

Aspects of Feeding, Burrowing, and Distribution of *Haploscoloplos elongatus* (Polychaeta: Orbiniidae) at Bodega Harbor, California¹

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ABSTRACT: *Haploscoloplos elongatus* in Bodega Harbor has an aggregated dispersion pattern correlated with sediments of relatively large grain size (0.149–0.42 mm). The association between algal cover and the presence of worms is not significant. The worm's soft, lobate proboscis is adequate for direct-deposit feeding and is not involved in burrowing. The prostomium is essential in formation of the penetration anchor and is used for enlargement of the burrow. Movement through the substratum is by retrograde waves by which the worm may move forward or backward.

THE BIOLOGY OF *Haploscoloplos elongatus* is poorly known although it has been described thoroughly (Hartman 1969, Johnson 1901 from Smith and Carlton 1975). It has previously been reported from Alaska to Mexico (Berkeley and Berkeley 1952, Hartman 1957, 1965, Hartman and Barnard 1960, Reish 1968) and occurs at varying depths (Hartman 1963, 1968, Pettibone 1957).

Haploscoloplos elongatus has been dredged from 10 to 30 fathoms off Vancouver Island (Berkeley and Berkeley 1952). In northern and central California it is common from intertidal down to 293 fathoms (Hartman 1957). In its more southern range it is found in the subtidal to 700 fathoms in sand and mixed sediments (Hartman 1963).

In submarine canyons off Santa Catalina Bay *H. elongatus* is more common in sand at an average depth of 198 fathoms [calculated from Hartman (1963)], although prior work by Hartman and Barnard (1960) in southern California showed *H. elongatus* attained maximum size and abundance in shallow (25 fathoms) depths. It is interesting to note that when it was found in mixed sediments in Hueneme and Newport canyons, abundance was greater in shallower depths (Hartman 1963).

Haploscoloplos elongatus is common in

very fine sands (Berkeley and Berkeley 1952), silts (Hartman 1965), silty sands (Reish 1968), mud and gravelly sands (Pettibone 1957), and sandy mud flats (Hartman 1957). In submarine canyons *H. elongatus* is commonly found in mud, sand, silty sand, mixed sediments, and occasionally in clay (Hartman 1963).

Little work has been published concerning burrowing, feeding, spatial distribution, or other aspects of its biology. This work concerns field and laboratory studies of burrowing, feeding, and distribution of an intertidal population of *H. elongatus* at Bodega Harbor, California. The mechanism of burrowing is compared to that of *Arenicola marina* (Seymour 1971, Trueman 1966) and other soft-bodied invertebrates (Trueman 1975, Trueman and Ansel 1969).

MATERIALS AND METHODS

Specimens of *Haploscoloplos elongatus* were collected using hand tools from the mud flat at Bodega Harbor, California, during -1.0 to -1.3 ft tides. In the laboratory they were kept in 1-pt specimen jars in a constant environmental chamber set at 15°C. Approximately 0.5 cm of mud from Bodega Harbor and small pieces of green algae were placed in the jars with the worms. The sediment was added to reduce the tendency of mucoid constrictions and severance

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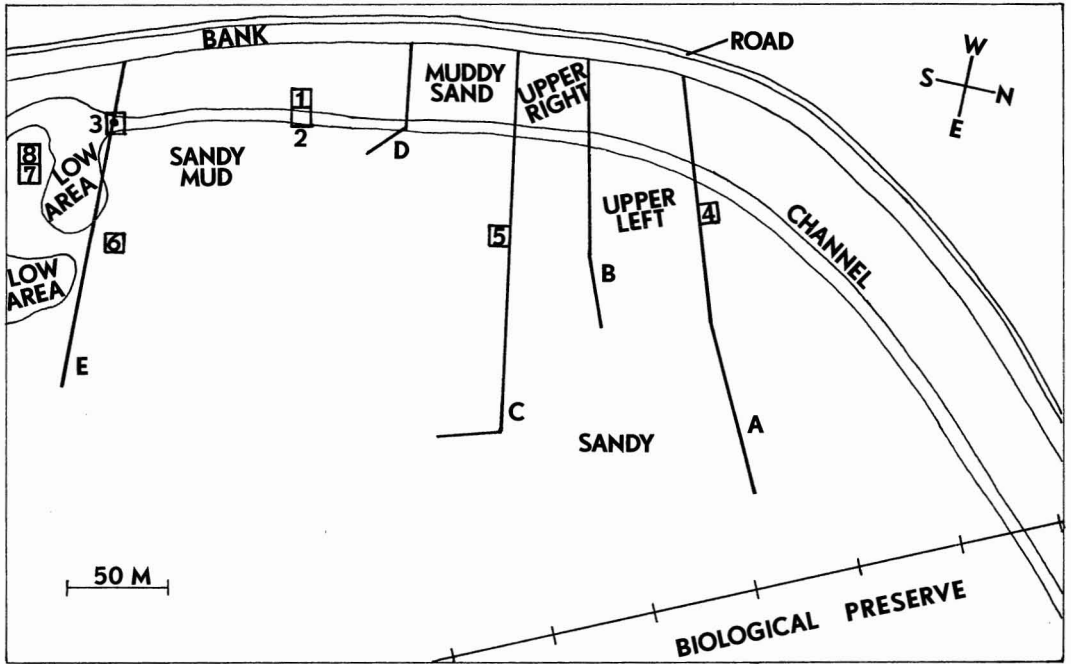


FIGURE 1. Illustration of study area along the northwest edge of Bodega Harbor, California, showing the relative position of each transect. Numbers 1–8 refer to 10×10 -meter transects; letters A–E refer to linear transects. The markers along the boundary of the University of California biological preserve are shown as reference points.

of the body at that point (Smith and Chanley 1975). The algae seemed to help reduce mortality. Observations of burrowing and feeding were made of worms in a burrowing chamber. This chamber was a 5-gal aquarium with a sheet of plexiglass inserted so that a worm had to burrow (and could be seen) in the front 2 cm of mud. Observations were recorded on Kodak Ektachrome movie film by a Bauer C. Boyd camera at 18 frames/sec.

Dispersion analysis (Poole 1974) was determined from specimens found in nature in 10×10 -meter transects selected from numbers in a random number table (Figure 1). A large shovelful (approximately $1/16$ m² surface area) of mud was dug and sieved, and worms were recovered from each of the random square meters sampled. Quadrats of $1/16$ m² from another 100 areas, each 1 m², along five different linear transects were also sampled for general distribution of *H. elongatus* on the mudflat (Figure 1).

The mudflat at Bodega Harbor during October and November was characterized by a great amount of algal cover (including

various species of *Ulva* and *Enteromorpha*). In January, April, and May, there was much less algal cover. During a low tide the water recedes to a small channel that drains the higher ground. The amount of algal cover and the position of quadrats in relation to the channel were recorded (Figure 1).

Sediments were collected from areas with worms (transects 1–3, 6–8) and areas with no worms (transects 4 and 5), and were dried and sieved to determine the percentage composition of different grain sizes. Sieves with mesh sizes of 1.0, 0.42, 0.149, 0.105, and 0.074 mm were used.

Specimens were brought back to the laboratory for dissection for study of septae and gut contents.

RESULTS

Distribution and Dispersion Pattern

A total of 46 specimens were found in 200 random 1-m² areas sampled in the eight 10×10 -meter areas (Table 1). Transect 1 revealed only one specimen. This area was

TABLE 1
BREAKDOWN OF EACH TRANSECT ASSOCIATING WORMS FOUND WITH ALGAL COVER

TRANSECT NUMBER	1	2	3	4	5	6	7	8
Average percentage of ulvoid cover, entire transect	90	20	30	0	5	0	40	5
Average percentage of ulvoid cover per $\frac{1}{16}$ m ² quadrat	40.8	8.2	11.4	0	0.08	0	17.4	4.6
Number of worms in transect	1	7	11	0	0	1	15	11
Average number of worms per quadrat	0.04	0.28	0.44	0	0	0.04	0.6	0.44
Percentage of worms with ulvoid cover	100	14	27	0	0	0	100	12
Percentage of worms without ulvoid cover	0	86	73	0	0	0	0	88

characterized by 90 percent algal cover and did not contain the channel. The substrate was a muddy sand, and water retention was low. Transects 2 and 3 were more rewarding, with 7 and 11 specimens, respectively. The channel traversed both. Of the 7 specimens taken in the second transect, 6 were found in sandy mud. The seventh specimen was uncovered in the upper right area (Figure 1) in muddy sand. The left bank of the channel consisted of much silt and had a strong odor. No specimens were found here. Algal cover of transect 2 was considerably reduced, with 86 percent of the worms taken associated without algae (Table 1). In transect 3 all 11 specimens were concentrated in the channel and peripheral area in sandy mud. Algal cover was between 0 and 50 percent, with only 27 percent of the worms taken associated with an algal cover (Table 1). Transect 4 was through mixed sediments of sand and mud, and algal cover was zero; no worms were found. In transect 5 the sediment was very sandy and infauna consisted mainly of *Phoronopsis viridis*. No orbiniiids were found. Transect 6 again was mostly sandy; the one orbiniiid found was in this sediment. Transects 7 and 8 were mixtures of sand and mud but far muddier than areas 5 and 6. Twenty-six specimens were found, usually (18 of 26) in areas with some algal cover.

In the 1/16-m² quadrats in 100 meters along linear transects A–E, only two specimens of *H. elongatus* were found. These two specimens were found in the same quadrat, in sandy mud in the streambed (area marked

with dot, transect E, Figure 1). Transects A–D, like transect 5, traversed a relatively high, dry, sandy area of the mud flat where infauna consisted mainly of *Phoronopsis viridis*. Transect E was in a mixture of sandy mud and silt; the two orbiniiids were found in sandy mud.

When sediments of the study area were qualitatively divided into muddy sand versus sandy mud, specimens of *H. elongatus* were found to be significantly more abundant in sandy mud substrata (9 worms in 59 muddy sand quadrats; 37 worms in 141 sandy mud quadrats; $\chi^2 = 184.35, P \ll 0.005$). Sediments from transect 5 contained no worms; sediments from transects 1 and 2 contained several worms. A comparison of particle size composition of these two areas using dried sieved sediments gave the following results:

Grain size (mm)	Percent of each grain size in transect 5	Percent of each grain size in transects 1 and 2
> 1.0	0.12	1.1
0.42–1.0	0.8	10.5
0.149–0.42	92.6	86.1
0.105–0.149	4.2	1.2
0.074–0.105	0.7	0.28
< 0.074	1.6	0.79

Sediments in which worms were common had a much higher percentage of larger grain sizes than areas tested for sediments without worms. Over the study area, *H. elongatus* showed a strongly aggregated dispersion pat-

tern (zero worms in 168 samples, one worm in 20 samples, two in 10 samples, three in 2 samples; average number of worms/sample = 0.23; $s^2 = 0.33879$; $\chi^2 = 24.84$, $P < 0.005$; see Poole 1974, pp. 103–105). From all the above data, distribution of *H. elongatus* is shown to be highly correlated with sediment type in this bay.

Haploscoloplos elongatus tended to be more abundant in areas with little algal cover (43 worms in areas with 20 percent or less algal cover; 3 worms in areas with 21 to 100 percent algal cover), but this association was not significant ($\chi^2 = 0.85$, $0.5 < P < 0.95$).

Feeding

The proboscis of *H. elongatus* is described as an unarmed, eversible, soft sac that is slightly lobate (Hartman 1957, Pettibone 1957). While in its burrow, *H. elongatus* was observed to evert its proboscis into the end of the burrow (Figure 2) and appeared to be eating; the proboscis is adequate for direct-deposit feeding. Gut contents from seven dissected worms included diatoms, foraminiferans, sand, and unidentified structures.

Burrowing

When first placed into the burrowing chamber, *H. elongatus* appeared disoriented for a short period of time before burrowing. Extension of the prostomium and a pumping action of the thorax ensued until the anterior end of the worm was anchored securely. Once this was accomplished, the more posterior portions were pulled in.

When it burrowed through a thin layer of silt, *H. elongatus* appeared to rest for short periods between pumping actions as if fatigued. The silt probably does not provide sufficient resistance against the body wall of the anterior region for a penetration anchor to form (see the Discussion below). To pull the rest of the body in, a terminal anchor must be made by dilation of the anterior end (Trueman 1975). Complete burial can then be made. *Haploscoloplos elongatus* moves through its burrow by elevating its parapodia when a peristaltic wave passes the associated



FIGURE 2. Drawing from a frame in a movie of *Haploscoloplos elongatus* in its burrow with the proboscis out. The finely stippled structure is the thin, membranous proboscis.

segments. If the wave is traveling from right to left (and the worm is moving from left to right, i.e., in retrograde waves), the region to the right is extended and the parapodia are lowered to allow passage. Segmented animals that use retrograde waves for locomotion must be completely segmented (Trueman 1975). As seen from dissection, *H. elongatus* has complete septae throughout the length of its body.

The animal constantly probed the area in its path with the prostomium as if to investigate the immediate area.

Widening of the burrow was observed from shearing by the prostomium against the burrow wall (Figure 3). The blind end of the burrow was enlarged, forming an area in which the proboscis was everted; the proboscis was not used in burrowing but only for feeding. Once the proboscis was retracted, *H. elongatus* either continued in its path or chose another direction.

DISCUSSION

Feeding

Proboscis eversion in the well-studied *Arenicola marina* is associated with feeding and burrowing; in the latter case, nothing enters the mouth (Wells 1954). The proboscis of *A. marina* is externally supplied with mucus glands that will cause adhesion of fine material and sand while materials of a coarser

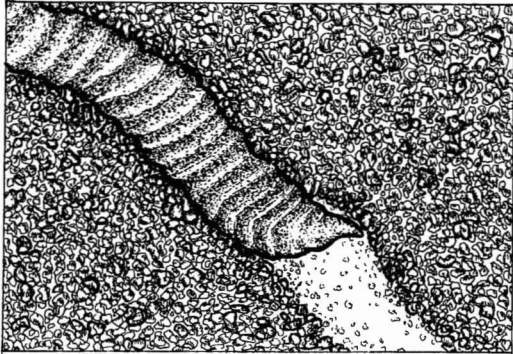


FIGURE 3. Drawing from a frame in a movie of *Haploscoloplos elongatus* widening its burrow by shearing action of the prostomium.

nature are pushed aside (MacGinitie and MacGinitie 1968). When inverted, the proboscis carries the entrapped material to the mouth, where it is ingested. As *Arenicola* burrows, little detritus adheres to the proboscis. *Haploscoloplos elongatus*, also a burrowing polychaete with a soft proboscis, can be compared to *Arenicola*. From observations and studies of movies of burrowing (Figures 2, 3), it was seen that the proboscis of *H. elongatus* is not involved in burrowing. It may be assumed that the eversion process occurs only for feeding, because the mouth of *H. elongatus* was not observed to be open when burrowing occurred.

Burrowing

Field and laboratory results of burrowing are compared to results from research done on burrowing of *Arenicola marina* (Seymour 1971, Trueman 1966) and reviews concerned with burrowing of soft-bodied animals (Trueman 1975, Trueman and Ansel 1969).

All soft-bodied animals burrow by utilizing a similar mechanism (Trueman 1975, Trueman and Ansel 1969). Primarily this is based on the formation of two types of anchors. First, the region above the extreme anterior end is dilated to form a penetration anchor; second, the distal anterior end is distended to form a terminal anchor (Trueman and Ansel 1969). The penetration anchor is essential because it prevents the animal from being

pulled upward by the contractions of the rest of the body.

Inability to form a penetration anchor initially accounts for the fatigue observed when *Haploscoloplos elongatus* attempted to burrow through the layer of silt in the burrowing chamber. This inability resulted in repeated burrowing failures; thus, fatigue set in. Once *H. elongatus* secured the penetration anchor, the terminal anchor was made. Applying these anchors alternately, the worm pulled its body into the burrow.

It should be noted that the prostomium is as important to *H. elongatus* in burrowing as the proboscis is to *A. marina*. Both worms have little weight in water, so these adaptations for initial penetration are essential.

A major problem arises in comparing results of burrowing in *Arenicola* to those of *H. elongatus* because the nature of the peristaltic waves in *H. elongatus* are retrograde whereas in *Arenicola* they are direct. It was found that *H. elongatus* has complete segments throughout its length; it also has retrograde waves when burrowing. *Arenicola* septation is incomplete, therefore it possesses a continuous trunk coelom (Trueman 1975). The importance of this lies in the fact that segmented animals must use peristaltic waves that are retrograde to burrow, but those with a continuous coelom may utilize either direct or retrograde waves.

Being of circular cross section, *H. elongatus* is well adapted for life in a burrow; the body wall is in contact with the substratum on all sides. Movement is made by contractions of the longitudinal muscles to form *points d'appui* (similar to the penetration anchor), while contractions of the circular muscles cause extension of the body. Waves of these contractions occur as peristalsis, causing erection and relaxation of the parapodia. It is the parapodia that form the *points d'appui*, allowing anchorage.

Distribution Patterns

The structure of *H. elongatus* and the nature of the parapodial position dictate that suitable substrate must be dilant (structured) enough to allow the worm resistance against

sand grains. But data (Hartman 1957, Reish 1968) show *H. elongatus* in a slightly thixotropic environment (i.e., sand grains of a small uniform size—silt). Thus, a sandy mud substratum is the most ideal and common environment in which *H. elongatus* is found.

In its southern range, *H. elongatus* has been found in mud and mixed sediments (Hartman 1965). Those taken in Santa Catalina Bay from mud and mixed areas were primarily from sublittoral depths. Its presence in sublittoral depths at the southern limit of its range may be correlated with lower temperatures, as those found in littoral depths at the northern end of its known range. Only when the range of *H. elongatus* in the north is better known can this correlation be made (Hartman and Barnard 1960).

The data accumulated from transects in an intertidal northern California bay established a number of findings. *Haploscoloplos elongatus* at this site is significantly associated with a sandy mud substratum, usually with low algal cover. It has an aggregated dispersion pattern and cannot be found over wide stretches of the mud flat.

If a species is truly aggregated, then this may be an intrinsic part of the behavior of the species or else the aggregating is caused by habitat heterogeneity (Poole 1974).

SUMMARY

1. Feeding in *Haploscoloplos elongatus* is by proboscis eversion while the worm is within its burrow. Gut contents consisted of sand, diatoms, foraminiferans, and unidentified structures.
2. The prostomium forms a penetration anchor to initiate burrowing, and burrowing is accomplished by retrograde peristaltic waves. Enlargement of the burrow is accomplished by a shearing action of the prostomium against the burrow wall.
3. Distribution of *H. elongatus* at Bodega Harbor is aggregated and is significantly correlated with a sandy mud substratum.

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