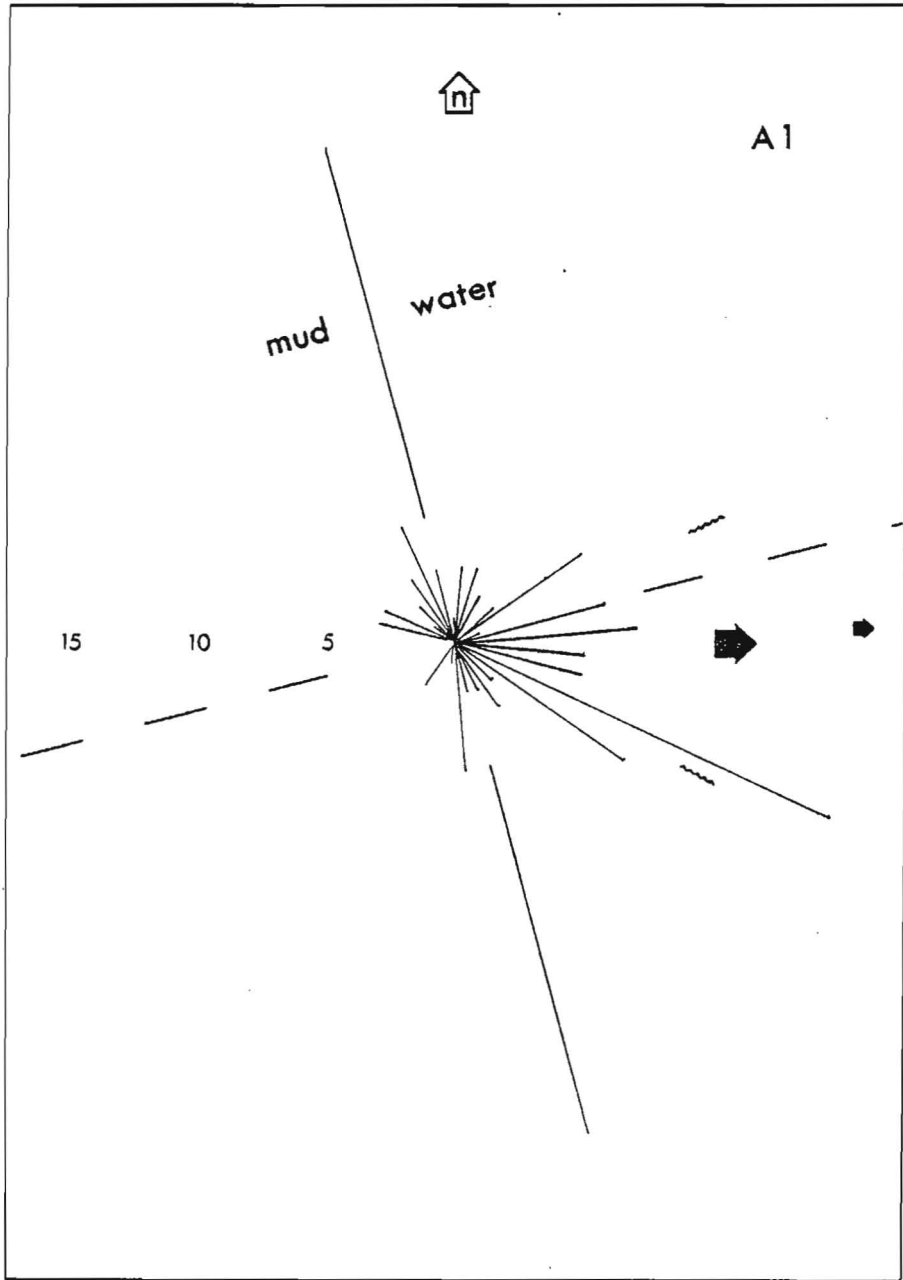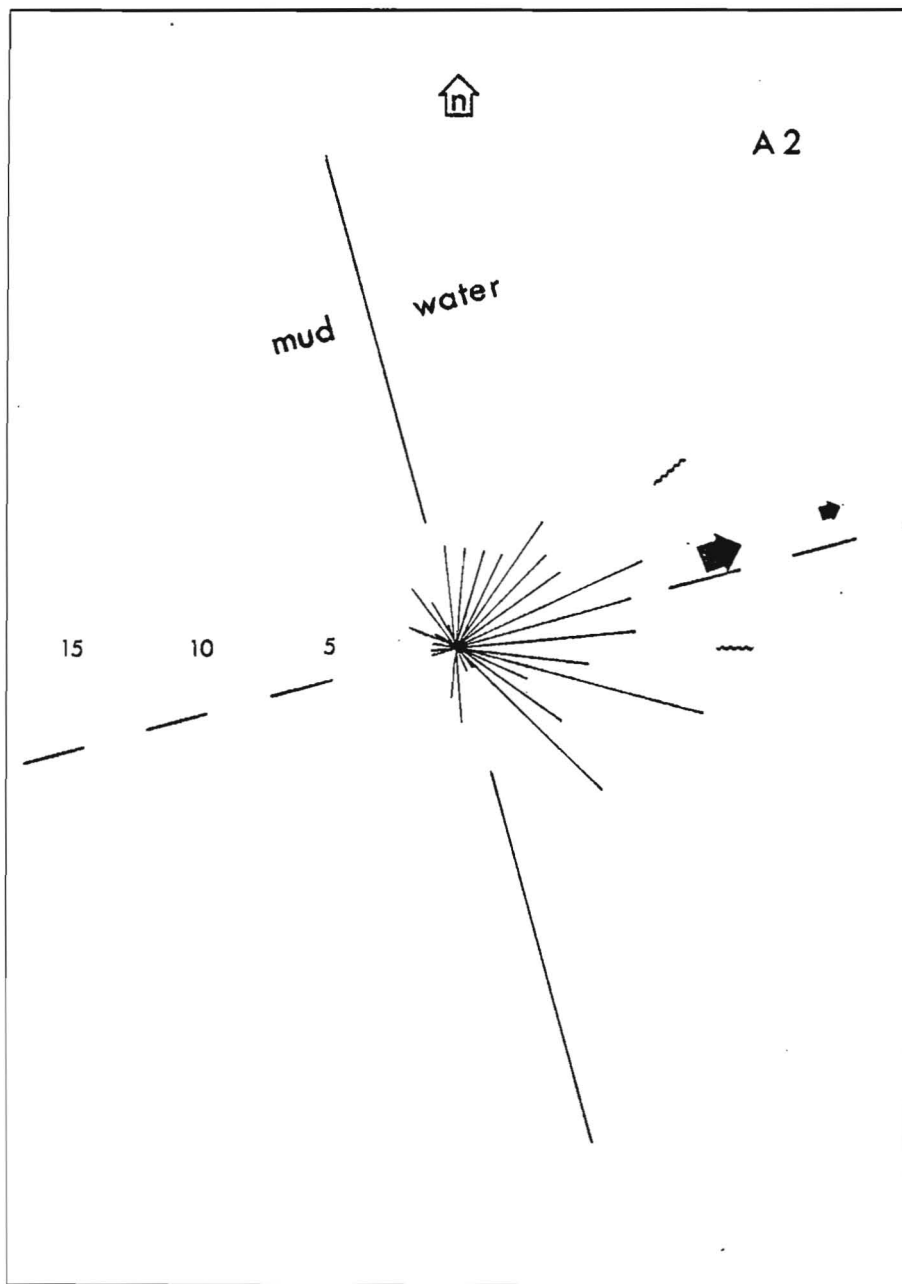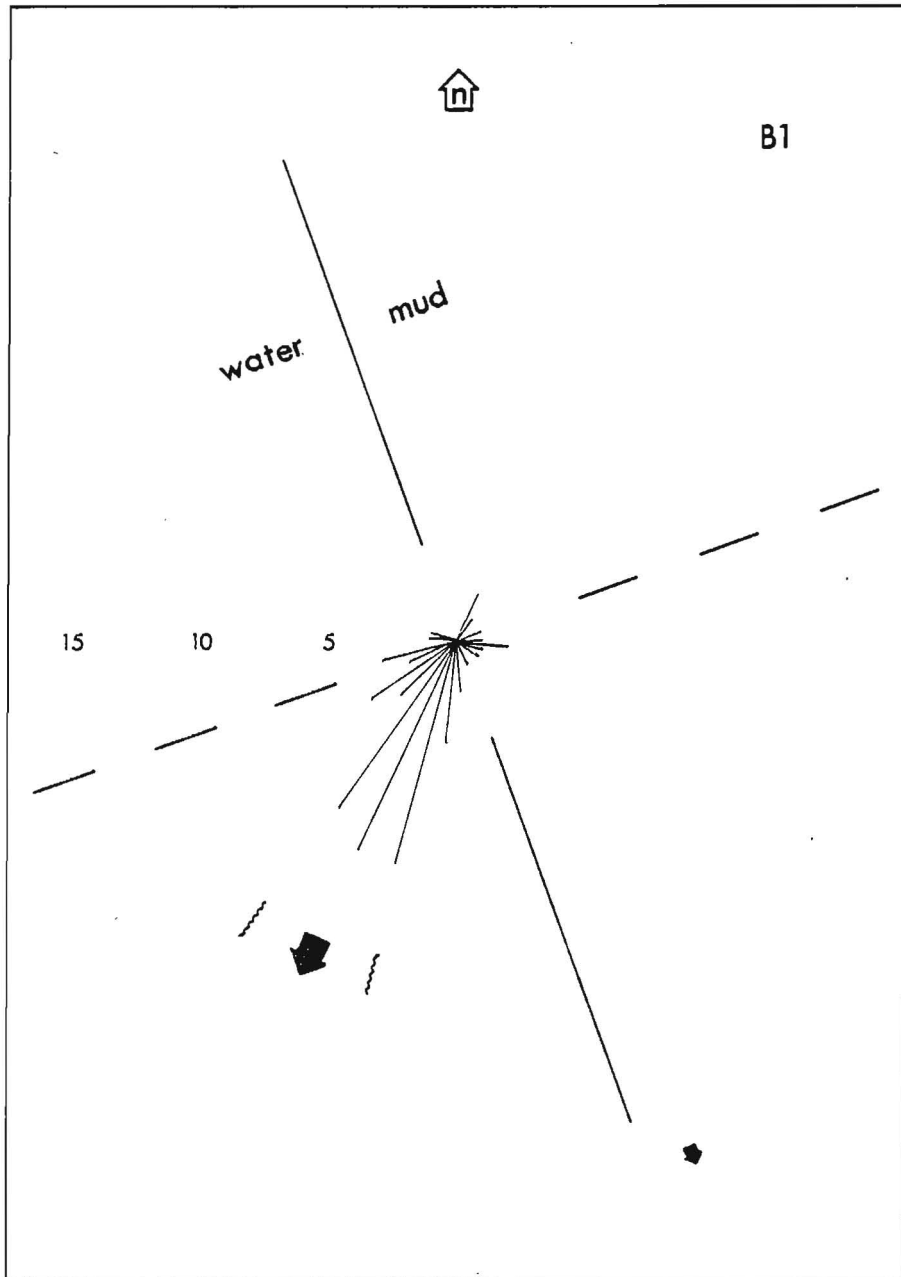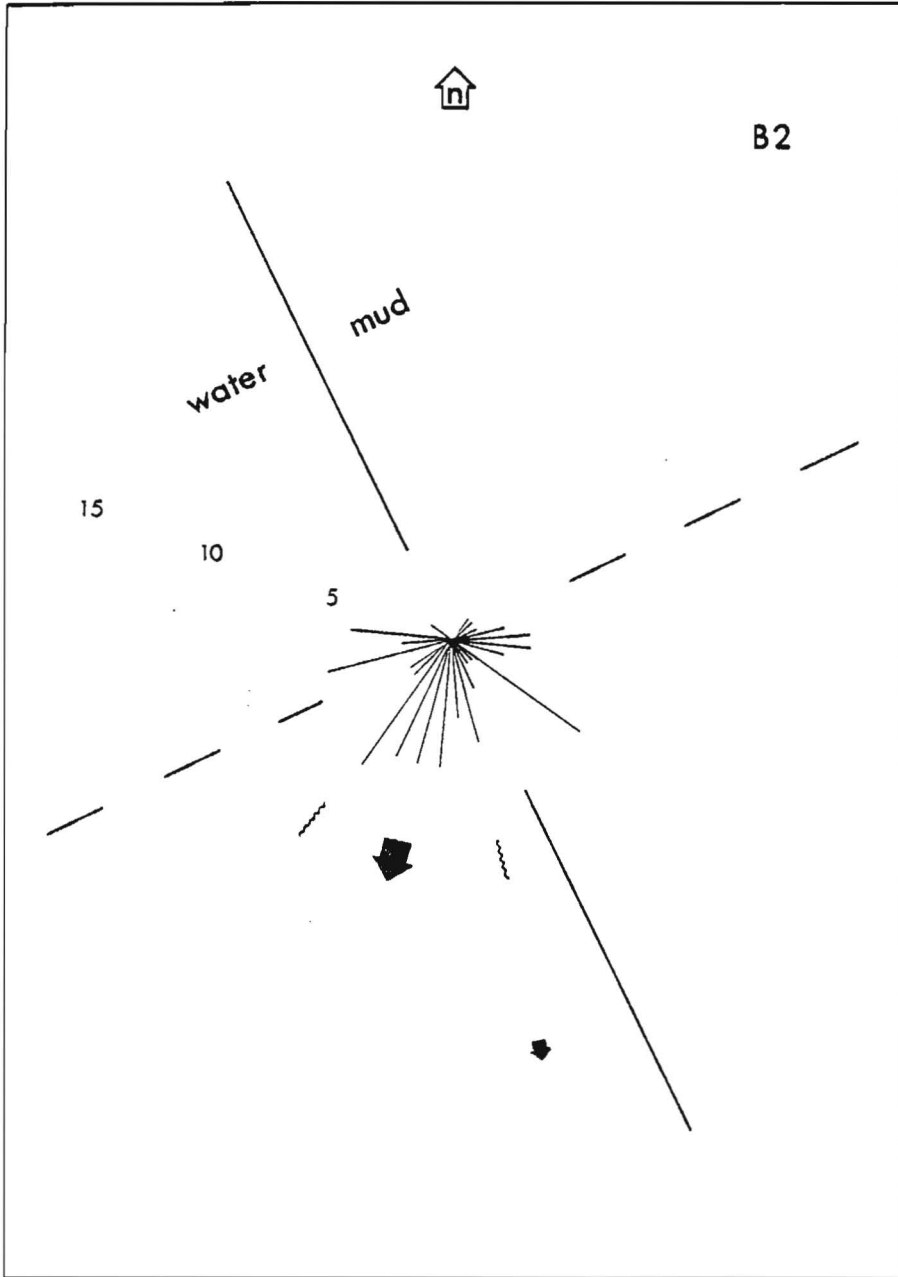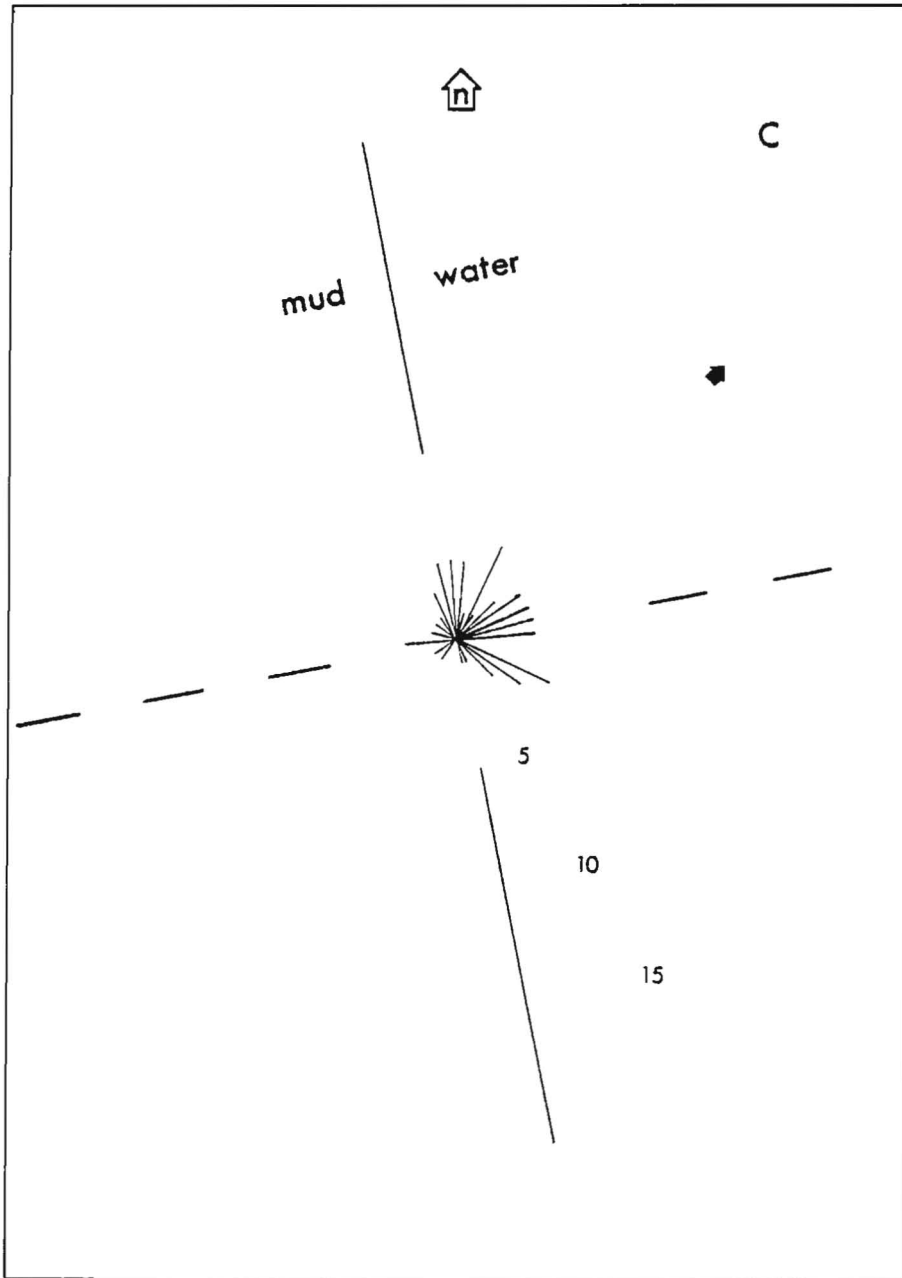
APPENDIX A

Notes on the Sample Areas

The sites were all sampled at lower-low water between November, 1978 and July, 1981. LENGTH refers to the length along the water's edge of the area sampled. At every 5 meters along the length of Site A1, a quadrat was placed randomly at 0 to 4 meters (inclusive) above the water's edge. Sites A2, B1, and C were sampled by positioning quadrats on an imaginary grid, as indicated in the METHOD column. The exact shape of this grid was adjusted to include only those areas where Pista pacifica occurred. The WIDTH in these cases refers to the maximum width of the grid, and thus the total area sampled is less than the LENGTH x WIDTH. At Sites B2, D and E all of the animals occurring in a given area were sampled. The dimensions of these areas are given in the LENGTH and WIDTH columns.

The density measurements should in no way be considered as representative of the population as a whole since the samples were taken at the upper limit of the animal's distribution, and since the boundaries of the sample areas were always arbitrarily established.

Site	Date	Description	Length	Width	Sample Area	Method	Number of Quadrats	n	Density
A1	11/78	- West side of South Slough C. - Fine mud sediment - Fairly dense Eel Grass - Some clear Areas - popular clam digging area - Straight shore line	210m	5m	a] 1050m²	a] - 0.25m² quadrat placed every 5m along beach, randomly along width of beach for 5m. b] - 0.25m² quadrats selected from Eel grass areas only. c] Worms selected from outside of quadrats	a] - 43 b] 61 c] —	a] 29 b] 62 c] 11 n = 102	a] 2.7/m² b] 4.1/m² c] —
A2	7/2/81 - 7/3/81	- West Side South Slough Channel - Fine Mud Sediment - Fairly dense Eel Grass - Some clear areas - popular clam digging area - straight shore line	250m	Max 6m	740m²	0.25m² quadrats placed on 2m×2m grid.	311	104	1.34/m²
B1	7/3/81	- East side South Slough Channel - Sandy Mud - No Eel grass in sample area - Straight shore line	60m-	Max 10m	600m²	0.25m quadrats placed on 2×2m grid	186	56	1.20/m²
B2	7/3/81	- East side South Slough Channel - Sandy Mud - Dense covering of Eel grass	15m	10m	150m²	All worms found in area were sampled rectangular	—	69	0.46/m²
C	4/26/79 - 4/27/79	- South Slough proper, west side. - Irregular shore line - Fine - sandy mud - Area divided into two subsamples seperated by 15m drainage channel. - Patches of Eel Grass	a] 80m b] 60m	Max 14m Max 20m	1010m² 720m²	a,b] 0.25m² quadrats placed on a 5m×2m grid. c] Worms selected from outside of quadrats	a] 125 b] 104 c] —	a] 12 b] 32 c] 8	a] 0.38/m² b] 1.23/m² c] —
D	4/29/79	- North Cove Tide Pool - See Figure 6. - Area submerged even at low tide	5m	7.2m	36m²	All worms in area sampled rectangular	—	27	0.75/m²
E	7/4/81	- North Cove Sandy Area - See Figure 7	24m	21m	490m²	All worms in Area sampled	—	16	0.063/m²

APPENDIX B

### Diagram of proposed flow chamber for eight tube worms

Water enters on the left and pushes through the diffusing screen (a ventilation filter) into the main chamber. Here the current is channeled by the curved plastic sheet into the experimental area. The water runs out the overflow on the right-hand side, and is recirculated.

Measurements in centimeters
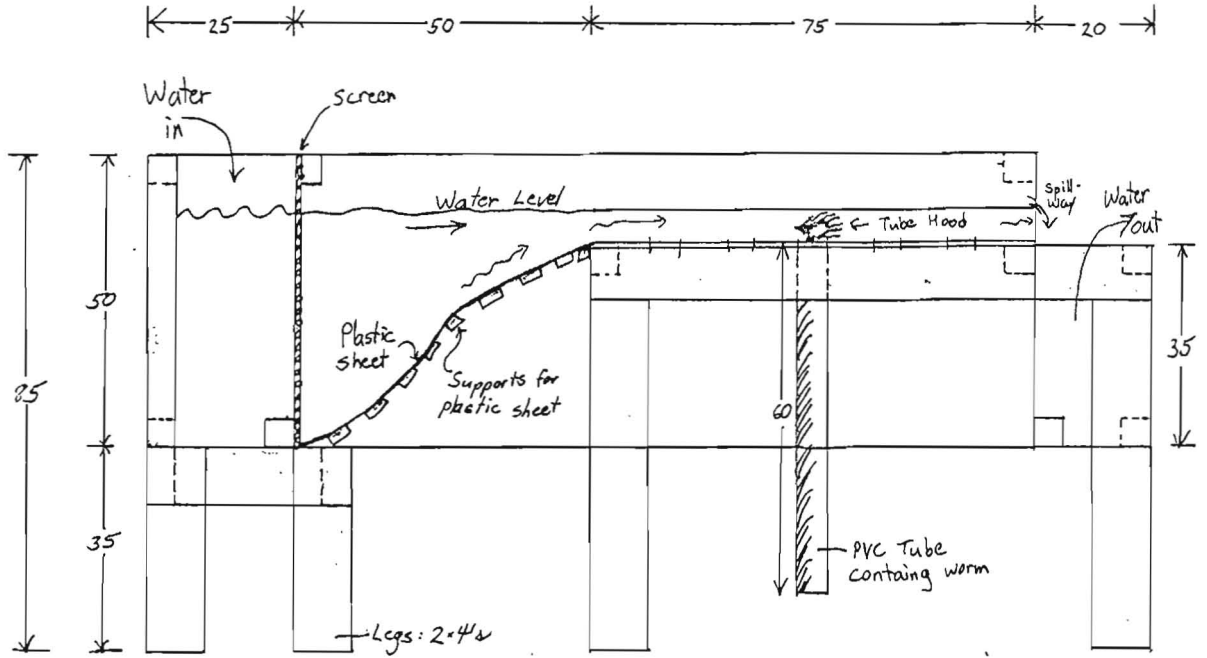
Side View - Shown with plywood sides removed. Plywood is 3/8"
Legs & major support members are 2"×4"s
Other supports are 2"×2"s

Top View
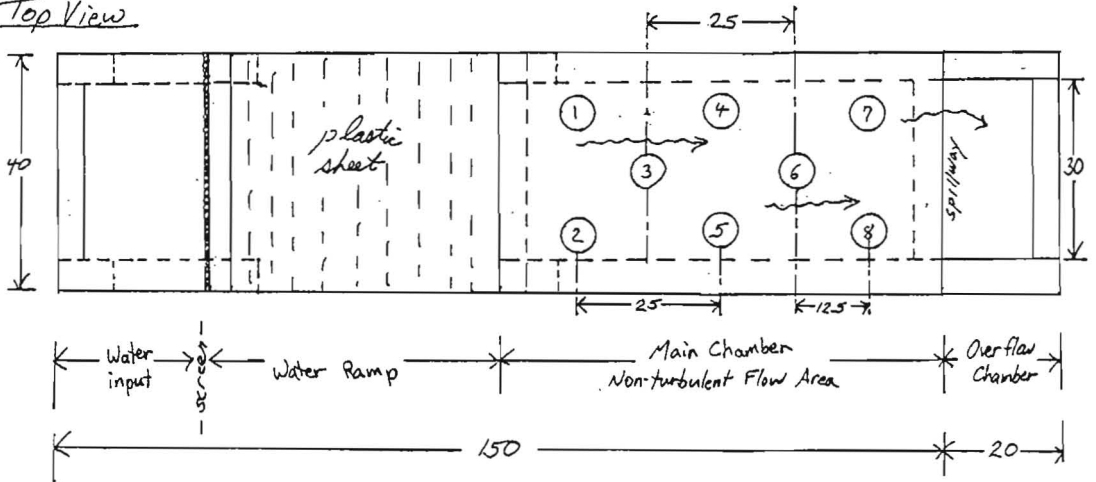
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