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Distribution and abundance of soft-sediment intertidal Polychaetes

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DISTRIBUTION AND ABUDANCE OF SOFT-SEDIMENT INTERTIDAL POLYCHAETES

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by
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INTRODUCTION

Experimental studies of rocky intertidal, epibenthic and other natural communities (Dayton 1971, 1975; Connell 1961a, 1961b, 1970; Paine 1966, 1969b; and others) have demonstrated the importance of interactions between the adults of component species of these communities in determining their abundance and distribution. Paine (1969a) coined the term "keystone species" for species of high trophic status that affect the distribution and abundance of other species in the community disproportionately, that is more than would be expected on the basis of the keystone species abundance, biomass, or other measure of dominance. Recently, Wooden (1974) attempted to study the interaction between infauna of soft-substrate communities, with special attention to polychaetes and found that competition for limiting resources was not important between tube builders or tube builders and burrowers and that other biological interactions were important determinants of polychaete infaunal species abundance patterns in soft-sediment environments.

Community regulation in the rocky intertidal zone was experimentally investigated by various workers. Paine (1966), Connell (1961a), and Dayton (1971) agreed that competition for space and predation were important factors in community regulation. However, Paine (1971) argued, that under many conditions predation is more important determinant of the broad patterns of community structure than competition.

Polychaetes are important components of the intertidal sandflat community in Lawson's Flat, Dillon Beach, California (Johnson 1970). Little is known about the factors that control the relative abundance of these species. In view of the extensive evidence of the importance of interactions between component species in intertidal communities it is of interest to obtain information that would facilitate future experimental work of such interactions. This study documents seasonal changes in the abundance of the polychaete component of the intertidal community. Attention is directed at possible factors that might affect seasonal changes in distribution. A major finding is that certain herbivorous polychaetes exhibit seasonal fluctuations in abundance that appear to be correlated with changes in algal cover. These findings might suggest more detailed future experimentation. Some aspects of recruitment of major species are considered and the presence of a parasite in one of the species is noted. Aspects of benthic community ecology are discussed.

MATERIALS AND METHODS

An intertidal sampling locality was chosen in a protected sand flat, locally known as Lawson's Flat, in Tomales Bay, California (Fig. 1). About 300 m of this flat are exposed during low tide. Characteristics of the area are described in Johnson (1965, 1967, and 1970), and in Clark and Haderlie (1962).

Samples of polychaetes were collected in a transect 10 by 100 meters in dimensions, the length running from high + 0.4m to low + 0.2m tide. Corners of this transect were marked by permanent stakes. The transect was divided into 10, 10x10 m quadrats, and replicate samples were taken within each month. Three replicates were taken in each quadrat for a monthly total of thirty samples. The sampling device was a brass core, sampling about 1/40 m^2 in area to a depth of 25 cm. Samples were taken every month from October 1974 to October 1975. Core locations were determined using a table of random numbers.

The core samples were returned to the laboratory and sieved through a 1 mm screen. The animals were picked, fixed in 5% sea-water formalin, preserved in 70% ethanol, and counted under a binocular dissecting microscope.

At each sampling time one sample was taken in each of the ten quadrats for sediment analysis; a coring tube of 3 cm in diameter was used to remove sediment 12 cm in depth. The sample coordinates were determined using a table of random numbers.

Sediments were analyzed using the techniques of Barnes (1959), and Twenhofer and Tyler (1941).

Sizes of four major species were obtained by measuring the width of the anterior setiger (Buchanan and Warwick 1974); Nichols (1975), using an eye-piece micrometer.

The gregarine parasite Lecudina longissima Hoshide 1944 described from the intestine of Lumbrineris zonata, (Johnson, 1901) from Santa Catalina Island, California (Levine 1974), was found in the intestine of Lawson's Flat L. zonata, probably for the first time in Tomales Bay (Blake pers. comm.). Infestation was estimated by opening the intestine of randomly selected hosts.

Identification of polychaetes was based on the keys of Hartman (1941, 1968, and 1969), Blake (1975), and Banse (1972). Other references were Blake and Woodwick (1975), and Blake (1969b).

Statistical computations used for data analysis were adapted from Sokal and Rohlf (1969). Calculations were performed on a Wang 500 computer.

COMPOSITION OF THE FAUNA

Results of the quantitave sampling from Lawson's Flat are shown in Table 1; the data were based on 390 samples comprising about 19,000 specimens, collected between October 1974 and October 1975. About 36 polychaete species were identified from the transect, among these 15 major species were found in varying abundances. Many species occurred sporadically, others were either seasonally distributed or present throughout the year.

Exogone lourei Berkeley and Berkeley, 1938

A herbivore species, builds tubes in the top sandy-mud substrate layer, or inside the stolons of *Enteromorpha*. The species was often found associated within *Enteromorpha* beds, and seldom incorporated into *Ulva*. Adults were found brooding their young on ventral surface between June and September; however, Wooden (1974) reported that brooding occurs in Washington between November and February.

E. Lourei was absent during winter months, but began to appear in the community between February and April, declined for a short period and then bloomed in July through October which coincides with the algal growth season (Fig. 2a). Abundances of the population were recorded in July-October period ranging from 585.6 to 1104.3/m^2; lowest densities occurred between October 1974 and January 1975 with less than 9.0/m^2. The species ranked the second in density after *L. zonata* (Table 2). Interaction between sampling months and intertidal level was significant, which means that E. lourei was abundant during particular season, in the summer, and distributed in the lower intertidal zone where algal cover offers viable habitat (Table 3).

Platynereis bicanaliculata (Baird, 1863)

A common tube-builder, nereid herbivore species; usually found in the mud flats associated with Ulva and Enteromorpha beds. The species also inhabits protected rocky intertidal within algal holdfasts, barnacles, and mussels (Blake 1975c).

Population distribution patterns showed significant fluctuations correlated with seasonal changes in algal cover in the lower intertidal zone, where Ulva and Enteromorpha dominate the area. Peaks of abundance were observed in the fall of 1974, spring and fall of 1975 (Fig. 2b). A sharp decline in population abundance occurred in the winter and in late spring.

Monthly abundances varied from the highest $321/m^2$ in October 1975 to the lowest $1.0/m^2$ in May. The monthly mean density of the population was $103.4/m^2$. Significant seasonal variations in abundance occurred (Table 4), and there were significant interaction between time and tidal level.

Brania limbata (Claparède)

A syllid herbivore species, builds tubes in sandy-mud, and often found associated to Enteromorpha. The young were observed brooded on the dorsal surface between June and September. Distribution of the population was restricted to the lower intertidal zone where algae are abundant.

The species was absent during most of the sampling period. Some individuals appeared in June followed by a sharp increase in July and continued fluctuating through October (Fig. 3a). Population abundance was high in July, $222.8/m^2$, when Enteromorpha beds were widespread; while during the first nine months the density never reached $2.0/m^2$. The monthly mean density was low compared to other species (Table 2). ANOVA computations did not show any differences between sampling months or quadrats (Table 5). Significant interaction was observed between seasons of the year and intertidal levels; this might explain the sudden July bloom of the population in the lower quadrats when algal community covered the total area.

Notomastus tenuis Moore, 1909

Common in sand and mud flats over a wide range of intertidal area, and in holdfasts of Phyllospadix (Hartman 1944b). The species was scattered all over the transect with an increasing abundance from the upper to the lower intertidal area. Distribution of the population was quite stable (Fig. 3b). Monthly abundances ranged from the highest $50/m^2$ to the lowest $20/m^2$, with a monthly mean density of $32/m^2$.

Abundances of the population were significantly different between the quadrats (Table 6). The last six quadrats showed a frequent appearance of individuals during all sampling period than the first four.

Lumbrineris zonata Johnson, 1901

A common lumbrinerid in the mud flats of Tomales Bay, along sandy beaches, and in sand or fine gravel under large beach boulders (Hartman 1939c). Distribution of the species within the transect is characterized by a dense population in the middle and low density at the extremes. The species dominated the polychaete community in abundance throughout the sampling period. Monthly abundances fluctuated between the highest 1207.7/m^2 in April to the lowest 709.8/m^2 in October 1975. The average monthly density recorded was 901.5/m^2; this high density ranked the species in the first place compared with any other species from the transect (Table 2).

In comparison with other species L. zonata appeared to be more stable in abundance throughout the year than most of the other species of polychaetes (Fig. 4a). Significant variations between months suggesting a time effect on abundance of the population (Table 7). Differences between quadrats over time were very significant. This variation was induced by a spatial fluctuation in abundance between the middle area of the transect and the extremes. No significant interaction found between time and space.

Nephtys caecoides Hartman, 1938

Common in muddy sand flats of Tomales Bay; description of the species was reported in Hartman (1938). Clark and Haderlie (1962), have surveyed the species distribution from Dillon Beach locality; an earlier survey was conducted in 1941 by Pitelka and Paulson, a summary of the results being reported in Ricketts and Calvin (1968).

Species distribution largely fluctuated during sampling period, all months deviated from the overall monthly average at 95% confidence intervals (Fig. 4b). Monthly abundances were low ranging from the lowest $1.2/m^2$ in March to the highest $113/m^2$ in October 1975, with a monthly mean of $19/m^2$. Temporal and tidal level distributions of the species were significant (Table 8), the last two months showing a big increase in abundance. A significant interaction observed between sampling period and quadrat level.

Pseudopolydora paucibranchiata (Okuda, 1937)

A tube-builder spionid, generally confined to sandy-mud substrate, and usually collected from the lower quadrats. Population distribution along the transect was restricted to the middle and lower intertidal zone. The species was sampled only between July and October (Fig. 5a), and the majority of the individuals were juveniles; marked absence was observed during several months of the sampling period. Blake and Woodwick (1975) reported the occurrence of the planktonic larvae between July and October in the years 1971-1972. The average monthly abundance was rather low, 52.7/m^2; however, maximum monthly mean density occurred in September with 255.5/m^2, while the minimum was recorded in all sampling months but the last four. Variation in abundance was significantly between times and levels (Table 9), and a significant interaction between time and levels occurred.

Axiothella rubrocincta (Johnson, 1901)

A maldanid deposit-feeder, live and build tubes in muddy-sand substrate; also known as a host of a commonest crab, Pinnixa longipes (Hartman 1944b). Ecology of the species was briefly reported by Johnson (1967a), and by Ricketts and Calvin (1968); Kudenov (MS.) has extensively investigated the morphology and ecology of A. rubrocincta.

Distribution of the population was quite stable throughout the year (Fig. 5b). Abundance of the species within the transect was extremely low, the average density was less than 4/m^2. Highest densities were recorded in June and September with 8 and 9/m^2 respectively; the lowest occurred in October 1975 with 1.3/m^2. ANOVA computations did not show any significant differences between times or levels (Table 10), reflecting stability in abundance and intertidal distribution of the species.

Anaitides williamsi Hartman, 1936

A herbivore phyllodocid species, confined to the lower intertidal zone within algae beds; also common in rocky intertidal localities and abundant in Zostera beds (Blake 1957c). Larval development was described in Blake (Ibid). Seasonal distribution of the population was generally stable except in winter and late spring (Fig. 5c). Monthly densities were low during several months with less than $2/m^2$, however the highest never reached $14/m^2$; the monthly mean density was extremely low compared to other species (Table 2). Differences between sampling months were significant, reflecting seasonal variations of species abundance (Table 11). Significance of time-level interaction may be due to the growth of algae in the lower zone during summer-fall period.

Mediomastus californiensis Hartman, 1944

Inhabits sandy mud flats, at low line, sometimes associated with N. tenuis (Hartman 1944b). Distribution of Mediomastus individuals was rather uniform except in the first quadrat where almost no individuals encountered. Distribution pattern of the population fluctuated largely during sampling months, seven of the 13 confidence intervals were not included in the overall mean (Fig. 6a). Abundances of the population was moderate with monthly densities ranging from $196.5/m^2$ in July to $9/m^2$ in November and December; the monthly mean density was $96.2/m^2$. Significant variations in abundance between sampling months and time-level interactions occurred (Table 12).

Polydora socialis (Schmarda, 1861)

Inhabits the intertidal zone, constructing tubes in sandy or muddy sediments; also in crevices and in rocky situations (Hartman 1941). Morphology of the species and records of its distribution were documented in Blake (1971).

The species is generally distributed in the middle and lower zones of the transect, and fluctuated seasonally in abundance (Fig. 6b). Seasonal abundances were low, ranging from 3 to 75/m^2, with mid summer and early fall densities being highest. Average monthly density was 17.4/m^2. Significant seasonal variations characterized the sampling period (Table 13). Time-level interactions were also significant.

Glycinde armigera Moore, 1901

Goniadid, common in Tomales Bay in muddy sand flats. Larval development of the species was described in Blake (1975c). Large fluctuations were observed during the survey (Fig. 6c); the species showed low density ranging from 1 to 36/m^2. The population was dispersed all over the transect except in the first quadrat. Differences in abundance between the seasons were significant (Table 14); low abundance occurred during fall 1974 and spring 1975, while the highest were recorded in mid-summer and fall of 1975. Significant time-level interaction was observed possibly due to the large numbers of individuals that appeared in the middle and lower intertidal levels in July through October.

Haploscoloplos elongatus (Johnson, 1901)

Orbiniid, common intertidally and subtidally in Tomales Bay, in sands and muds. Distribution of the species was mostly concentrated in the middle of the transect, and fewer individuals encountered in the extremes. The population was distinguished by a stable abundance distribution (Fig. 7a). Monthly densities were high compared to most of the other species, the range was from 147 to 290/m^2; monthly mean abundance ranked the species in the third place (Table 2). Temporal changes in abundance were significant (Table 15), highest densities occurred in October and December 1974, and March-April 1975. Spatial and temporal interactions were significant.

Armandia brevis (Moore, 1906)

A common burrower and deposit-feeder opheliid, inhabits sandy mud and silt. Distribution of larvae in Tomales Bay in the years 1971-73 was generally sparse, but a continuous occurrence reported between May and November and rare cases spotted in February (Blake pers. comm.). Extensive studies from Washington Coast suggested that the species may have 2 or 3 generations per summer season (Herman 1964, 1966; in Wooden 1974).

Species distribution in the transect was rather uniform; individuals from the first quadrat were never collected. Monthly distributions fluctuated moderately, only seven months were included in the overall mean and in two, May and July, no specimens were found (Fig. 7b). Abundance of the population calculated on a monthly basis averaged between 6.7/m^2 in October 1974 and 59/m^2 in December, while the overall mean was less than 23/m^2. Differences between monthly abundances were significant (Table 16), and a significant interaction between seasons and sampling locations was also present.

<u>Capitella capitata</u> (Fabricius, 1909)

A cosmopolitan capitellid, tube-builder and deposit feeder species; encountered in fine sand, mud and muddy sand, usually collected from the lower quadrats. The species showed little fluctuation and was present almost throughout the year (Fig. 7c). A steady decline of population abundance began in November, started to increase gradually from February to April, and then another decline occurred in May which continued through June. Monthly mean density was very low compared with other species (Table 2). Maximum monthly density reached in July and September with 38 and 28.8/m^2 respectively; the minimum was recorded in January with 2.8/m^2. Significant time and time-level interactions occurred (Table 17).

Description of Other Species

Twenty-one species represent the rest of the polychaete infaunal community. The majority of these did not exceed $2/m^2$ per month, and only six species having densities between 2 and $4/m^2$. Tentatively these populations may be grouped, according to their abundance in the transect, into four groups.

I- Group averaging less than $1.0/m^2$: This group comprises twelve rare species, all seem to occur seasonally (Table 1). Very few individuals, mostly under 9 specimens per species, were collected during the survey period. Such species do not contribute much to the infauna, but do have some effect on the diversity of the whole community.

II- Group having less than $2.0/m^2$: There are four species representing this group: two spionids, Polydora ligni and Pygospio elegance, Chone mollis, and Hemipodus borialis. None of these species exceeded 18 individuals during the total sampling period. These species appeared to be seasonal, and generally confined to the lowest quadrats, suggesting that algal community and sediment type may have some distributional effect on these populations.

III- Group represented by less than $3.0/m^2$: Three species constituting this group, Eteone californica, Eupolymia crescentis, and Boccardia proboscidea. Their abundances mostly occurred in the summer and fall for the first two species, and in the fall and winter for the third.

IV- Group averaging less than $4.0/m^2$: Two species in this group, Magelona pitelkai collected during all months but three; most individuals were found between July and October (Table 1). Spatial distribution of this species was not restricted to particular areas. Pseudopolydora kempi was encountered only in July and October; that is when the majority of the spionids collected during this time. The species was principally confined to the lowest three quadrats, suggesting a possible interaction between algal beds and muddy sediments.

RECRUITMENT IN FOUR DOMINANT POLYCHAETE SPECIES

Recruitment of the four most abundant species was investigated. One sample was chosen from each tidal level every month for measurement of worm size. Usually the sample having the largest number of worms was picked. The width of the first setiger was used as a standard parameter. The smallest size-class observed was between 0.25 and 0.375mm in width, the largest varied according to species. The smallest size class, expressed as percent of the total, was used as a measure of recruitment.

Separation of polymodal frequency distributions was attempted using probabilty paper. The technique is described in Harding (1949); Cassie (1954); Lewis and Taylor (1967). As Warwick and Price (1975) pointed out, this technique requires that the data for each year-class conform to a normal size frequency distribution although size selective pressures such predation or differential rates of migration to the site may skew the size frequency curve to the left or to the right. Warwick and Price (1975) proposed another approach in place of Harding's method, but their new procedure seems to be more complicated and requires more information than Harding's method.

Platynereis bicanaliculata

Data on size distribution of the species is summarized in Figure 8. Roe (1971) (in Wooden 1974) reported that spawning of

P. bicanaliculata in Washington occurred between June and September; however, massive spawning was observed during late July and early August (Roe 1975). Planktonic larvae of this species were collected in abundance in Tomales Bay in March 1972 (Blake 1975c). However, during the years 1971-73 larvae occurred also between July and August (Blake pers. comm.). Adults were abundant from October to December 1974, and March 1975; none were found between July and September, which coincides with the post spawning mortality period.

Size distribution of the population was rather stable between October 1974 and March 1975. In the fall of 1974 recruitment was low compared with other seasons. During 1975 the smallest class represented 35% of the population in July and more than 50% in September; a sharp decline in recruitment occurred in October with 15% of the population, represented by the smallest size class.

The results estimated from the graphical inflexion method showed that after-spawning mortality eliminated the larger individuals, and the large recruitment of young revealed only one size-group, July and September. Data of other months suggest an overlapping of either two or three populations of different size-individuals, mixed in unequal proportions.

Lumbrineris zonata

Mature adults were scarce, only one ripe specimen found in each month of November, December and March. About 1.4% and 0.6% of the population were encountered in June and August respectively.

Larval abundances are still unknown and no previous studies in Tomales Bay reported their distribution.

Size distribution was stable during October 1974 through June 1975 (Fig. 9a,b). Significant increase in juveniles occurred in July and August. Bimodal distribution characterized the period October-June and October 1975 during which the overlapping populations were represented at about 90:10% in favor of smaller and middle sizes. In the other months, a polymodal distribution was the general pattern; larger individuals contributed less than 10% in any particular month, although the smaller and middle size share the 90% left in approximately equal proportions.

Haploscoloplos elongatus

In comparison with P. bicanaliculata, the size distribution of H. elongatus is quite stable (Fig. 10). There are no clear periods dominated by adult mortality or extensive juvenile recruitment. The smallest size class never represented more than 10% of the total population.

Ripe specimens, recognized by the presence of large yolky-eggs beneath the skin, were found between June and October. About 31% of July individuals had eggs, 19.7% in August, and 11.4% in September; the lowest number recorded was in June with 6.6%.

Population classes in Figure 10 demonstrated a single modal distribution in all months except August. The mean width of the individuals during these periods never exceeded 0.6mm.

August bimodal pattern showed 97.5% of the individuals were smaller than 0.75mm, and the average width was 0.562mm.

Mediomastus californiensis

The size-frequency data is shown in Figure 11. While middle sizes were present throughout the year, the young were recruited in various seasons with a peak in October 1974 and none in April 1975. Maximum abundance of breeding adults, also distinguishable by their small size eggs visible through the skin, occurred in June with 15.7% of the population; the minimum was in August with 1.9%. Between 1971-73 M. californiensis larvae were most abundant during the summer months and always present between June and November, being rare in January (Blake pers. comm.). Mediomastus californiensis is the only species among the four having all size classes represented by a single mode. All individuals were smaller than 0.875mm, and the average size ranging between 0.400 and 0.555mm in width.

SEDIMENT ANALYSIS

Results of dry-sieving analysis showed that the sediment of the transect is characterized by a fine well-sorted sand of average diameter 0.220mm. These two parameters did not differ between the quadrats. Similar results were obtained earlier from Lawson's Flat by Clark and Haderlie (1962) and Johnson (1967a).

As the flat is considered a well protected area (e.g. Clark and Haderlie 1962) these conclusions support Morgans (1956) argument that fine sediments deposited under more sheltered conditions tend to be more uniform in diameter.

DESCRIPTIVE ACCOUNT OF THE PARASITE INFESTATION

Lecudina longissima Hoshide, 1944 is an eugregarine monocyst of the family Lecudinidae. Levine (1974) described the morphology of this species in California, although the original description and life cycle were reported from the host Lumbrineris japonica by Hoshide (1944). Mode of reproduction of Lecudina is exclusively by gamogony, and earlier developmental stages of the genus are intracellular (Grassé 1953). Early intracellular development of L. longissima is known (Hoshide 1944, in Levine 1974).

Description of the parasite as reported by Hoshide and by Levine does not apply exactly to the type found in L. zonata of Tomales Bay, which raises some doubts about identification. However, the identity of the parasite is accepted here with some precautions and additional information on certain morphological differences is discussed.

Living specimens of L. zonata were collected from the sampling site in April 1976. The worms were kept alive in a glass finger-bowl containing sea water. Worms were dissected and living gregarines removed and mounted on slides covered with cover-slips. Some slides were examined under a Tiyoda compound microscope, others were checked under a Zeiss compound microscope equipped with Nomarski Phase Interference. Specimens were photographed under the latter.

Different body shapes of the parasite were seen; a wrinkly type showing one or more wrinkles and having an oval or round nucleus (Fig. 12). According to Hoshide (1944) is an attached trophozoite form of a cephalont. A similar specimen was observed occupying an oval transparent pouch (Fig. 13a); once freed, a wrinkled type body was seen which will presumably develop into a smoother shape (Fig. 13b). The second type is a lance-shape form, a sporont (e.g. Hoshide 1944) or a gamont (e.g. Levine 1974). Some of these were seen attached to the tissue by means of a long epimerite; when detached, the epimerite remaining in the body for a short time (Fig. 14a). The free living gamont was observed undergoing extensive morphological changes. It took the gamont 10 minutes to absorb the epimerite, while the cytoplasm of the body gradually became denser as a result of this absorption process (Fig. 14b, 15a,b). Disappearance of the epimerite did not leave any trace of its original location (Fig. 16a). Different sizes of gamonts were observed, with little morphological variations. The largest sizes being the oldest (Fig. 16b). Rare cases were observed having a median fold which were thought to represent a septum (Fig. 17), but one specimen examined revealed a non-septate body suggesting the fold disappears later. Cyst formation was also observed undergoing slow transformation. About six hours elapsed without completion of cyst formation; unfortunately the observations were terminated due to death of the organism (Fig. 18a,b).

HOST INFESTATION SURVEY

About 3000 specimens of L. zonata were examined for parasite infestation. The results are shown in Figure 19. Infestation of the host began at earlier stages, demonstrated by infected young in July and August. As individuals grow the parasites increase in numbers. Larger hosts were observed having fewer gregarines, in proportion to their sizes, than middle sizes. Individuals larger than 1.0mm in width had very low infestation rate.

The lowest infestation for all size-classes was recorded in July with 57% of the population. The highest was in February, April, and October 1975 with 98% in each month. Intermediate sizes, between 0.50 and 1.0mm, showed the largest infestation rate.

DISCUSSION

The distribution of any species in nature is the result of the action of various environmental factors (Sanders 1958). The community structure is determined by both physical and biological factors (Stickney and Stringer 1957/ Sanders 1960, 1968; and others). However, Green and Hobson (1970) concluded that the structure of certain intertidal communities is determined principally by spatial and temporal variations in temperature. McIntyre (1969) and Nichols (1970) argues that the most significant of the physical environmental factors affecting the distribution of benthic fauna are temperature, salinity, and grain size. Diurnal temperature change is caused by incoming tide, rather than temperature range as such, and some surface living animals are known to be forced deeper by temperature changes. Variations of tidal heights affect substrate temperature. Johnson (1965) concluded that sediment temperatures become more variable with increasing elevations on the beach coincident with decreasing numbers of species and individuals.

According to stability-time hypothesis (Sanders 1968), when physiological stresses have been historically low, biologically accomodated communities evolve, and when stress is high predominantly physically controlled communities develop. Whenever control of population size is seldom the result of changes in physical environment or any disturbances it can be said that the community is biologically accomodated rather than physically regulated (Grassle and Sanders 1973).

Species in predictable environments tend to be more specialized than those in unpredictable environments so that "unpredictable" environment species may be expected to be kept out of high predictability environments by competition (Slobodkin and Sanders 1969). Whether it is legitimate to consider the lowest zone of the transect dominated by algae a predictable environment is a questionable matter, because of lack of information on temperature variations of the substrate, daily oxygen changes and degree of other disturbances.

According to Grassle and Sanders (1973) adaptation to unpredictable environmental change may be accomplished by having large population size which is directly related to the advantages resulting from the maintenance of a high degree of genetic variability. Large population size prevents loss of genetic variability through inbreeding, and a high level of genetic variability is insurance that some individuals in the population will be well adapted to unpredictable events. In these species high mortality is an essential component of the adaptation that enables a population to shift rapidly to a new adaptive peak through short-term selection.

Holme (1961) suggested that the distribution of some benthic groups is determined to a lesser degree by the extent of larval dispersal than by conditions encountered at the bottom during metamorphosis and early juvenile growth. Recruitment of new generations and establishment of benthic populations were regarded as a function of food supply, temperature and type of substratum (Thorson 1966).

The sediments of Lawson's Flat are fine well sorted sands. Sanders (1958) argued that predominantly silt and clay sediments support small numbers of filter feeders; these sediments accumulate in areas having weak currents which allow fine particles, including the organic matter, to settle out thus favoring infaunal substrate feeding. The lowest two quadrats of the transect contain a fairly large percentage of silt and clay (5-7% in each).

Areas with well sorted fine grained sediments are, according to Sanders (1958), stable environments. Lawson's Flat is a sheltered, well protected area and wave action is weak (Clark and Haderlie 1962); however, earlier studies (e.g. Johnson 1970) and personal observations showed that the area was frequently disturbed by clam diggers, bat rays, predators, and certain physical disturbances such as storms, temperature fluctuations, sediment erosion and deposition. The effect of bat ray may be extensive. Fager (1964) concluded that large beds of tube-building Owenia fusiforms were destroyed by bay rays. It could be argued, therefore that the area is typically unstable and the major instability factor is probably the shifting of dune-sand into the mud flat (or due to bat ray feeding activities.). Newell (1970) considered the stability of the substratum as a principal factor determining the overall nature of the organisms of the intertidal zone. He also regarded the grain size of the sediment as an important parameter in determining the type of animals living there.

The influence of sediment types on distribution of benthic communities was regarded an important matter to be considered (e.g., Holme 1949; Sanders 1958; Gibbs 1969; Nichols 1970; Young and Rhoads 1971; Bloom, Simon, and Hunter 1972; and others). Feeding types of the infauna are correlated to the sediment type (Sanders 1958; Rhoads and Young 1970; Bloom, Simon, and Hunter 1972). The major feeding types are suspension feeders, deposit feeders and a facultative feeding types represented by relatively few species. Rhoads and Young (1970) proposed a classification of feeding types taking into consideration the degree of food selectivity among deposit feeders and the level of feeding above the bottom by the suspension feeders. Although different types of feeding were recorded in benthic studies (Sanders 1958, 1960; Sanders et al 1962; Banse and Hobson 1968; Santos and Simon 1974; Wooden 1974), observations on many species are inconclusive (e.g. Sanders 1960; Banse and Hobson 1968).

Rhoads and Young (1970) have suggested that organisms that feed exclusively on deposited food would, a priori, be expected to reach maximum diversity and biomass on fine-grained organic muds containing an abundant food supply. Suspension feeders seem to be the least affected by the type of substrate. Rhoads and Young believed that a population feeding on suspended material may be less influenced in its distribution by the type of substratum than by the quantity and quality of the suspended material in the water column.

Most polychaetes in Lawson's Flat appear to be deposit-feeders and a few are herbivores. Other feeding types are also represented by occasional species. Deposit-feeders such as spionids, *A. rubrocincta*, *N. tenuis*, and *H. elongatus* showed wider ranges of distribution even though some species fluctuated seasonally. The sediment reworking effect of deposit feeders is an indication of a physical instability of the environment, which according to Rhoads and Young (1970) may discourage the settling of the larvae of many suspension feeders, and therefore reduce or eliminate such species from the area.

Herbivore species represented by *P. bicanaliculata*, *E. lourei*, and *B. limbata* were confined to *Ulva* and *Enteromorpha* beds. In this study seasonal changes in algal cover were correlated with changes in the density of herbivore polychaete populations. The most dominant species in space and time was *L. zonata*. The feeding type of this species is still uncertain; other species of the genus have different types of feeding. For example, *L. tenuis* is an omnivore (Santos and Simon 1974), *L. inflata* is a herbivore (Wooden 1974), and *L. californiensis* is a carnivore (Banse and Hobson 1968). *Lumbrineris zonata* possesses well developed jaws suggesting a herbivore or carnivore feeding type, but the stomach was observed to contain sand; therefore the species tentatively may be considered an omnivore. This kind of feeding is probably the most efficient of all types in the sense that species having such feeding type could expand its range, as food becomes a minor limiting factor, if it can compete for space and other requirements. Omnivore species could also control population densities of other species particularly at their early stages of development. Chances of larvae passing alive through stomach of benthic carnivores are high according to Mileikovsky (1974), but they will play no important role in the process of maintenance and recruitment of the species and communities involved nor of the marine benthos as well (Mileikovsky 1974). The major difficulties will be competition for space, and as Frank (1965a) pointed out, the time available for feeding rather than the existing food concentration may be the most significant.

Communities inhabiting intertidal seaweeds seem to be controlled by the type of algal species. Wieser (1952) pointed out that the principal factor controlling the nature and abundance of these communities is the growth form of the particular species of weed. He argued that different species of seaweeds are of different growth form, thus they give different degrees of protection from stress such as wave action, desiccation and temperature fluctuation. In the study area Ulva and Enteromorpha were the dominant algae forming a broad bed at the lower intertidal zone. They offer a convenient shelter and abundant food supply to various species. The effect of this algal community is to change the physical properties of the sediment, by periodical reduction of the amount of oxygen on the substrate, and thus to reduce the number of species of limited tolerance.

The most significant species, in terms of abundance, confined to these algae were the three herbivores, P. bicanaliculata, E. lourei, B. limbata, and the spionid P. paucibranchiata.

The most tolerant species existed under these beds was C. capitata which was not found outside them. The herbivore species did not seem to control algal community, probably because of their smaller sizes and relatively lower numbers compared with the fast growing algae. However, the rocky intertidal algae Lessoniopsis littoralis, as Dayton (1975) showed, were unable to recruit among Mytilus californiensis at least from one particular area. The effect of algae on species abundance was demonstrated to be crucial for certain populations. Wooden (1974) showed that A. rubrocincta population in natural algal cover was reduced to 44% of that found in an area where algae were removed, and concluded that this low abundance is presumably due to an inability to withstand anoxia and the failure to remove and/or to extend its tubes up through the algae.

Distribution of algae in the transect appeared to be seasonal. From about mid-summer to mid-winter the algae were constantly present, but they disappeared in the other periods.

Future experimental studies of the dependence of some intertidal polychaetes on distribution of algae should confirm present observations that abundance fluctuations of P. bicanaliculata, E. lourei, B. limbata and P. paucibranchiata are strongly correlated with changes in algal cover.

Infestation of L. zonata by the parasite Lecudina longissima was quite high, ranging between 57-98% of the worm population. The parasite were too dense in the bodies of the worms to permit estimation of their densities. There is some doubt remaining about the identity of the parasite. The presence of a transitory epimerite strongly contradicts the classification of the species. Grassé (1953) reported the presence of a transitory epimerite in some families, like the Stylocephalidae. Possession of this organ does not, obviously, permit classification of the species observed in L. zonata in the Stylocephalidae, because of other characters have to be considered which do not apply to this family.

The effect of the parasite on its host is expected to modify the metabolism of the host. The presence of many parasites that feed in the lumen might require frequent feeding of the host from the environment which, consequently, may affect the food supply for the population and for other species as well. Lecudina longissima did not show any apparent effect on L. zonata, but if the parasite is completely dependent on the host for nourishment, which is the case here, deleterious effects are expected. Hopkins (1957) suggested the possibility for parasites to affect host population without extensive morphological effects on the parasitized individuals. Further studies of the effect of the parasite on its host would be of interest.

Information on reproduction of L. zonata is unknown, and if the species manifests post-spawning mortality, parasites will not be transmitted into other hosts. In such cases the parasite must have a cyst-forming stage that can be released outside the host into the environment, and these cysts must tolerate habitat stresses to some degree until once again ingested by new hosts. As a cyst-formation case was observed occurring in L. longissima, the previous possibility may apply in this case.

SUMMARY

1. Thirty samples were taken at monthly intervals from October 1974 to October 1975, at Lawson's Flat in Tomales Bay, California.

2. Thirty-six polychaete species were identified, among these 15 species comprised the major portion of the infauna, and twenty-one were poorly represented during sampling.

3. The most characteristic members of the community were those which occupied a wider range and were constantly present. These were L. zonata, H. elongatus, M. californiensis, N. caecoides, and N. tenuis.

4. A large number of species did not seem to have a clear distribution in relation to tidal height; N. caecoides, M. californiensis, and L. zonata are examples to name. However, many others were restricted to the lower intertidal zone, for example P. bicanaliculata, E. lourei, and C. capitata.

5. Species confined to algal beds showed fairly large seasonal fluctuations related to changes in algal cover.

6. Species of restricted distribution within the algal community outnumbered those of unrestricted habitat beyond the algal range.

7. Most species showed significant changes in population density over time.

8. Recruitment of four major species was investigated. Platynereis bicanaliculata recruited in July and September,

L. zonata recruited in July and August. Recruitment in H. elongatus and M. californiensis occurred throughout in H. elongatus and M. californiensis occurred throughout the year.

9. Characteristics of the sediment were a fine well-sorted sand of a median size of 0.220mm.

10. The parasite Lecudina longissima infecting the host L. zonata was described. Identity of the parasite is in some doubt, and additional information on some morphological characters was obtained.

11. Seasons and size of the host appeared to have little influence on the incidence of the parasites. High infestation occurred at all times of the year.

12. Infestation of the host began at earlier stages and decreased with age; younger individuals were the most infected.

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Table 1. Abundances of Polychaete infauna: October 1974 to October 1975

Species	O	N	D	J	F	M	A	M	J	J	A	S	O	Mean no./m^2
Anaitides williamsi	5	5	--	--	3	--	--	--	1	1	1	10	10	3.6
Armandia brevis	10	11	45	42	18	42	6	--	--	17	5	20	5	22.3
Axiothella rubrocincta	1	--	2	2	3	--	3	2	6	4	4	7	5	3.9
Boccardia proboscidea	--	--	--	--	--	--	--	--	13	2	3	3	2	2.32
Brania limbata	1	--	--	--	--	--	--	--	1	150	24	44	16	25.8
Capitella capitata	3	14	7	2	3	6	10	7	--	29	14	22	5	12.3
Chone mollis	1	1	1	2	--	--	--	1	--	1	2	2	7	1.81
Dorvillea rudolphi	1	--	1	--	--	--	--	1	--	--	--	1	1	0.5
Eteone californica	2	--	--	--	--	--	--	--	--	1	9	8	9	2.92
Eteone dilatae	--	--	--	--	--	--	--	--	--	--	--	1	--	0.10
Eupolymia crescentis	3	1	5	2	--	--	--	--	--	--	3	8	3	2.52
Exogone lourei	7	--	--	3	45	152	246	14	35	843	447	722	462	300.0
Glycera americana	--	5	1	--	--	1	--	--	1	--	--	--	--	0.81
Glycera tenuis	--	--	--	--	--	--	3	2	1	--	--	--	--	0.79
Glycinde armigera	2	1	1	6	7	10	4	3	4	20	24	23	28	13.3
Haploscoloplos elongatus	205	161	221	164	197	216	145	184	181	142	142	158	112	224.5
Hemipodus borealis	--	--	3	1	1	4	--	1	--	4	--	--	1	1.51
Hespernoe adventor	--	1	1	--	--	--	--	--	--	--	--	--	--	0.20
Lumbrineris zonata	708	550	820	546	598	746	922	828	759	616	633	678	542	901.5

Table 1. (Cont.)

Species	O	N	D	J	F	M	A	M	J	J	A	S	O	Mean no./m^2
Magelona pitelkai	--	1	--	3	1	4	1	--	6	5	7	7	2	3.83
Mediomastus californiensis	59	7	7	52	41	47	72	72	116	150	105	130	97	96.2
Naineris dendritica	--	--	--	--	--	--	--	--	1	--	--	--	--	0.1
Nerinides tridentata	--	--	--	--	--	--	--	--	--	--	--	--	2	0.2
Nephtys caecoides	7	4	6	7	4	1	4	1	3	3	7	56	86	19.0
Notomastus tenuis	25	15	18	21	38	25	24	21	31	24	22	30	30	32.6
Pectinaria californiensis	--	--	--	--	1	--	--	--	--	--	--	3	1	0.5
Platynereis bicanaliculata	148	188	32	12	2	108	14	1	--	24	6	227	265	101.4
Polydora brachycephala	--	--	--	--	--	--	--	--	--	1	--	--	--	0.1
Polydora ligni	--	--	--	--	--	--	--	--	--	1	15	--	--	1.61
Polydora socialis	21	10	3	4	5	--	2	10	6	58	27	20	8	17.4
Pseudopolydora kempi	--	--	--	--	--	--	--	--	--	5	16	6	7	3.43
P. paucibranchiata	1	--	--	--	--	--	1	--	1	98	186	185	51	53.7
Pygospio californica	--	--	--	--	--	--	--	--	--	--	--	--	1	0.1
P. elegans	--	--	--	--	--	--	--	--	--	5	--	2	4	1.11
Sphaerosyllis californiensis	--	--	--	--	--	--	--	--	--	--	--	2	--	0.2
Spiophanes missionensis	--	--	--	--	--	--	--	--	--	1	--	--	--	0.1

Table 2

Monthly mean density/m^2 of major species

Species	Density (mean no./m^2)	S.D.
Lumbrineris zonata	901.5	159.23
Exogone lourei	300.0	387.66
Haploscoloplos elongatus	224.5	42.80
Platynereis bicanaliculata	101.4	122.13
Mediomastus californiensis	96.2	58.20
Pseudopolydora paucibranchiata	53.7	94.93
Notomastus tenuis	32.6	8.01
Brania limbata	25.8	61.76
Armandia brevis	23.3	21.10
Nephtys caecoides	19.0	33.98
Polydora socialis	17.4	20.26
Glycinde armigera	13.3	12.89
Capitella capitata	12.3	11.06
Axiothella rubrocincta	3.9	2.81
Anaitides williamsi	3.6	4.80

Table 3

Two-way ANOVA of *Exogone lourei*

Source of variation	Degrees of freedom	Sum of Squares	Mean square	F ratio
Between months	12	35034.4974	2919.5415	3.5200[b]
Between quadrats	9	9344.3179	1038.2575	1.2518[n]
Interaction (months x quadrats)	108	288061.3487	2667.2347	3.2157[c]
Error	260	215650.6666	829.4256	

b - $P \leq 0.01$

c - $P \leq 0.001$

n - Not significant at 0.05 level

Table 4

Two-way ANOVA of *Platynereis bicanaliculata*

Source of variation	Degree of freedom	Sum of squares	Mean square	F ratio
Between months	12	3481.4410	290.1201	1.9029[a]
Between quadrats	9	1997.7974	221.9795	1.4560[n]
Interaction (months x quadrats)	108	36618.3025	339.0583	2.2239[c]
Error	260	39639.3333	152.4590	

a - $P \leq 0.05$

c - $P \leq 0.001$

n - Not significant at 0.05 level

Table 5

Two-way ANOVA of *Brania limbata*

Source of variation	Degrees of freedom	Sum of squares	Mean square	F ratio
Between months	12	887.6256	73.9688	1.5824^n
Between quadrats	9	500.1128	55.5681	1.1888^n
Interaction (months x quadrats)	108	8644.8870	80.0453	1.7124^c
Error	260	12153.3333	46.7436	

c - $P \leq 0.001$

n - not significant at 0.05 level

Table 6

Two-way ANOVA of *Notomastus tenuis*

Source of variation	Degrees of freedom	Sum of squares	Mean square	F ratio
Between months	12	19.3974	1.6165	1.7320^n
Between quadrats	9	128.1128	14.2348	15.2521^c
Interaction (months x quadrats)	108	120.6539	1.1172	1.1970^n
Error	260	242.6667	0.9333	

c - $P \leq 0.001$

n - not significant at 0.05 level

Table 7

Two-way ANOVA of *Lumbrineris zonata*

Source of variation	Degrees of freedom	Sum of squares	Sum square	F ratio
Between months	12	24521.5359	2043.4613	9.2956^{c}
Between quadrats	9	98926.9461	10991.8829	50.0016^{c}
Interaction (months x quadrats)	108	19135.3872	177.1795	0.8060^{n}
Error	260	57156.0000	219.8308	

c - $P \leq 0.001$

n - not significant at 0.05 level

Table 8

Two-way ANOVA of *Nephtys caecoides*

Source of variation	Degrees of freedom	Sum of square	Sum square	F ratio
Between months	12	267.8410	22.3200	22.4638^{c}
Between quadrats	9	24.7900	2.7544	2.7721^{b}
Interaction (months x quadrats)	108	167.4400	1.5504	1.5604^{c}
Error	260	258.3400	0.9936	

b - $P \leq 0.01$

c - $P \leq 0.001$

Table 9

Two-way ANOVA of *Pseudopolydora paucibranchiata*

Source of variation	Degrees of freedom	Sum of squares	Mean square	F ratio
Between months	12	2099.2000	174.9333	10.5041^{c}
Between quadrats	9	366.2333	40.6926	2.4434^{a}
Interaction (months x quadrats)	108	7701.1333	71.3068	4.2817^{c}
Error	260	4330.0000	16.6538	

a - $P \leq 0.05$

c - $P \leq 0.001$

Table 10

Two-way ANOVA of *Axiothella rubrocincta*

Source of variation	Degrees of freedom	Sum of squares	Mean square	F ratio
Between months	12	1.8666	0.1555	0.9479^{n}
Between quadrats	9	0.2795	0.0310	0.1892^{n}
Interaction (months x quadrats)	108	18.2872	0.1693	1.0318^{n}
Error	260	42.6666	0.1641	

n - not significant at 0.05 level

Table 11

Two-way ANOVA of *Anaitides williamsi*

Source of variation	Degrees of freedom	Sum of squares	Mean square	F ratio
Between months	12	5.4102	0.4508	1.8127[a]
Between quadrats	9	1.9077	0.2119	0.8522[n]
Interaction (months x quadrats)	108	40.6923	0.3768	1.5149[c]
Error	260	64.6666	0.2487	

a - $P \leq 0.05$

c - $P \leq 0.001$

n - not significant at 0.05 level

Table 12

Two-way ANOVA of *Mediomastus californiensis*

Source of variation	Degrees of freedom	Sum of squares	Mean square	F ratio
Between months	12	789.1744	65.7645	12.2571[c]
Between quadrats	9	439.8077	48.8675	9.1079[c]
Interaction (months x quadrats)	108	842.4923	7.8009	1.4539[c]
Error	260	1395.0000	5.3654	

c - $P \leq 0.001$

Table 13

Two-way ANOVA of *Polydora socialis*

Source of variation	Degrees of freedom	Sum of squares	Mean square	F ratio
Between months	12	267.8410	22.3200	22.4638^c
Between quadrats	9	24.7900	2.7544	2.7721^b
Interaction (months x quadrats)	108	167.4400	1.5504	1.5604^c
Error	260	258.3400	0.9936	

b - $P \leq 0.01$

c - $P \leq 0.001$

Table 14

Two-way ANOVA of *Glycinde armigera*

Source of variation	Degrees of freedom	Sum of squares	Mean square	F ratio
Between months	12	38.6769	3.2231	8.3804^c
Between quadrats	9	14.2846	1.5872	4.1269^c
Interaction (months x quadrats)	108	64.6821	0.5989	1.5572^c
Error	260	100.0000	0.3846	

c - $P \leq 0.001$

Table 15

Two-way ANOVA of *Haploscoloplcs elongatus*

Source of variation	Degrees of freedom	Sum of squares	Mean square	F ratio
Between months	12	426.0359	35.5030	3.1985^c
Between quadrats	9	8493.6821	943-7425	85.0218^c
Interaction (months x quadrats)	108	2955.1179	27.3622	2.4651^c
Error	260	2886.0000	11.1000	

c - $P \leq 0.001$

Table 16

Two-way ANOVA of *Armandia brevis*

Source of variation	Degrees of freedom	Sum of squares	Mean square	F ratio
Between months	12	103.8667	8.6556	4.3127^c
Between quadrats	9	59.9718	6.6635	3.3190^c
Interaction (months x quadrats)	108	369.9262	3.4252	1.7060^c
Error	260	522.0000	2.0077	

c - $P \leq 0.001$

Table 17

Two-way ANOVA of *Capitella capitata*

Source of variation	Degrees of freedom	Sum of squares	Mean square	F ratio
Between months	12	28.4359	2.3696	1.8632[a]
Between quadrats	9	18.4513	2.0501	1.8120[n]
Interaction (months x quadrats)	108	302.2820	2.7989	2.2007[c]
Error	260	330.6666	1.2718	

a - $P \leq 0.05$

c - $P \leq 0.001$

n - not significant at 0.05 level

Figure 1. Sampling area at Lawson's Flat.

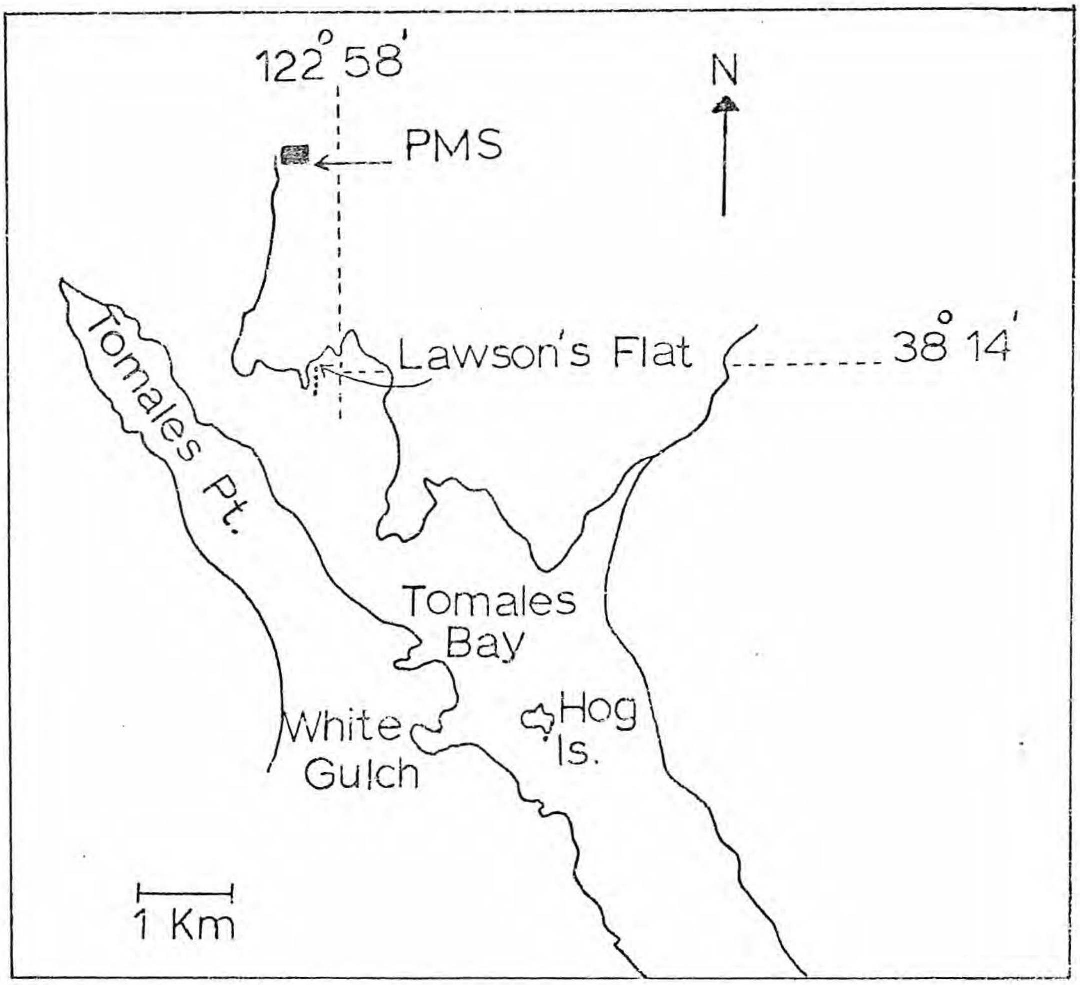

122°58'
N
PMS
Lawson's Flat
38°14'
Tomales Pt.
Tomales Bay
White Gulch
Hog Is.
1 Km

Figure 2. a- Estimates of population abundance of *Exogone lourei*. Horizontal bar represents monthly mean, the vertical line the 95% confidence interval, and the dashed line the overall mean.

b- Estimates of population abundance of *Platynereis bicanaliculata*. Symbols as above.

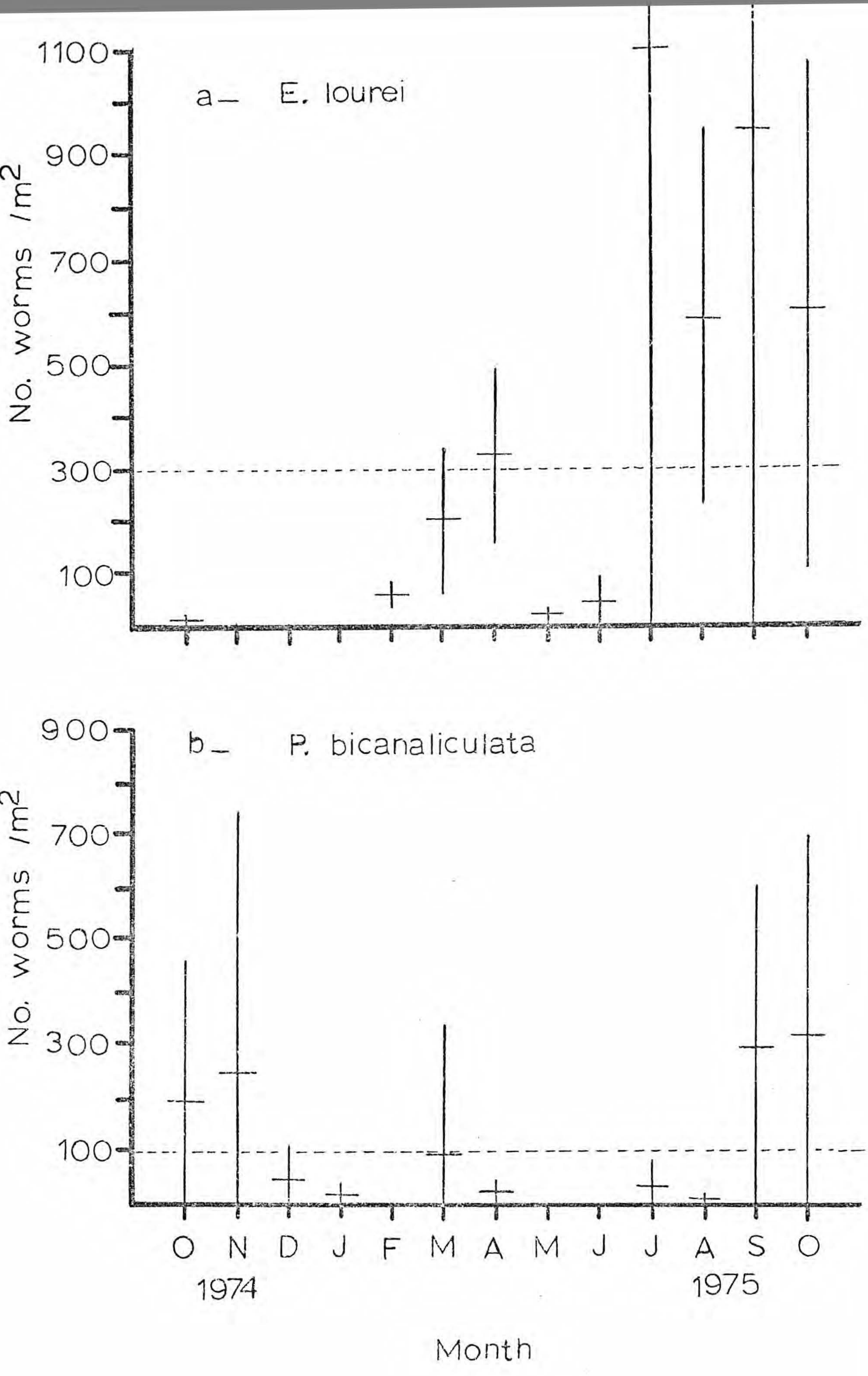

a— E. lourei
b— P. bicanaliculata
No. worms /m^2
1100
900
700
500
300
100
No. worms /m^2
900
700
500
300
100
O
N
D
J
F
M
A
M
J
J
A
S
O
1974
1975
Month

Figure 3. a- Estimates of population abundance of _Brania limbata_. Symbols as in Figure 2.

b- Estimates of population abundance of _Notomastus tenuis_. Symbols as in Figure 2.

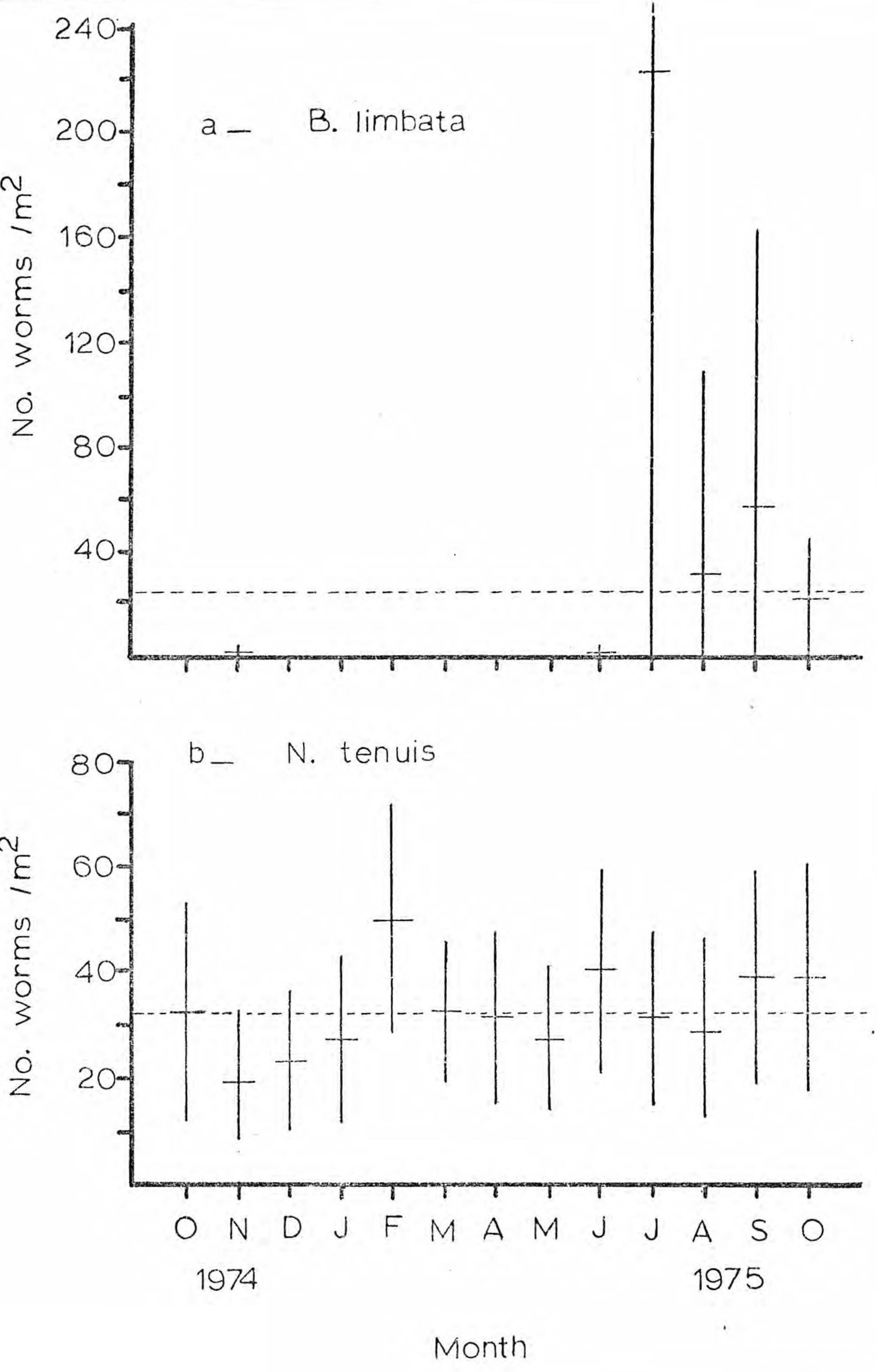

a — B. limbata
b — N. tenuis
No. worms /m^2
240
200
160
120
80
40
80
60
40
20
O
N
D
J
F
M
A
M
J
J
A
S
O
1974
1975
Month

Figure 4. a- Estimates of population abundance of *Lumbrineris zonata*. Symbols as in Figure 2.

b- Estimates of population abundance of *Nephtys caecoides*. Symbols as in Figure 2.

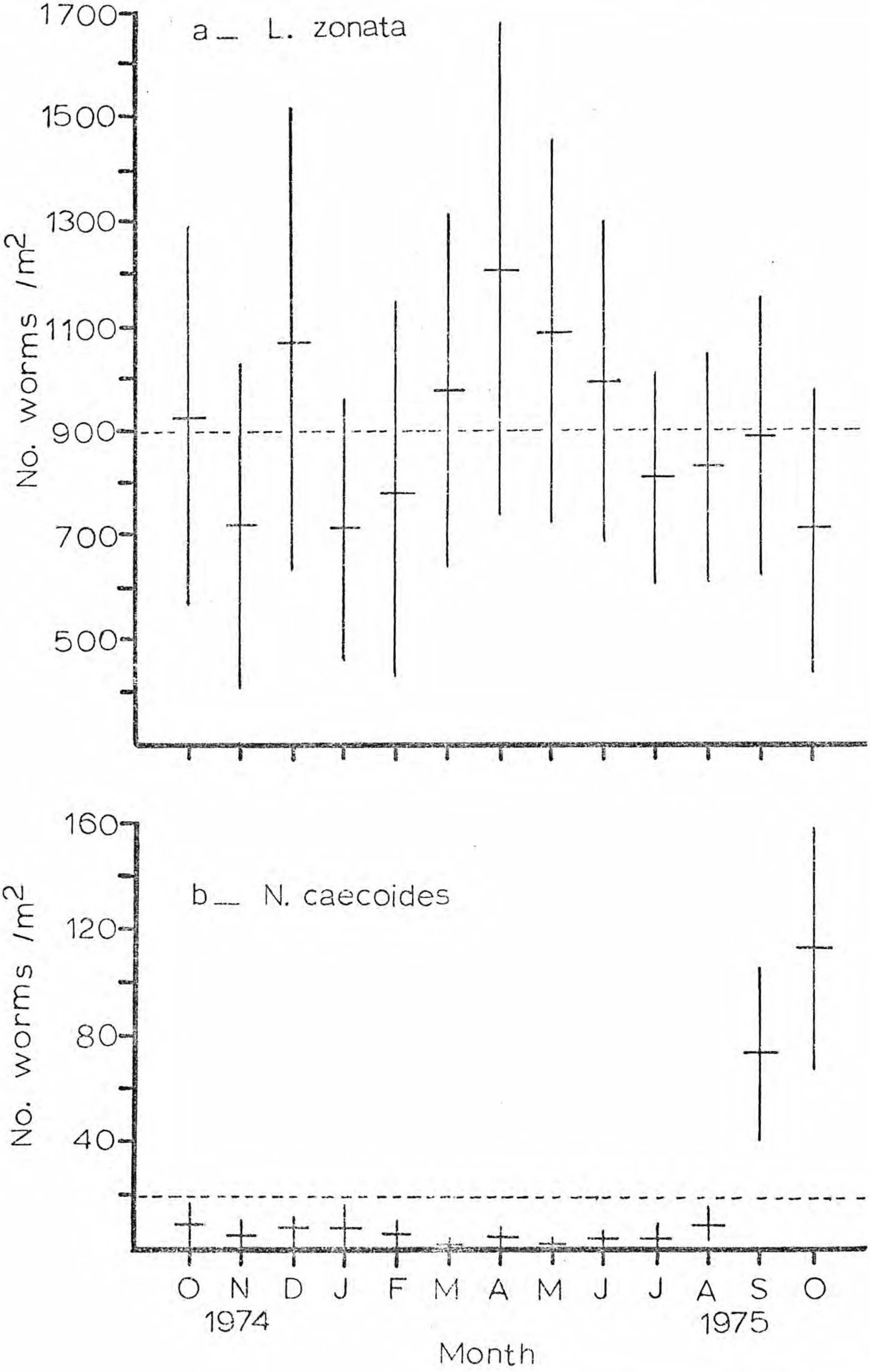

a _ L. zonata
No. worms /m^2
1700
1500
1300
1100
900
700
500
b _ N. caecoides
No. worms /m^2
160
120
80
40
O N D J F M A M J J A S O
1974
1975
Month

Figure 5. a- Estimates of population abundance of *Pseudopolydora paucibranchiata*. Symbols as in Figure 2.

b- Estimates of population abundance of *Axiothella rubrocincta*. Symbols as in Figure 2.

c- Estimates of population abundance of *Anaitides williamsi*. Symbols as in Figure 2.

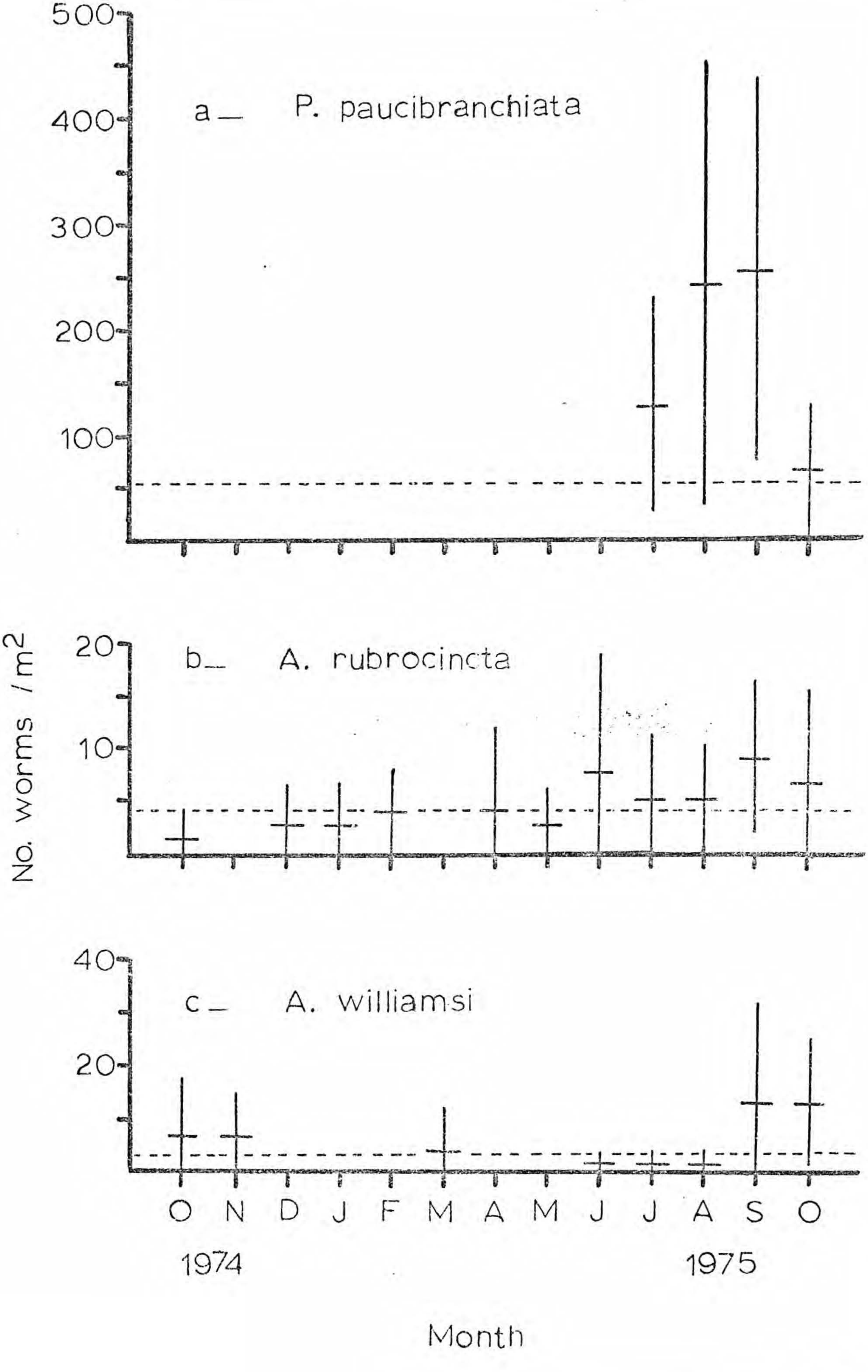
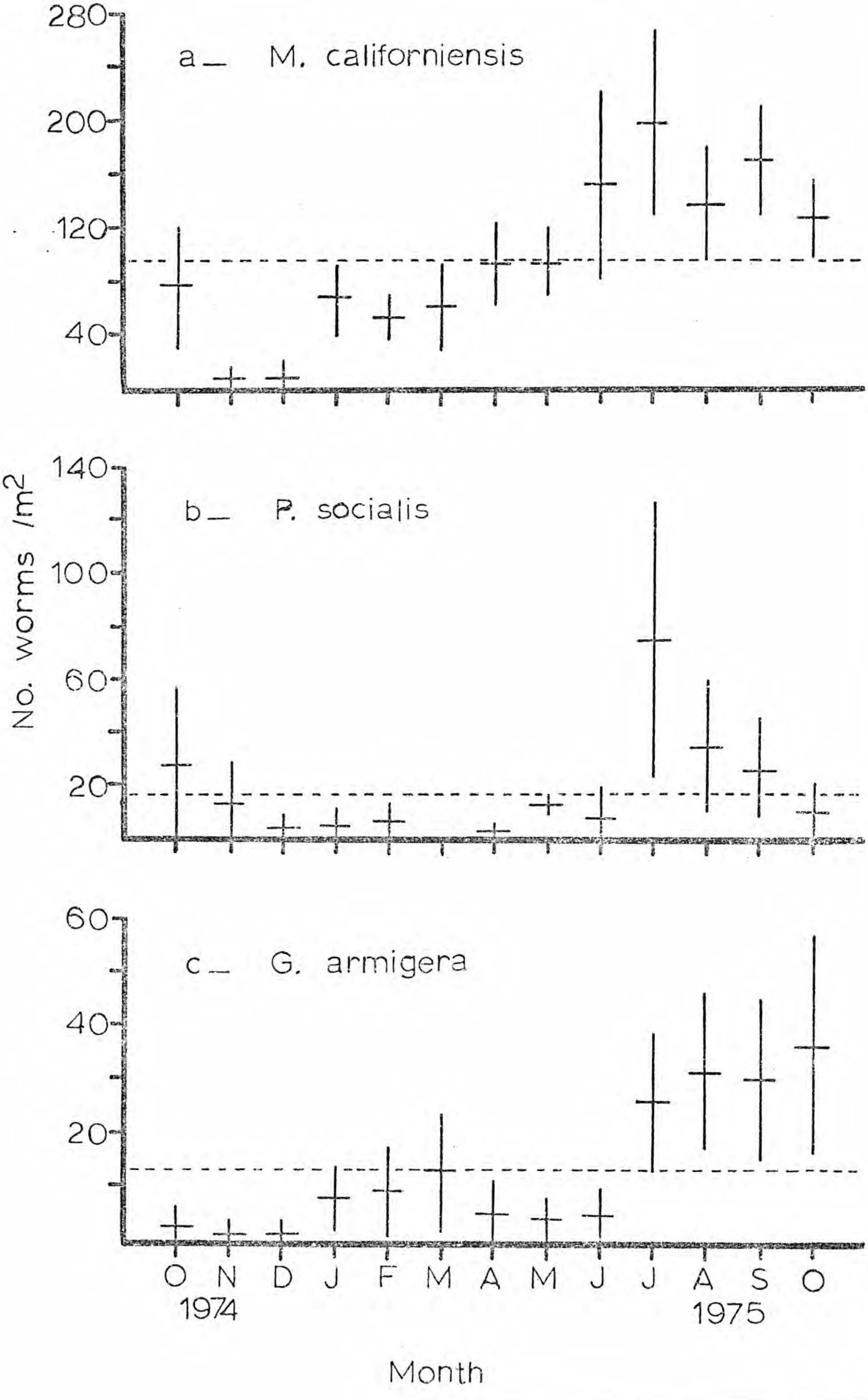

500
400
300
200
100
a — P. paucibranchiata
20
10
b — A. rubrocincta
40
20
c — A. williamsi
No. worms / m^2
O N D J F M A M J J A S O
1974
1975
Month

Figure 6. a- Estimates of population abundance of *Mediomastus californiensis*. Symbols as in Figure 2.

b- Estimates of population abundance of *Polydora socialis*. Symbols as in Figure 2.

c- Estimates of population abundance of *Glycinde armigera*. Symbols as in Figure 2.



280
200
120
40
a — M. californiensis
140
100
60
20
b — P. socialis
No. worms /m²
60
40
20
c — G. armigera
O N D J F M A M J J A S O
1974
1975
Month

Figure 7. a- Estimates of population abundance of *Haploscoloplos elongatus*. Symbols as in Figure 2.

b- Estimates of population abundance of *Armandia brevis*. Symbols as in Figure 2.

c- Estimates of population abundance of *Capitella capitata*. Symbols as in Figure 2.

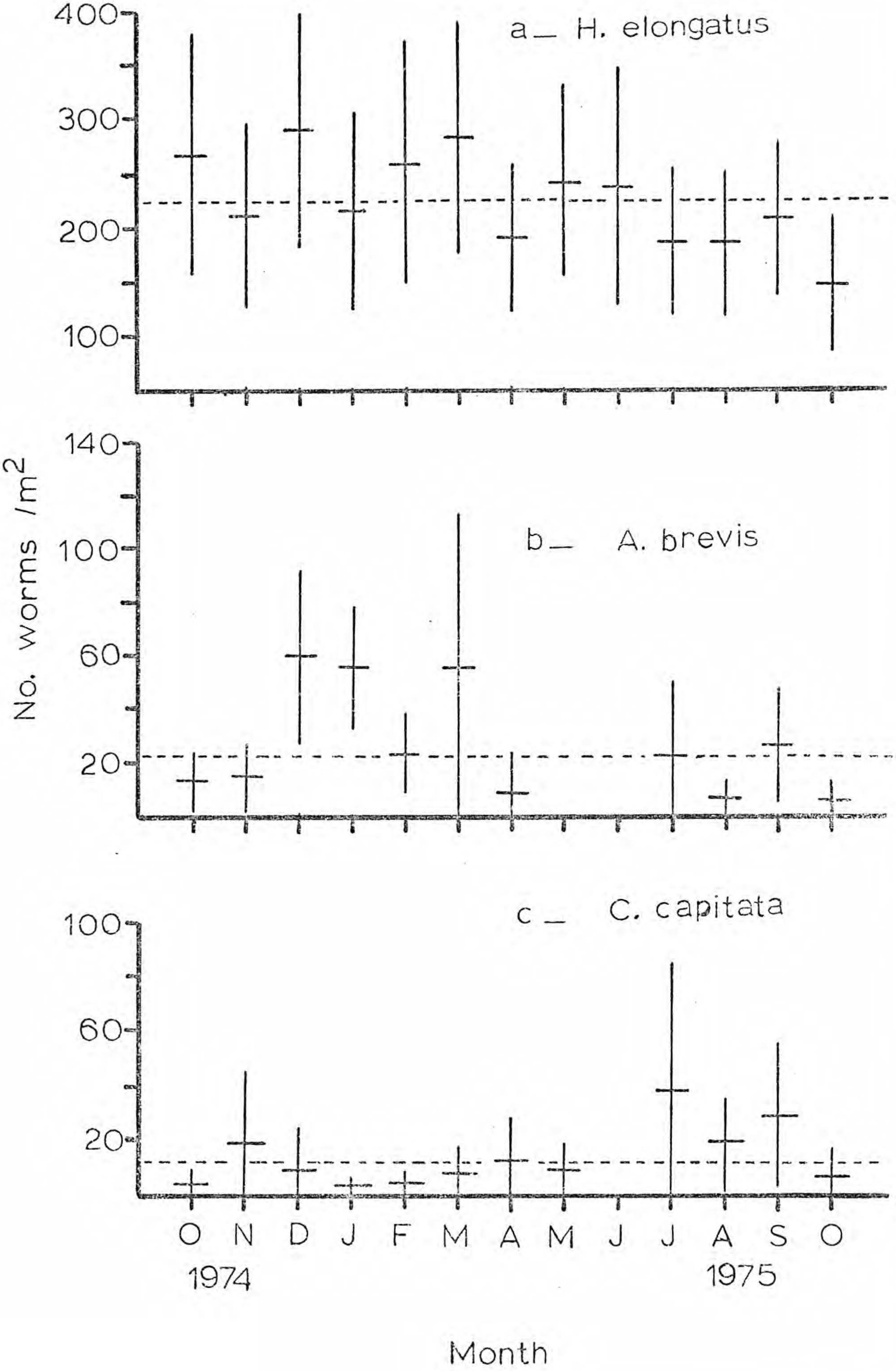

a_ H. elongatus
400
300
200
100
b_ A. brevis
140
100
60
20
c_ C. capitata
100
60
20
No. worms /m^2
O N D J F M A M J J A S O
1974
1975
Month

Figure 8. Size-frequency distributions of _Platynereis bicanaliculata_. Solid area represents recruitment, and dashed line average size-group determined by graphical inflexion method.

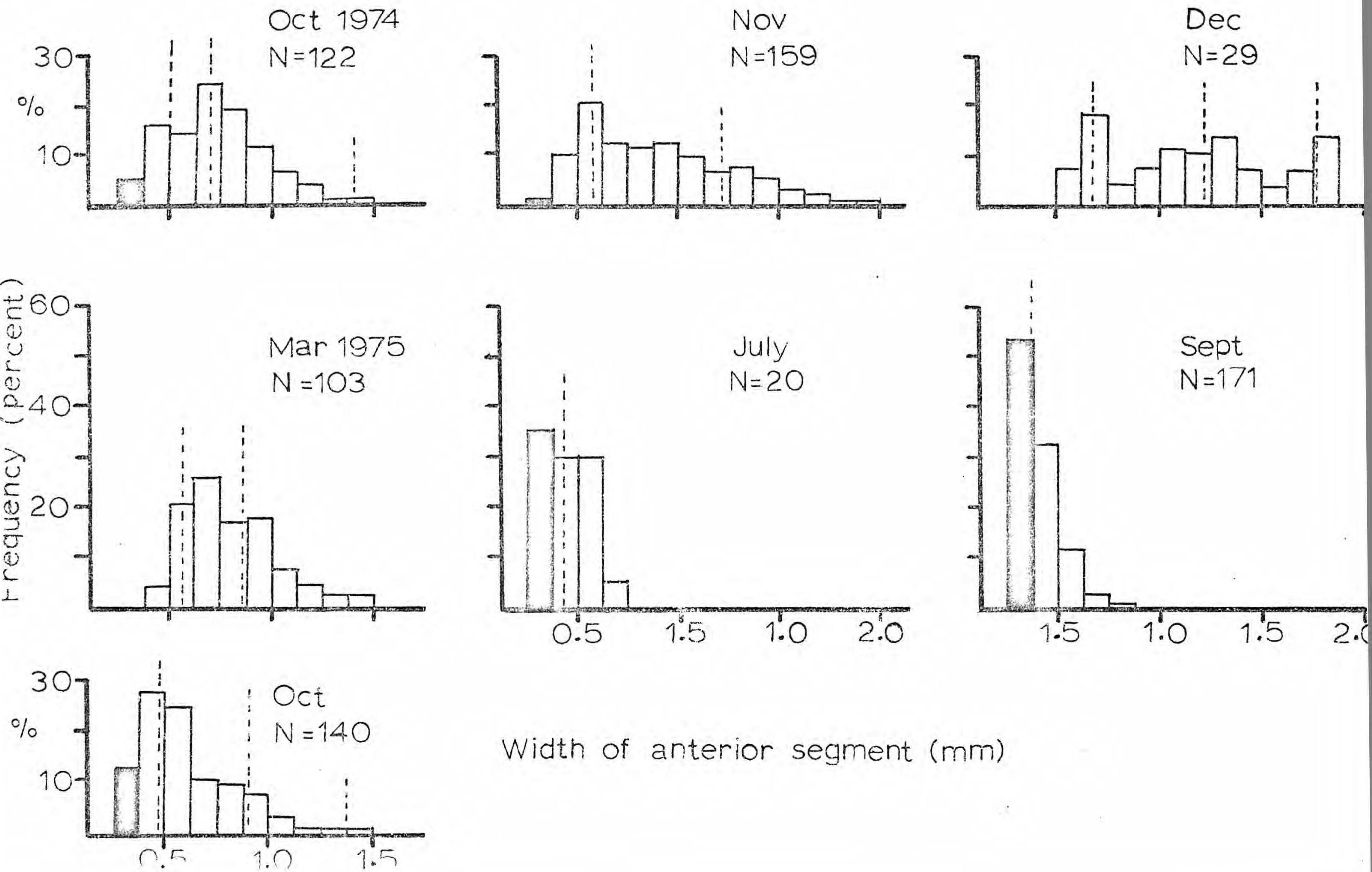
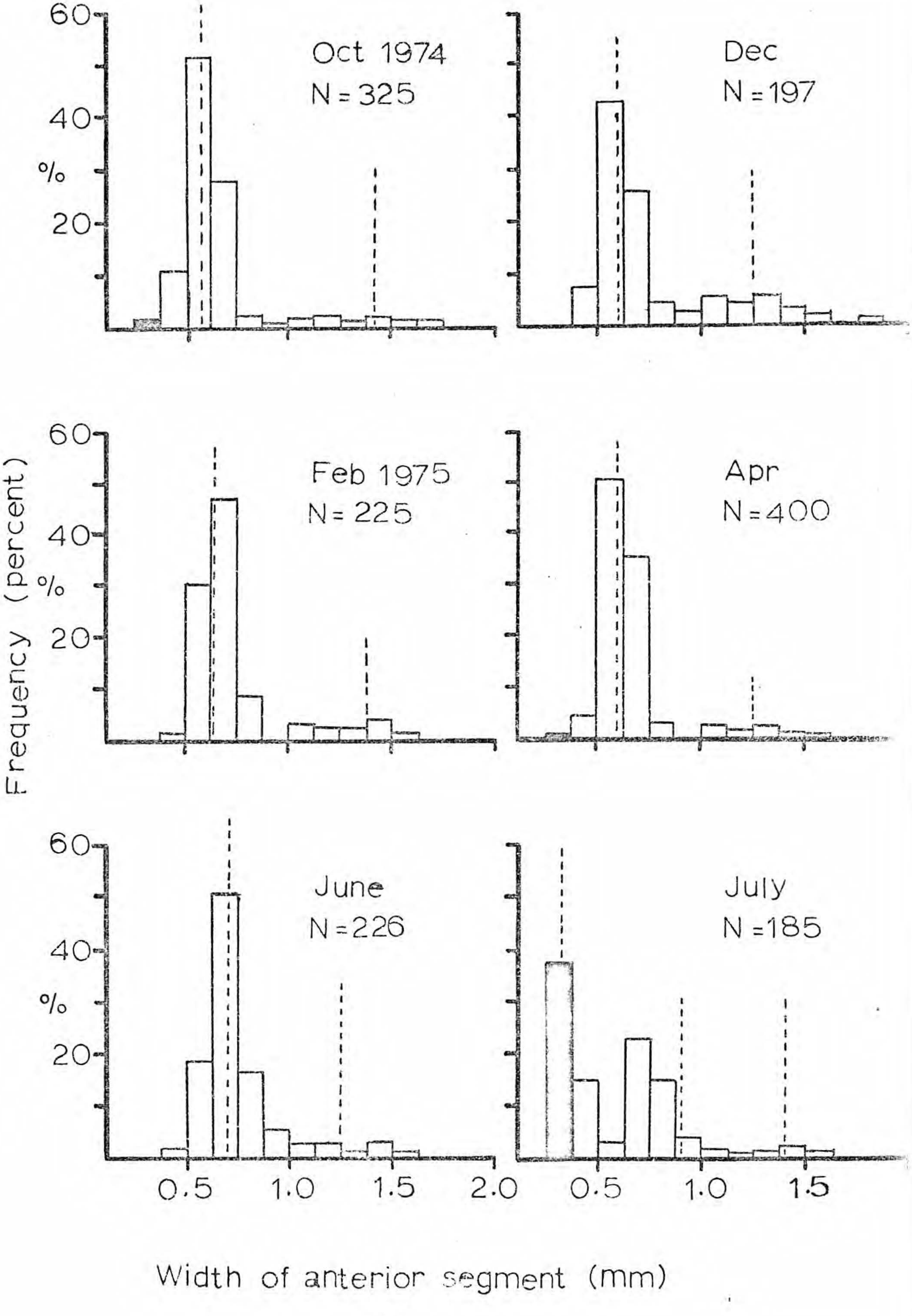
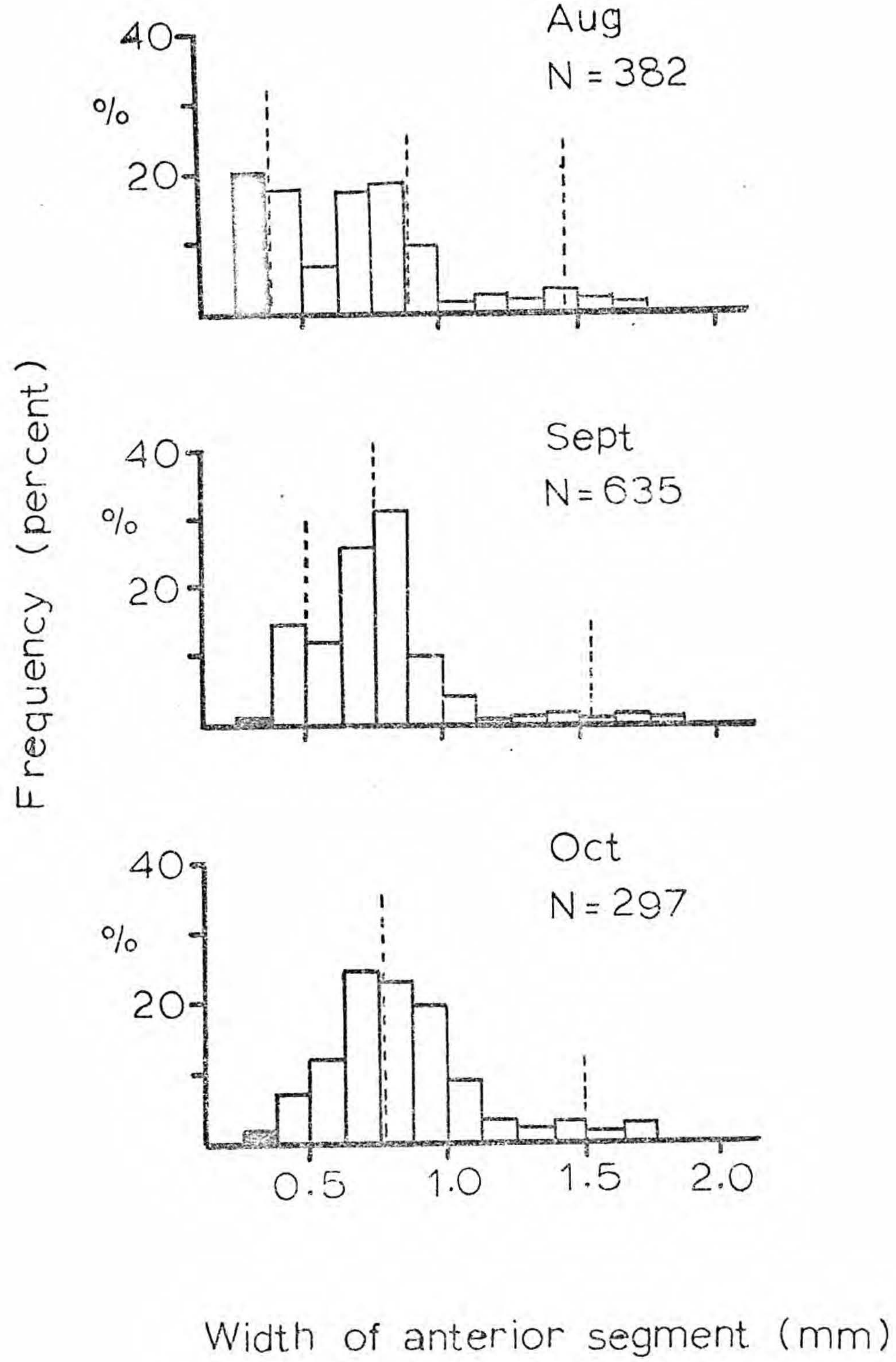

Oct 1974
N=122
Nov
N=159
Dec
N=29
30
%
10
Mar 1975
N=103
July
N=20
Sept
N=171
Frequency (percent)
60
40
20
0.5
1.5
1.0
2.0
1.5
1.0
1.5
Oct
N=140
30
%
10
0.5
1.0
1.5
Width of anterior segment (mm)

Figure 9 a, b. Size-frequency distributions of *Lumbrineris zonata*. Legends as in Figure 8.

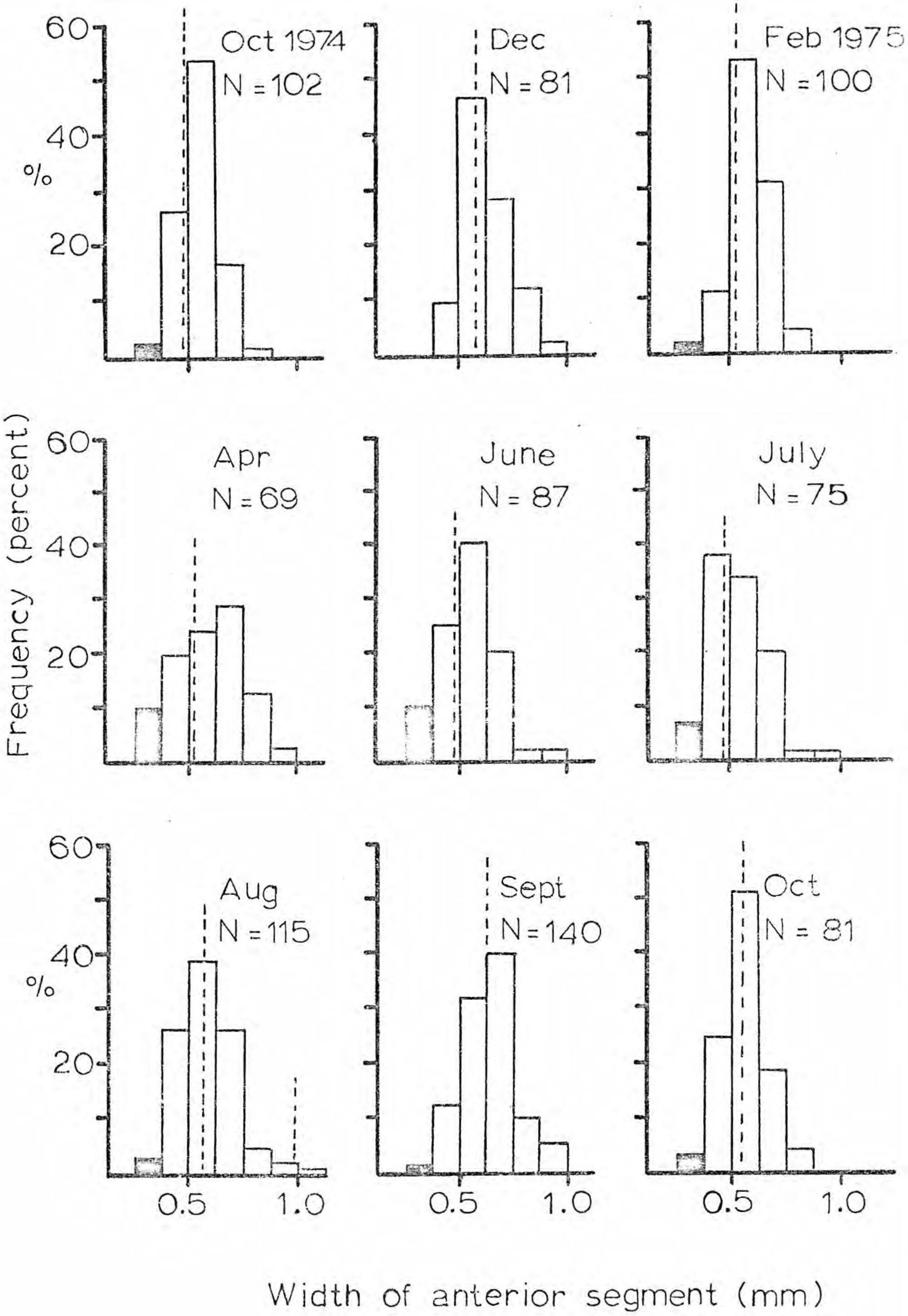

60
40
%
20
Oct 1974
N = 325
Dec
N = 197
Feb 1975
N = 225
Apr
N = 400
June
N = 226
July
N = 185
Frequency (percent)
0.5
1.0
1.5
2.0
Width of anterior segment (mm)

(a)


Aug
N = 382
Sept
N=635
Oct
N=297
40
%
20
Frequency (percent)
0.5
1.0
1.5
2.0
Width of anterior segment (mm)

(b)

Figure 10. Size-frequency distributions of _Haploscoloplos elongatus_. Legends as in Figure 8.



60
40
20
%
Oct 1974
N = 102
Dec
N = 81
Feb 1975
N = 100
Frequency (percent)
60
40
20
Apr
N = 69
June
N = 87
July
N = 75
60
40
20
%
Aug
N = 115
Sept
N = 140
Oct
N = 81
0.5
1.0
0.5
1.0
0.5
1.0
Width of anterior segment (mm)

Figure 11. Size-frequency distributions of *Mediomastus californiensis*. Legends as in Figure 8.

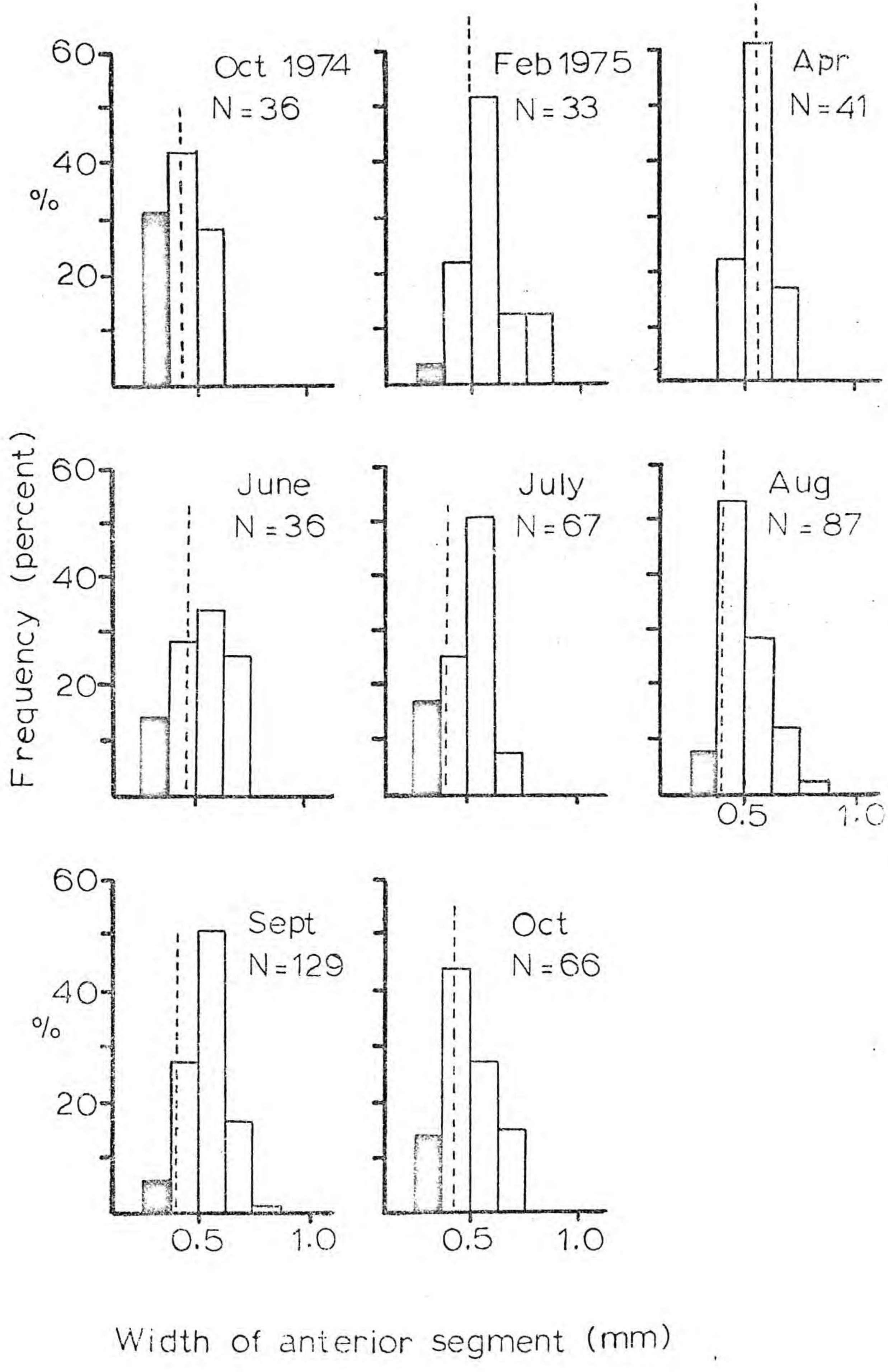
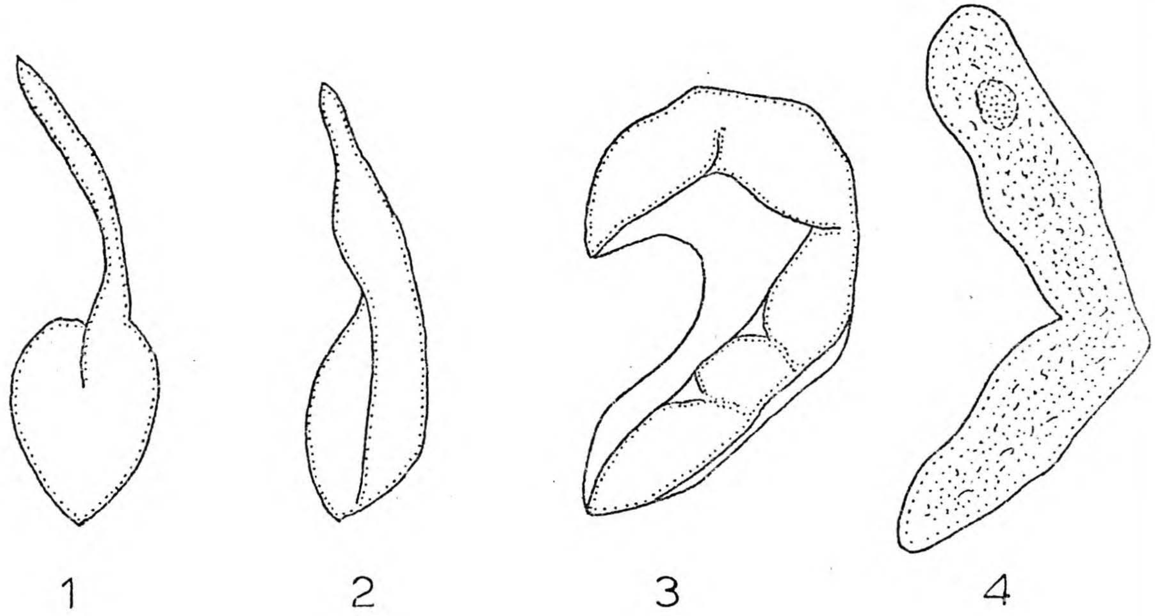

60
40
20
%
Oct 1974
N = 36
Feb 1975
N = 33
Apr
N = 41
Frequency (percent)
60
40
20
June
N = 36
July
N = 67
Aug
N = 87
0.5
1.0
60
40
20
%
Sept
N = 129
Oct
N = 66
0.5
1.0
0.5
1.0
Width of anterior segment (mm)

Figure 12. Photograph of wrinkled trophozoites of *Lecudina longissima*.

a. 1-3 A trophozoite occupying a pouch; 4, a freed wrinkled trophozoite.

Figure 13.

b. Photograph of a smooth trophozoite body of *Lecudina longissima*.

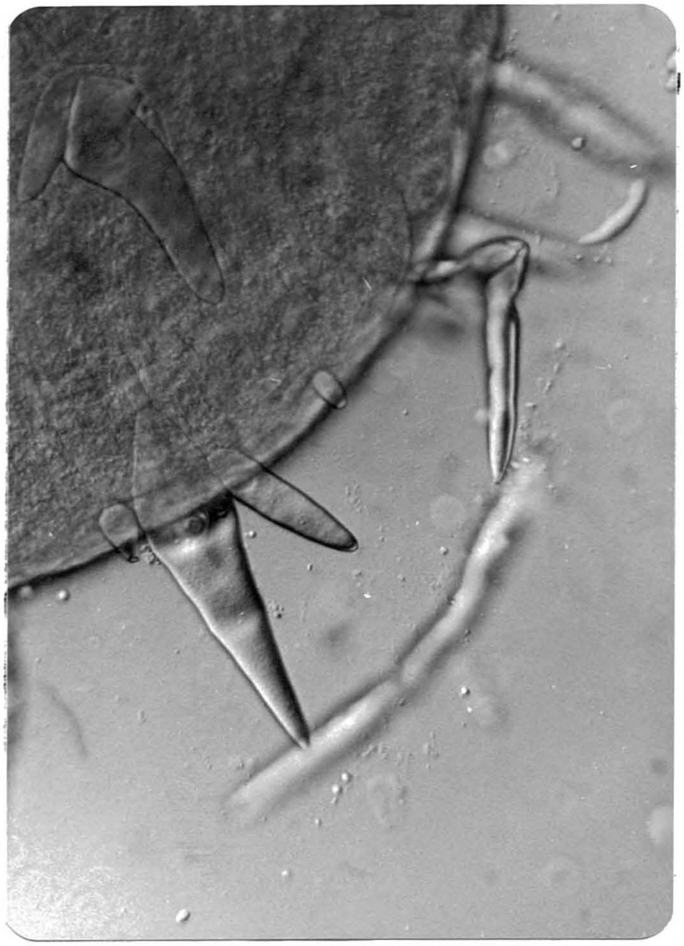

a
1
2
3
4


b

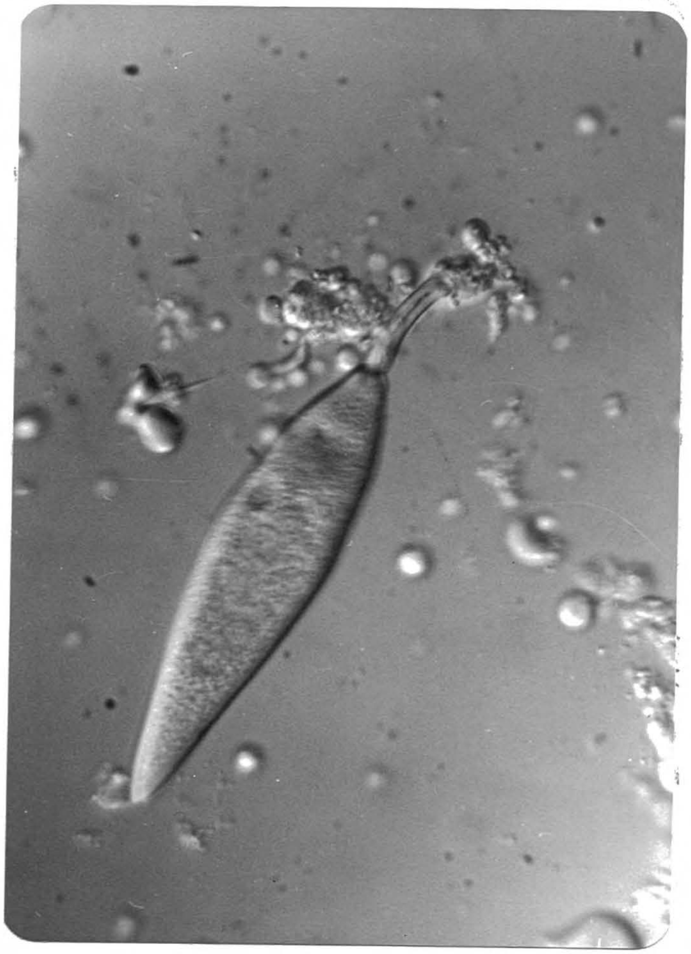
a. Photograph of a lance-shape sporont (gamont) of *Lecudina longissima* attached to tissue by an epimerite.

Figure 14.

b. Photograph of a free gamont of *Lecudina longissima* with a long anterior epimerite.



a

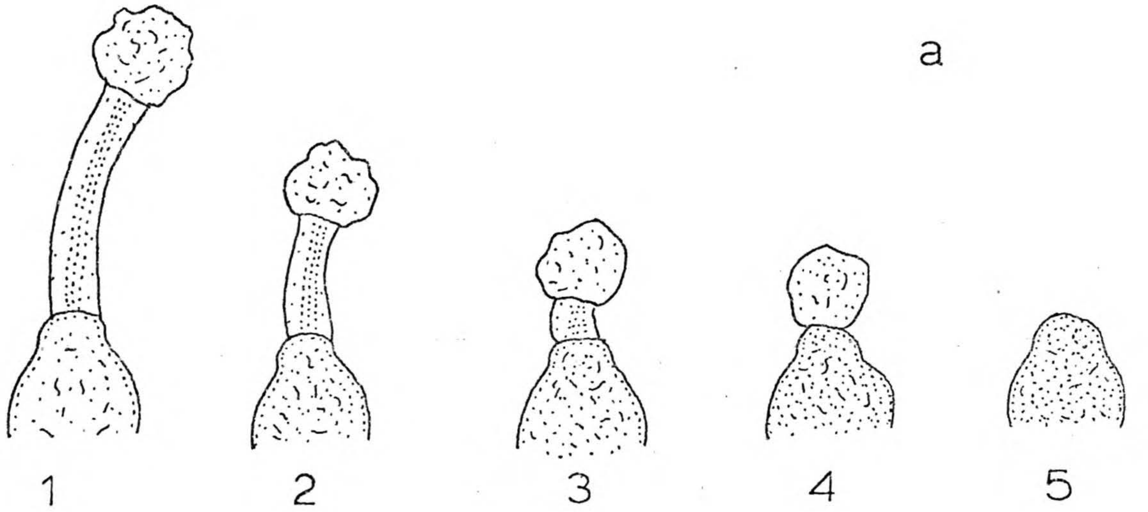


b

a. 1-5, Morphological changes of the epimerite of _Lecudina longissima_.

Figure 15.

b. Photograph of a gamont undergoing epimerite morphological changes of _Lecudina longissima_. Step 4 above is shown here.



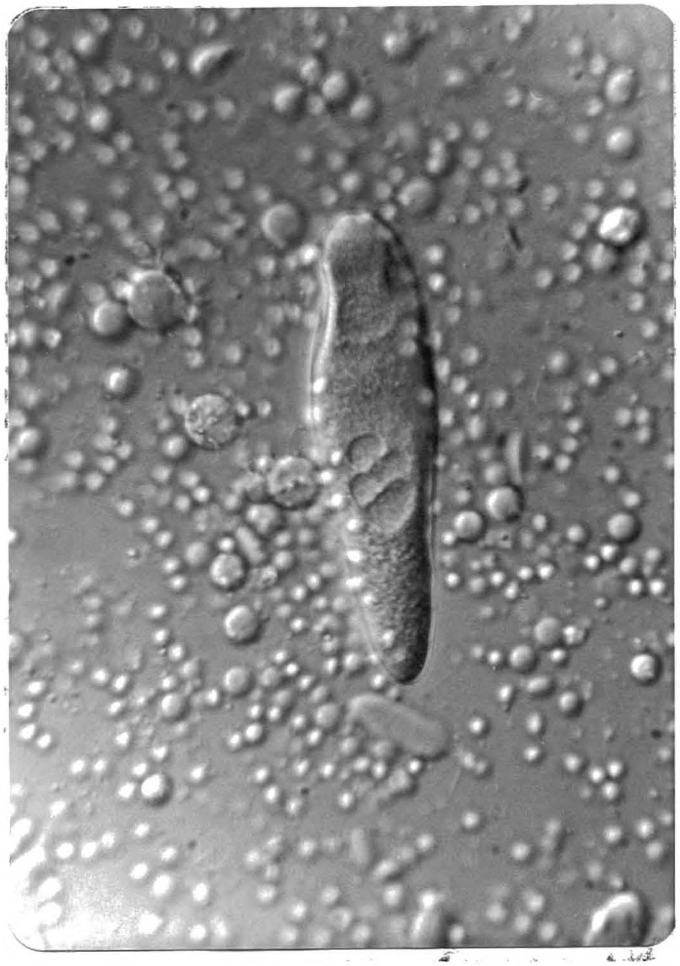
a

b

a. Photograph of a gamont of *Lecudina longissima* without epimerite. Body showing multiple nuclei.

Figure 16.

b. Photograph of different sizes of gamonts of *Lecudina longissima*.

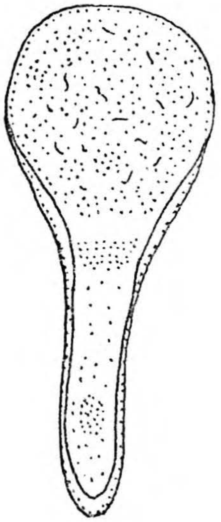


a

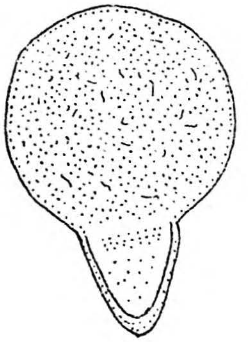
b

Figure 17. Photograph of a gamont of *Lecudina longissima* showing a median fold.

Figure 18. a,b. Cyst formation of a gamont of *Lecudina longissima*. Six-hour period between steps a and b.

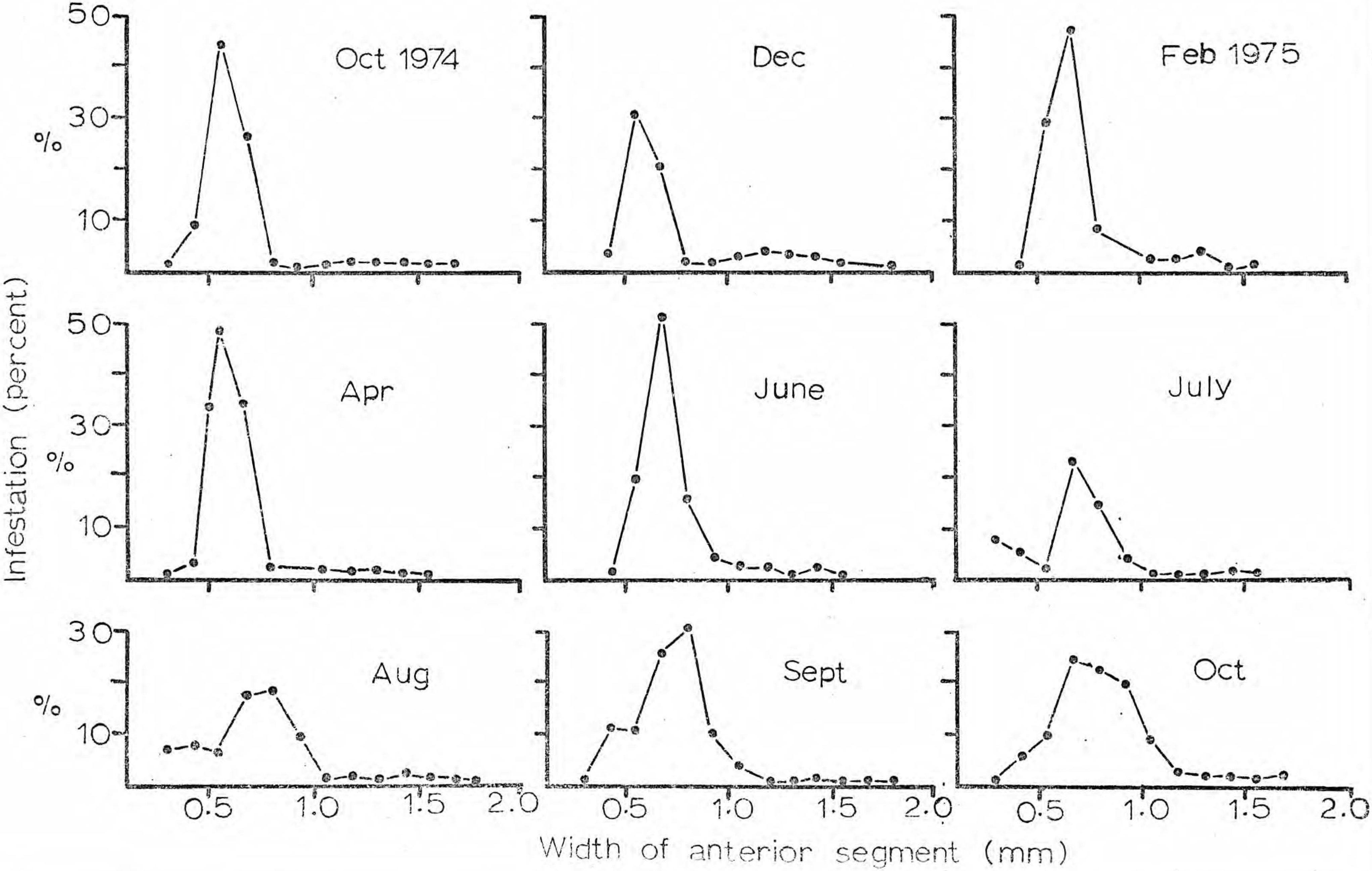


a



b

Figure 19. Frequency of parasite infestation by size-class in *Lumbrineris zonata*.


Oct 1974
Dec
Feb 1975
Apr
June
July
Aug
Sept
Oct
50
30
10
%
Infestation (percent)
0·5
1·0
1·5
2.0
Width of anterior segment (mm)