The Annual Cycle of Oogenesis, Spawning, and Larval Settlement of the Echiuran *Listriolobus pelodes* off Southern California[1]

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ABSTRACT: *Listriolobus pelodes* lives in aggregated populations in fine-grained sediments along the mainland shelf from northern California to Baja California, Mexico. This echiuran forms U-shaped burrows and uses its proboscis to feed on the uppermost layer of sediment deposited around the burrow apertures. The bacterial flora of the sediment may be an important food source. Commensals in the burrow include a polychaete, a pinnixid crab, and a small bivalve.

The annual reproductive cycle of a population off Palos Verdes, California, is defined in terms of coelomic oocyte dynamics, spawning, and larval settlement. Small oocytes are released from the gonad through most of the year but fully grown oocytes are present only from mid-fall through spring. It is estimated that the coelomic phase of oogenesis lasts about 5 months. Fully grown oocytes are removed from the coelomic fluid in the germinal vesicle stage and accumulate in the storage organs until spawning. Spawning takes place in winter and spring and individuals are spawned out by summer. An annual influx of small juveniles into the population occurs in late winter and spring. The newly settled juveniles reach sexual maturity when they are 6 months to 1 year old.

Listriolobus pelodes (Fisher 1946) is a deposit-feeding echiuran found in 18–155 m depths along the west coast of North America from northern California to Baja California, Mexico. Barnard and Hartman (1959) described a unique area of fine-grained sediments dominated by this animal near Santa Barbara, California. The more peripherally located members of this population were considerably smaller than the centrally located ones. These "small phase" echiurans were considered to be similar to the larger echiurans in all aspects except size. In 1970, during an investigation of a large oil spill which occurred at Santa Barbara, it was found that the number of *L. pelodes* had decreased dramatically (Fauchald 1971). Populations of *L. pelodes* are found in other areas off the southern California coast (Fauchald and Jones 1976; Green and Smith 1975). All of these populations share three characteristics: (1) *L. pelodes* is a dominant macroinvertebrate, (2) they are highly aggregated, and (3) they are located in areas composed of fine-grained sediments with a high organic content.

In spite of its prominence in localized benthic communities, surprisingly little is known about the biology of *Listriolobus pelodes*. The purpose of this paper is to provide a compendium of information about the natural history and behavior of *Listriolobus pelodes* and, further, to describe its reproductive biology in terms of coelomic oocyte dynamics, spawning, and larval settlement. Reproductive cycles have been studied in related phyla such as the annelids

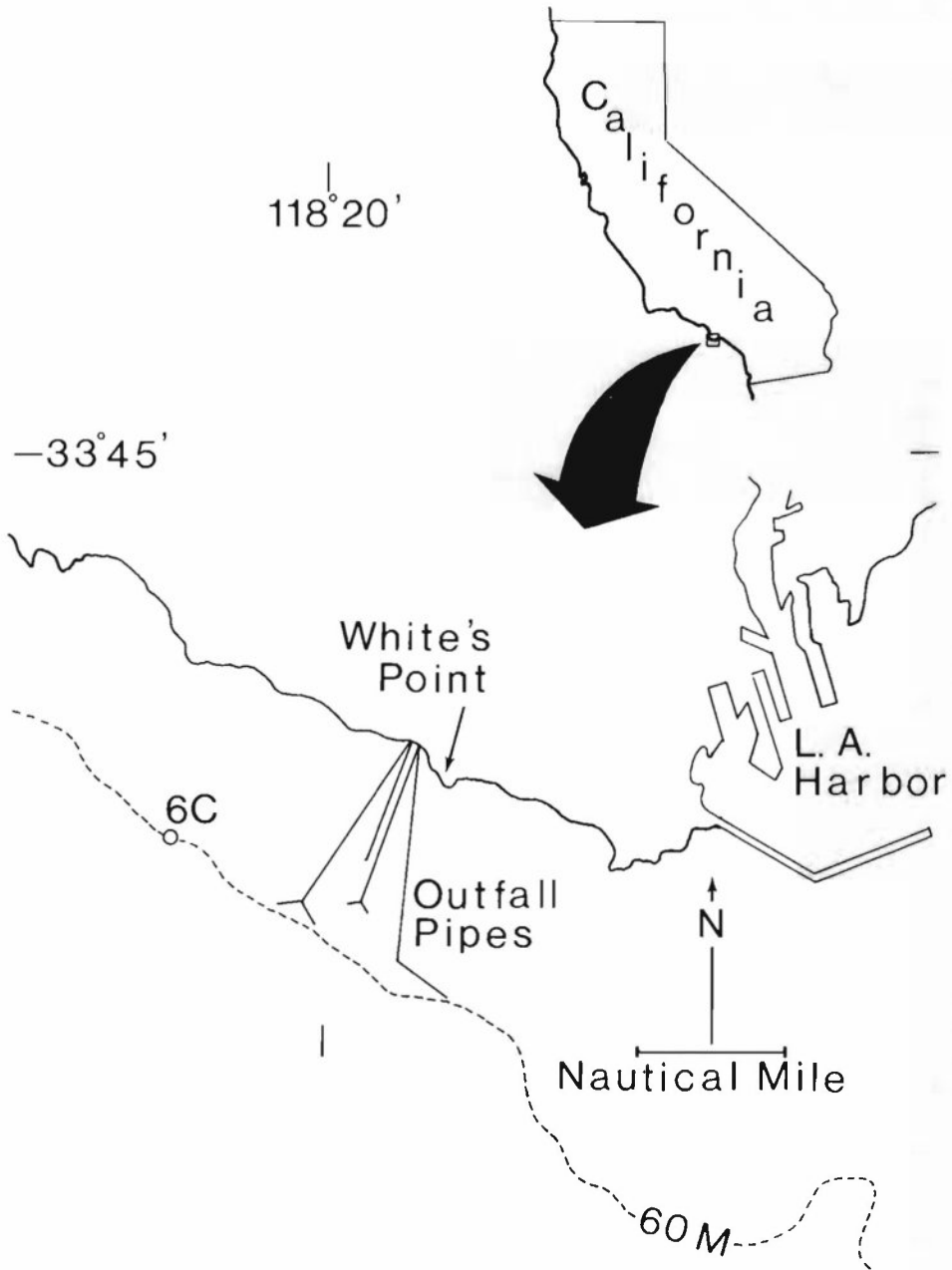[2] Smithsonian Institution, Fort Pierce Bureau, Route 1, Box 194-C, Fort Pierce, Florida 33450.

FIGURE 1. The collecting site, station 6C, at White's Point, California. Inset of California showing the location of the White's Point area.
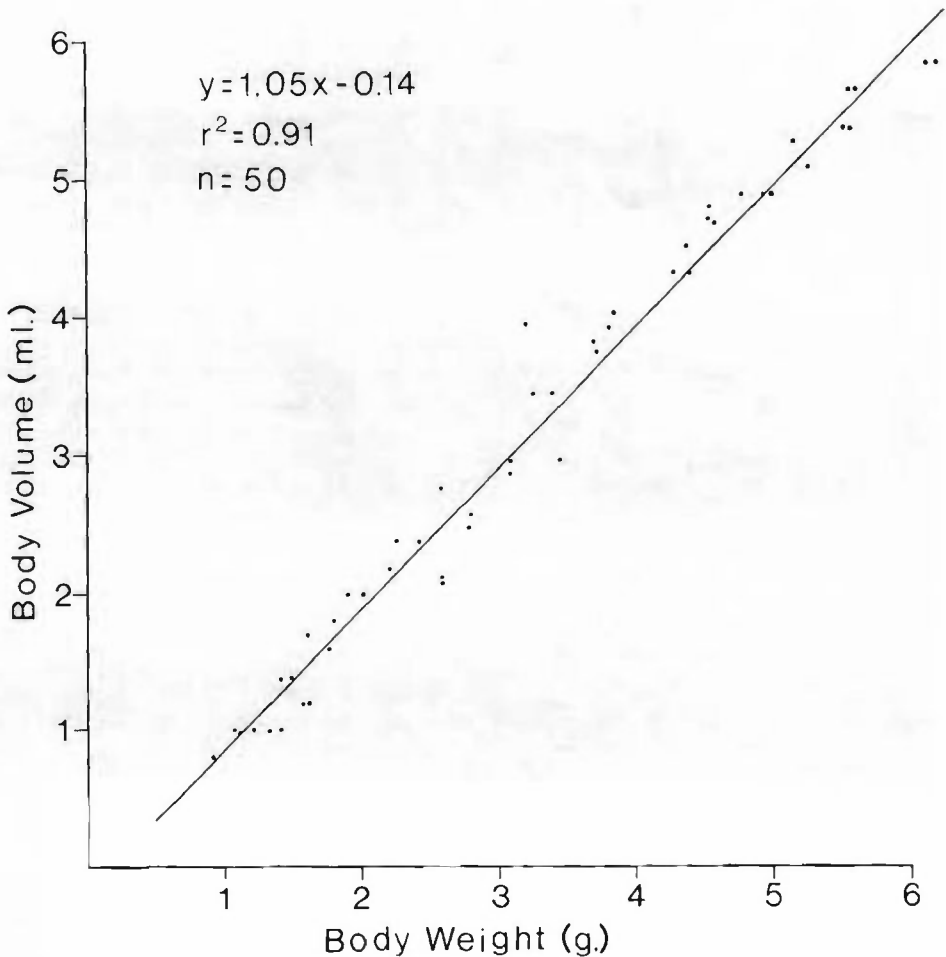
$$y = 1.05x - 0.14$$
$$r^2 = 0.91$$
$$n = 50$$

FIGURE 2. Regression of body volume against wet body weight of *L. pelodes* collected from station 6C.

(see Schroeder and Hermans 1975 for a review; Olive 1977, 1978) and sipunculans (see Rice 1975 for a review; Gibbs 1976), but they have never been investigated in the Echiura. It is hoped that this information will provide a basis from which further studies of this interesting echiuran will emerge.

METHODS

Specimens of *L. pelodes* were collected from a depth of 60 m at station 6C of the Los Angeles County Sanitation District,

near White's Point, California (33°42.5' N, 118°20' W; Figure 1). Supplementary information for certain aspects of this study was obtained by using large specimens collected from the Santa Barbara, California, *L. pelodes* population which was described by Barnard and Hartman (1959; 34°23' N, 119°38' W). Live animals and sediment were obtained with a Shipek grab or box corer and maintained in flow-through seawater aquariums in a laboratory at the Catalina Marine Science Center, University of Southern California.

Adults of *L. pelodes* are poor burrowers and will die if a burrow is not constructed.
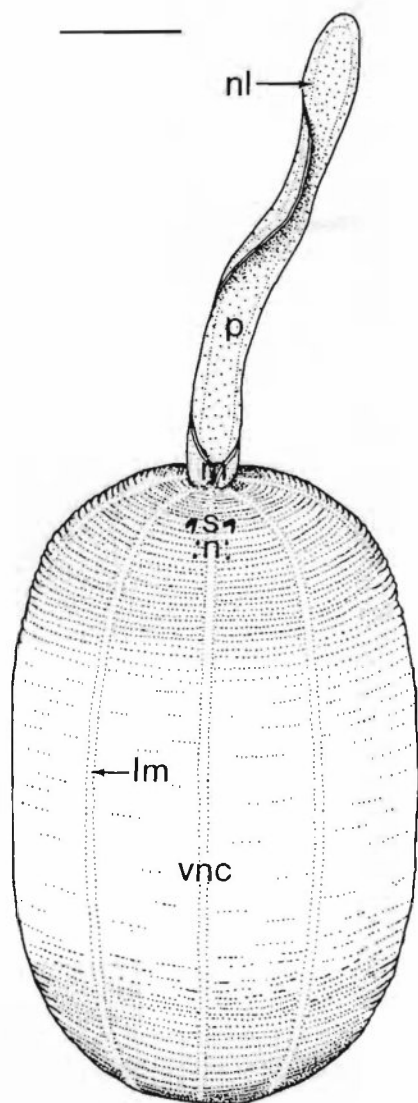
FIGURE 3. Ventral view of *Listriolobus pelodes*. *lm*, longitudinal muscle band; *m*, mouth; *n*, nephridiopores; *nl*, anterior nerve loop; *p*, proboscis; *s*, setae; *vnc*, ventral nerve cord on mid-ventral muscle band. Scale equals 5 mm.

The number of casualties from this problem was minimized by artificially constructing U-shaped burrows for some, and by maintaining others in glass or plastic tubing and providing sediment for feeding. Burrows in narrow glass-sided boxes filled with mud facilitated the observation and understanding of aspects of the animal's behavior which take place within the burrow.

Diameter of coelomic oocytes was used as the primary index of gametogenic activity. On a monthly basis from January 1975 through December 1976, a sample of coelomic fluid was withdrawn with a syringe from 5 females; 40 oocytes were measured in each specimen. The frequency distribution of these diameters was plotted on a time scale.

Differentiated gametes accumulate in 2 pairs of storage organs (modified nephridia) until spawning. These organs become greatly enlarged by the accumulation of gametes within them. A relative decrease in the volume of these organs can indicate the time of spawning. For each individual, the 4 organs were measured and their total volume calculated. This volume was divided by the animal's wet body weight to correct for differences in individual size. It was not possible to make these measurements on the specimens from White's Point because they were collected as part of a County Sanitation District study which precluded their dissection. To get some idea of the spawning period, however, data were obtained from specimens collected from Santa Barbara, California, as reported by Barnard and Hartman (1959) and others (Pilger 1977).

The size-frequency distribution of echiurans in the samples taken at station 6C indicated the period of larval settlement. Wet body weight was used as an index of size. This measurement was found to be directly related to body volume (Figure 2) and could be determined accurately and rapidly.

RESULTS

Natural History Observations

The body of *Listriolobus pelodes* (Figure 3) is subspherical to ovoid and measures up to 4 cm long and 2 to 3 cm wide. A green pigment usually is present on the anterior and posterior ends of the body and 8 regularly-spaced longitudinal muscle bands are visible in the body wall. The mouth is located

ventrally at the base of the dorsoventrally flattened, highly extensible proboscis. Two hooked setae straddle the ventral midline behind the mouth. A pair of nephridiopores open on each side of the ventral nerve cord posterior to the setae.

Using a box corer, 10 intact *Listriolobus pelodes* burrows were collected from Santa Barbara, California. Careful examination of these burrows showed all of them to be U-shaped with exactly 2 openings to the surface. Peristaltic contractions of the body pump respiratory water through the burrow. The anal vesicles (paired hind-gut diverticulae) intermittently "inhale" and "exhale" portions of this water.

Listriolobus feeds on deposited sediment that surrounds the burrow apertures. While feeding, the body remains within the burrow and the proboscis extends onto the substrate with its ventral side up. The top layer of sediment is picked up by the proboscis and transported by ventral cilia to the mouth. Laboratory observations showed that certain areas of sediment are grazed while others are disregarded. This may indicate that some degree of qualitative discrimination takes place in food selection.

Fecal pellets (0.5 × 1.0 mm ellipsoids) remain in the burrow for a while after their release. The combined effect of the water currents from the body's peristaltic contractions and the "exhalations" from the anal vesicles intermittently expels the pellets from the burrow. The feces accumulate on the sediment around the burrow apertures and give rise to the hummocky topography of an *L. pelodes* bed (R. Given, personal communication). Since these pellets typically are reingested after a short exposure on the sediment, a rapidly regenerating food resource is implied (e.g., bacteria and associated microorganisms).

The proboscis is highly extensible and large specimens of *L. pelodes* have been observed to feed on the sediment as far as 20 cm from the burrow aperture. *L. pelodes* intermittently turns around in its burrow, thus feeding on the sediment surrounding both burrow apertures. These observations indicate that up to 0.25 m² of substrate surface

is available for feeding by individual echiurans and imply that in dense *L. pelodes* populations (approximately 100 individuals · m^{-2}) all of the sediment surface is regularly grazed. Clearly, the potential impact of the presence of *L. pelodes* on sediment reworking and the trophic structure of the benthic community is great.

At least 3 commensal organisms were found to be living in the burrow of *Listriolobus pelodes*: the polychaete *Hesperonoe laevis* (Hartman 1961), the pinnotherid crab *Pinnixa schmitti*, Rathbun 1918, and the bivalve *Mysella tumida* (Carpenter 1864). Although there does not appear to be any direct interaction between these commensals and the echiuran, the burrow may afford them some protection, and nutritional benefit may be derived from the water and associated organisms which are pumped through it (Fisher and MacGinitie 1928). A peritrichous ciliate was discovered in the coelomic fluid of a few specimens and a helminth parasite was found embedded in the proboscis musculature of another. Neither of these was identified further.

Oogenesis

Echiuran oogenesis may be divided into 3 distinct phases. The oocytes begin their differentiation in the gonadal phase. They enter the second, or coelomic, phase when they detach from the gonad and continue their growth in the coelomic fluid. Finally, as germinal vesicles, they enter the storage phase when they are removed from the coelomic fluid and accumulated in the modified nephridia.

In *Listriolobus pelodes* the gonad is situated on the ventral blood vessel in the posterior region of the body (Figure 4). The blood vessel is attached to and follows the ventral nerve cord posteriorly. Near the rectum the vessel separates from the nerve and attaches to the intestinal caecum. The germ cells arise from the tissue surrounding the blood vessel in this region.

Small primary oocytes (5–7 μm) are released from the gonad in clusters of 20 to 30 cells (Figure 5a). One to 3 of these cells begin
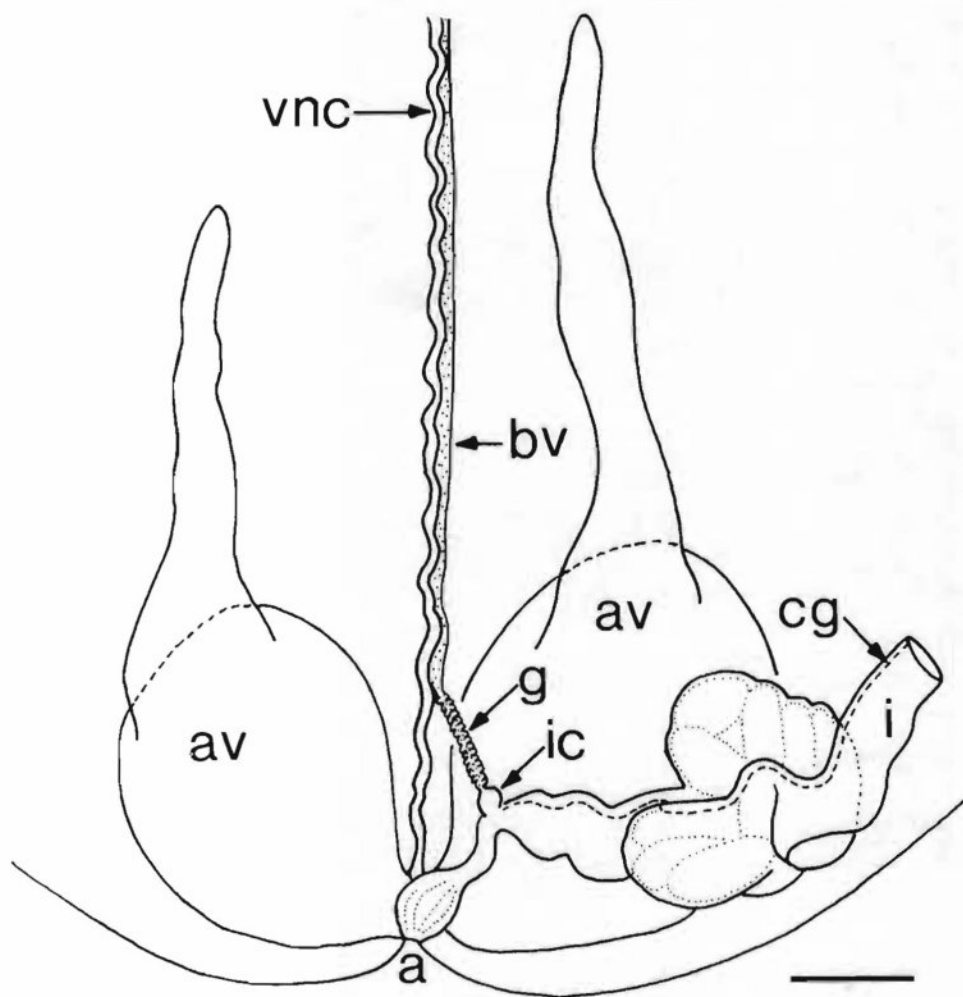
FIGURE 4. Dorsal view of the posterior internal anatomy of *L. pelodes* showing the location of the gonad. *a*, anus; *av*, anal vesicles; *bv*, blood vessel; *cg*, ciliated groove; *g*, gonad; *i*, intestine; *ic*, intestinal caecum; *vnc*, ventral nerve cord. Scale equals 1 mm. Adapted by permission of the Smithsonian Institution Press from *United States National Museum Proceedings*, Volume 96, "Echiuroid Worms of the North Pacific Ocean," by W. K. Fisher, April 11, 1946, pages 215–292, Figure 12. Washington, D.C.: U.S. Government Printing Office, 1948.

to differentiate and are distinguishable by their increased diameter (Figure 5b). The remainder do not differentiate but remain attached to the definitive oocytes. When an oocyte reaches a diameter of 40 μm it separates from the cluster to continue differentiating as a single cell (Figure 5c). Upon attaining a diameter of about 100 μm the oocytes are selectively removed from the coelomic fluid by the long coiled nephrosto-

mal lips (collecting threads). These threads lead to the nephridia (storage organs) where oocytes are stored until spawning. The oocytes are spawned in the germinal vesicle stage.

Gametogenic Cycle

The data presented in Figure 6 show the annual cycle of coelomic oocyte growth in
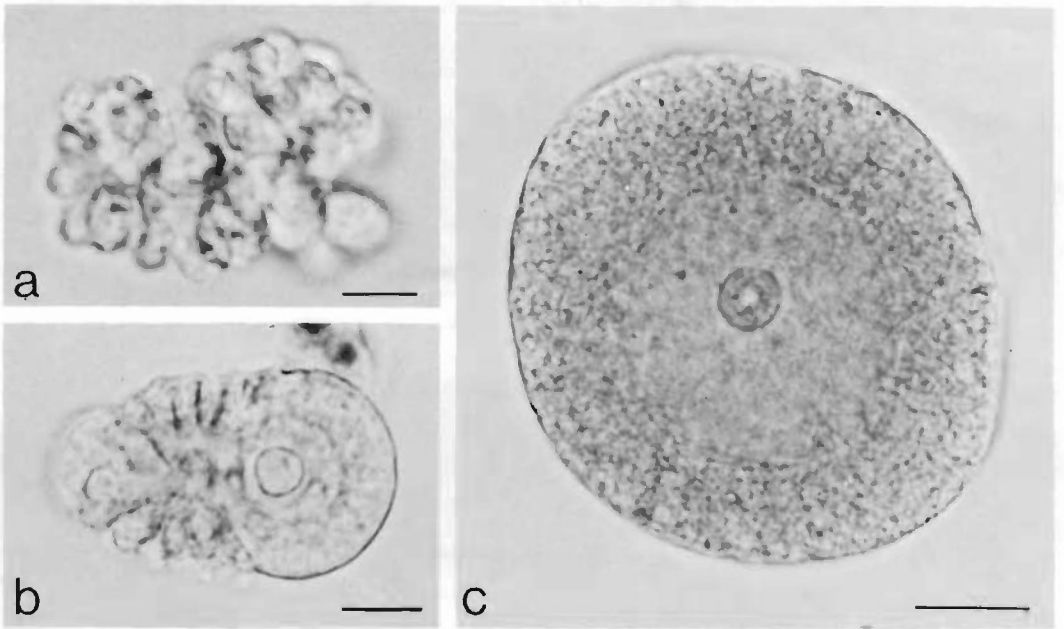
FIGURE 5. Coelomic oocytes from *L. pelodes.* *a*, a cluster of small primary oocytes recently released from the gonad. Scale equals 10 μm. *b*, two differentiating oocytes still attached to the cluster of small cells. Scale equals 10 μm. *c*, a coelomic oocyte that has dissociated from the cell cluster and is undergoing the remainder of oogenesis as a single cell. Scale equals 20 μm.
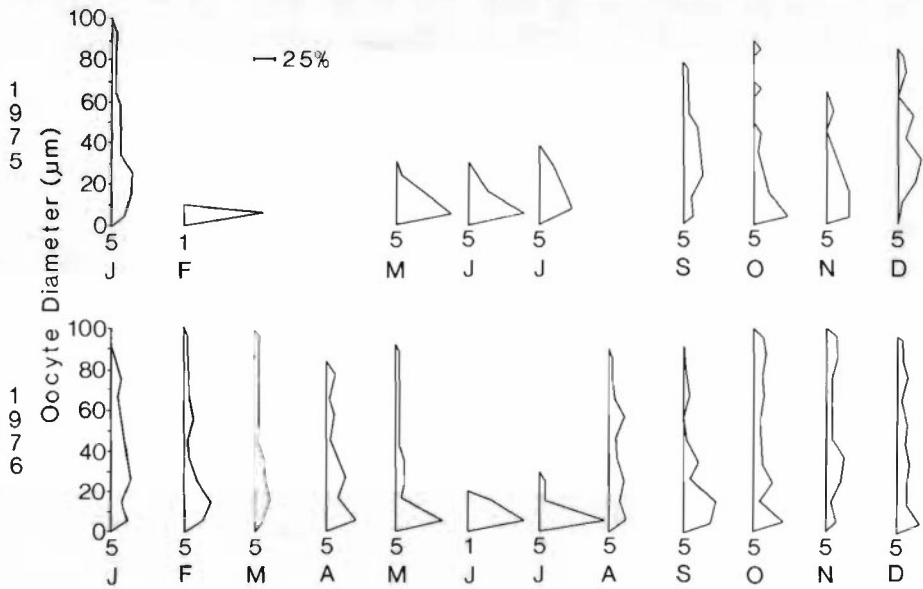

FIGURE 6. Relative frequency distributions of oocyte diameters in *L. pelodes* collected from January 1975 through December 1976 at station 6C. The number of females examined is indicated below each month. Scale equals 25 percent.
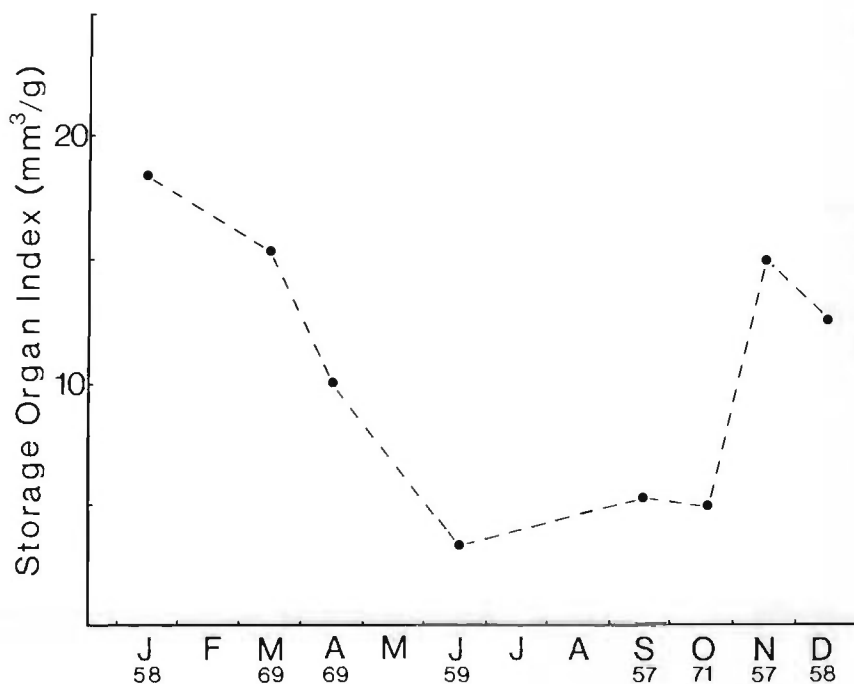
FIGURE 7. Index of storage organ volume taken from *L. pelodes* collected at Santa Barbara, California, in the years indicated below each month.

L. pelodes at White's Point during the study period. In May, June, and July 1975, the coelomic oocyte population consisted exclusively of small oocytes. By October, some of these oocytes had reached maximum diameter while growth of the remaining oocytes continued into winter. The production of small oocytes by the ovary continued through the fall, winter, and probably part of spring so that differentiating oocytes of all sizes were present in the coelom through May 1976. During June and July 1976, the coelomic oocyte population again had only small cells. The most advanced of these reached maximum size in October while those produced in succeeding months differentiated in November, December, and after the study had ended.

The data show that the ovary released small oocytes into the coelom more or less continuously through the year. This interpretation may not be correct, however, since only those individuals that contained recognizable oocytes could be included in the results. Individuals that were large enough to be sexually mature (>0.82 g), but lacked coelomic gametes altogether, were sometimes present in the samples but could not be sexed. The samples contained a greater percentage of individuals lacking coelomic gametes in winter (26 percent) and spring (29 percent) than in summer (2 percent) and fall (11 percent). This indicates that in many individuals the coelomic gamete population became depleted in winter and spring. This was probably due to the accumulation of fully differentiated gametes in the storage organs prior to spawning (see *Gamete Accumulation and Spawning* below). By summer, the coelomic gamete population in most of the individuals had been replenished with small gametes released from the gonad. These data suggest that the gonad of *L. pelodes* may have undergone a period of quiescence which was obscured by slight asynchrony in the population and the sampling bias described above. To test such a hypothesis would require examination of the gonad and careful repeti-

tive monitoring of the coelomic gamete population in single individuals over time.

Duration of Oogenesis

The entry of oocytes into the coelomic fluid during the summer defines periods of oocyte growth which can be used to estimate the duration of oogenesis (Figure 6). In May, June, and possibly July, 1975, small oocytes were released into the coelom. The first of these became fully differentiated by October, indicating that the duration of oogenesis was roughly 5 months (May to October). In a similar manner, the oocytes that reached maximum diameter in October 1976 are assumed to have been released into the coelomic fluid in April or May of that year. Thus, the term of oocyte growth was estimated as having been 5–6 months. Estimates from oocytes released at other times during the year are not practical since the growth of discrete size classes could not be followed with certainty.

Oocytes that have reached maximum diameter are removed from the coelomic fluid and accumulated in the storage organs from October through May.

Gamete Accumulation and Spawning

Annual fluctuations of the storage organ volume in specimens collected in different years from Santa Barbara, California, were pooled and are shown in Figure 7. The data indicate that the storage organs are small and empty in summer. The volume increases sharply in fall and continues through midwinter as more and more gametes become fully differentiated and are removed from the coelomic fluid. The steady decline in storage organ volume noted throughout the spring is assumed to be the result of spawning. By summer the animals are spawned out and the storage organs are empty again.

Juvenile Settlement

During late winter and early spring 1975, a large influx of very small juveniles (<0.25 g) appeared in the population at White's Point

(Figure 8). These were assumed to be recently settled individuals. By April and May they accounted for as much as 75 percent of the population (by numbers). With time these individuals grew and appeared in progressively larger size classes or died. The number of individuals in the smallest size class remained very low from fall 1975 through early spring 1976. Another influx of juveniles occurred in May and June 1976. This settlement involved fewer individuals than the one in 1975, was restricted to a narrower time-frame, and was recognizable as a distinct size class for a shorter time.

Growth to Sexual Maturity

The growth of newly settled juveniles during their first year can be predicted from the data presented in Figure 8. Since the population size frequency distributions are noticeably skewed by the influx of newly settled juveniles, changes in the arithmetic mean weight for the entire population are a poor indication of growth during the first year. In this case, fluctuation of the most frequent size class (i.e., the mode) more adequately represents the weight changes of individuals in these small size classes.

Growth of newly settled juveniles in the population is seen graphically as a progression of the modal size class toward heavier weight classes. The difference in weight of the modal class in the 12 months following settlement gives an indication of juvenile growth during the first year. In July 1975, the modal class was 0–0.25 g and comprised individuals which had settled in the preceding few months. By January 1976, this class had increased to 0.75–1.0 g and was still quite distinct. In June–July 1976, the mode for the individuals which had settled in 1975 was about 1.50 g. Thus, in the 12 months following their settlement in 1975, the juvenile *L. pelodes* had attained a weight of approximately 1.5 g.

Based on the examination of several hundred individuals of various sizes, the smallest individual in this study having differentiating gametes in the coelomic fluid weighed 0.82 g and was assumed to have been about 6
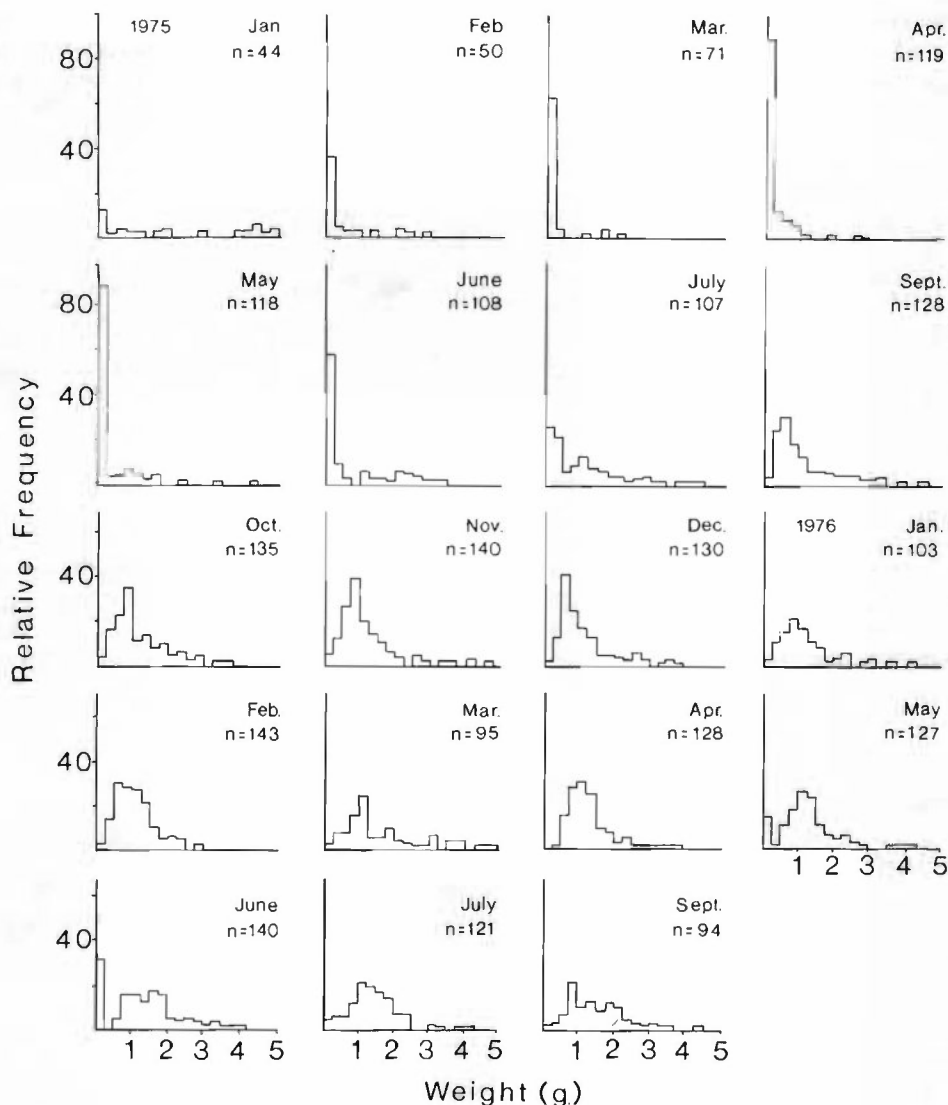
FIGURE 8. Relative size frequency distributions of *L. pelodes* collected from January 1975 through September 1976 at station 6C. The size classes are in 0.25 g increments of wet body weight.

months old. Thus, it is hypothesized that *L. pelodes* juveniles from White's Point reach sexual maturity when they are 6 months to 1 year old.

DISCUSSION

Listriolobus pelodes was first described from the stomach of flounders (Fisher 1946)

and at White's Point it is known to be the main food item of the dover sole, *Microstomus pacificus* (Lockington 1879; J. Allen, personal communciation). The bat ray, *Myliobatis californicus*, Gill 1865, is a suspected predator also since it is present with *L. pelodes* at White's Point and it is known to eat other echiurans elsewhere (Fisher and MacGinitie 1928).

Listriolobus pelodes uses its proboscis

to feed on sediment deposits in a manner similar to that described for *Echiurus echiurus* (Gislén 1940), *Ochaetostoma erythrogrammon* (Chuang 1962), and *Bonellia viridis* (Jaccarini and Sehembri 1977a, 1977b). Since *L. pelodes* feeds on sediment in some areas while leaving other areas undisturbed, it is hypothesized that the proboscis is able to discriminate qualitatively between different sediment types. Jaccarini and Schembri (1977b) re-reported that *Bonellia viridis* has a feeding preference for nutrient-rich fine sediments. The sensory structures that are involved in this discrimination have not been described. Recent evidence indicates that this type of selectivity is not restricted to adults since echiuran larvae show similar substrate preferences at the time of settlement (L. Suer, personal communication; see also Pilger 1978).

Risk (1973) stated that the burrow of *Listriolobus pelodes* is a gallery consisting of as many as 4 openings to the surface. This study has shown, however, that the burrows are U-shaped with exactly 2 openings to the surface. U-shaped burrows with only 2 openings have also been described for the mud-dwelling echiurans *Urechis caupo* (Fisher and MacGinitie 1928) and *Echiurus echiurus* (Gislén 1940). *Bonellia viridis*, on the other hand, lives in rock burrows having multiple openings (Schembri and Jaccarini 1978), but these dwellings are formed by the action of *Upogebia deltura*; *B. viridis* is only a secondary resident that makes few, if any, modifications to the burrow system (Schembri and Jaccarini 1978).

The location of the gonad is known only in a couple of echiuran species. Spengel (1879) described the gonad of *Bonellia viridis*, Rolando 1821, as being an area of differentiating peritoneal cells surrounding the posterior part of the ventral blood vessel. More specifically, the gonad covers the blood vessel where it extends from the intestine to the ventral nerve cord and a little farther anteriorly. In *Lissomyema mellita* (Conn 1886) the gonad surrounds a posterior muscle band which "extends from the intestine to the ventral nervous chord." Conn (1886) clearly described the gonad as being in the same

location as in *Listriolobus pelodes* but interpreted the underlying structure as being muscular rather than vascular. The association of *L. pelodes*' gonad with the posterior ventral blood vessel corresponds well with what is known in these 2 other echiuran species. However, the location of the gonad in echiurans which lack a vascular system (e.g., *Urechis caupo*) remains an enigma.

Scant information is available on the reproductive rhythms of echiurans other than *L. pelodes*. From this study and the parenthetical remarks by others on 3 additional echiurans, it is known that gamete production is seasonal in some species, and in at least 1 other species it is continuous. Hiraiwa and Kawamura (1936) mentioned that egg production in *Urechis unicinctus* occurs during winter off Japan. The oogonia of *Ikedosoma gogoshimense* first appear in the coelomic fluid in May and June and differentiation continues into winter (Sawada and Ochi 1962). *Urechis caupo* off southern California, on the other hand, produces gametes continuously (MacGinitie 1935) and contains all oocyte size classes in the coelom simultaneously throughout the year (Gould 1967).

Miller and Epel (1973) attempted to determine the time course of oogenesis in *Urechis caupo* by radioactive labeling and subsequent monitoring of coelomic oocytes. This approach failed because it required that the animals be retained in the laboratory for an extended period and *Urechis caupo* is not able to maintain oogenesis during such a treatment. Das (1976) calculated the rate of ribosome production for different oocyte stages and, considering the total amount of ribosomal material in a fully differentiated *U. caupo* oocyte, predicted that oogenesis continues for 135 days. The value determined for *Listriolobus pelodes* in this study (5–6 months) is considerably longer; the methods used in this study were also cruder than those used by Das. It is not possible to evaluate such differences without more specific information about the process of oogenesis in *L. pelodes*.

Assuming continuous gamete production in *Urechis caupo*, Gould-Somero (1975) reasoned that the frequency of each oocyte size

class is proportional to the relative amount of time an oocyte spends in that particular size range during oogenesis. Her data suggest that the rate of oocyte growth varies during oogenesis. Specifically, the larger oocytes seem to grow faster than the smaller ones. Since gamete production by the gonad of *L. pelodes* may not be a continuous event, the reasoning used by Gould-Somero (1975) cannot be applied here. It can be argued, however, that differential oocyte growth may occur in *L. pelodes*, since a preponderance of small oocytes was present in the coelomic fluid during several months of the study period though there never was a month when large ones prevailed.

The accumulation of ripe oocytes in the storage organs of *L. pelodes* takes place in fall, winter, and part of spring. Spawning, on the other hand, is limited to the spring months. Thus, it is probable that at least the first batch of oocytes produced in the reproductive season remain in the nephridia for a few months before they are spawned. The metabolic requirements of these oocytes may be low since growth is negligible during this phase. From November through March specimens can be obtained routinely which contain large quantities of gametes in the storage organs. This observation is in contrast to the situation in the Sipuncula where gametes are rarely found stored in the nephridia (Rice 1975).

Judging by the conditions of the storage organs, Fisher (1946) noted that a specimen of *L. pelodes* that was collected in June had recently spawned. His observation corresponds with the period defined by the present study. The only other information on echiurans available for comparison concerns *Urechis caupo*. This echiuran is reported to undergo partial or complete spawning in late summer (Ricketts and Calvin 1962) despite the fact that its gamete production is continuous.

In studying the *L. pelodes* population at Santa Barbara, Barnard and Hartman (1959) stated that "mature individuals are those measuring 25 mm or longer." According to their data (Table 6, p. 13), these individuals should weigh about 6 g. Personal observa-

tions of echiurans from the same area (though 13 years later) reveal that the lower weight limit of sexual maturity is closer to 0.8 g.

Fisher (1946) noted that his smallest sexually mature specimen was just 7 mm long. Since individuals of that size usually are contracted as small spheres (Pilger, personal observation), the volume of his specimen probably was about 0.2 ml and weighed about 0.2 g (see Figure 2). Barnard and Hartman's data support this conversion (1959:13, Table 6). Fisher's observation is inconsistent with the findings of this study that sexually mature individuals weigh at least 0.8 g. A possible reason for this difference is that Fisher's specimen probably was one of the "small phase" individuals which had been loaned to him by Hartman (Fisher 1946, pp. 238–239). If this is true, then caution must be exercised in extending the reproductive information in the present study beyond populations of normal-sized individuals.

SUMMARY

1. *Listriolobus pelodes* lives in U-shaped burrows which it fashions in soft muddy bottoms off southern California. The proboscis is a highly extensible structure adapted for feeding on the uppermost layer of sediment around each of the burrow apertures. Some degree of nutritional discrimination may take place. The ability of these echiurans to feed regularly on large areas of the sediment surface implies that the impact of their presence on the trophic structure of the benthic community is great.
2. The gonad of *L. pelodes* surrounds the most posterior portion of the ventral blood vessel. Early in oogenesis clusters of primary oocytes detach from the ovary and differentiate in the coelomic fluid. When an oocyte reaches 40 μm diameter it separates from the cell cluster and completes oogenesis as a single cell. Fully grown oocytes are selectively removed from the coelomic fluid and accumulated in the modified nephridia (storage organs)

until spawning. The oocytes are spawned in late prophase of the first meiotic division but complete their maturation prior to syngamy.

3. Gametes are released by the gonad during most of the year but fully grown oocytes are present only in late fall, winter, and spring. The duration of oogenesis is estimated to be 5–6 months.

4. Spawning takes place over an extended period from late winter through spring and individuals are spawned out by summer.

5. Juvenile recruitment occurs in late winter and spring. Newly settled juveniles become sexually mature when they are 6 months to 1 year old.

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