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Reproduction and Larval Development of *Typosyllis pulchra* (Berkeley & Berkeley) (Polychaeta: Syllidae)[1]

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ABSTRACT: The reproductive biology of *Typosyllis pulchra* from the coast of Washington has been investigated based on observations of animals in the field and stolonization in the laboratory by both field-collected and cultured animals. Like most Syllinae, *T. pulchra* reproduces by stolonization, i.e., each individual produces 3–4 posterior, detachable, gamete-bearing stolons during consecutive 30-day intervals. Although some regenerating segments are incorporated into the stolons, in this species new stolons consist primarily of stock body segments. Reproductive animals occur in the field from late January through July; maximum reproductive activity is between April and June. Long days apparently promote reproduction, but lunar synchronization of spawning could not be demonstrated.

Larval development is described based on light and scanning electron microscopy. Fertilization is external; developing larvae settle within 75 hr. The development of cephalic structures (eyes and antennae) is precocious compared to other Syllinae that have been studied, and the sequence of parapodium formation is unusual.

LITTLE INFORMATION IS AVAILABLE concerning reproduction or larval development of any syllid polychaete; there is almost none for species from the northeastern Pacific. Most reports on western American syllids are limited to descriptions of reproductive individuals and contain little or no additional reproductive data (Pettibone 1954, MacGinitie 1955, Pettibone 1963, Banse 1972). Brooding has been described in the exogonine *Exogone lourei* (Woodin 1974) and the eusylline *Syllides japonica* (Heacox and Schroeder 1978).

Larval development has been investigated in a number of syllids; many of these studies concern brooding species of Exogoninae, Autolytinae, and Eusyllinae. All the Syllinae studied have been European species: *Typosyllis hyalina* (Malaquin 1893), *Syllis amica* (Herpin 1925), *Typosyllis variegata* (Cazaux 1969), and *Typosyllis prolifera* (Franke 1979).

This paper describes reproduction and development in *Typosyllis pulchra*, based on field observations on the coast of Washington and laboratory spawning of collected and cultured animals.

MATERIALS AND METHODS

Collection

Typosyllis pulchra (Berkeley & Berkeley) was collected from the rocky intertidal, near the Slip Point Light Station, Clallam Bay, Washington, within the root–rhizome system of the marine angiosperm *Phyllospadix scouleri*. Every 6–8 weeks, for a period of 18 months, *Phyllospadix* samples were collected, placed in plastic bags, packed on ice, and transported to the laboratory in Pullman, Washington, for sorting. Water temperature was recorded and samples for salinity determination were taken at each

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collection. Samples awaiting sorting were kept in aerated plastic dishpans in artificial seawater (Instant Ocean®, density 1.020, ASW) at 10°C. The syllids were sorted by hand with the aid of a dissection microscope. Animals were identified with Banse and Hobson (1974) and checked against the descriptions of *T. pulchra* provided by Berkeley and Berkeley (1948), Hartman (1968), and Banse (1972).

Maintenance

Ten to fifteen individuals were kept in 4-inch covered fingerbowls with 150 ml ASW and a small amount of sand from the original biotope. Animals were kept either at 8 ± 1°C with a 12L/12D light/dark cycle or at 10 ± 1°C with an 18L/6D light/dark cycle (Hauenschild 1972). Forty watts of indirect fluorescent lighting were used to initiate the light cycle. After the first hour, a step increase in illumination was provided by the addition of 120 watts of direct fluorescent lighting. Light intensity was also decreased in a similar fashion at the onset of the last hour of light to simulate periods of dawn and dusk, respectively (Gidholm 1969). In addition, a 15-watt light bulb was on during the dark cycle of the five consecutive days corresponding to the natural full moon of each month.

Polychaetes in culture have been maintained on a variety of natural and artificial foods (Muller 1962, Goerke 1971, Hauenschild 1972, Dean and Mazurkiewicz 1975). The following foods were offered: frozen spinach (Åkesson 1967); powdered alfalfa (D. Reish, personal communication); frozen *Artemia* (Hauenschild 1972); Tetramin®, a commercial dried fish food (Reish, personal communication); the green alga *Dunaliella* (Dean and Mazurkiewicz 1975); the diatom *Phaeodactylum*; and hyroid polyps (Hamond 1974). Feeding trials were also made with Tetra® squid flakes and the mussel *Mytilus californianus*. The hydroid polyps *Tubularia* and *Garveia* were used in this study because of their abundance in the intertidal zone where *T. pulchra* was collected. All foods with the exception of *Dunaliella* and *Phaeodactylum* were macerated in a tissue grinder and centrifuged before being added to the cultures. Worms were routinely fed once a week, and the water in the bowls was changed 24 hr after feeding.

Worms were determined to be reproductive when gametes were observed in the posterior end or when signs of stolonization (stolon eye spots; swimming setae) were present. Animals showing signs of reproduction within 10 days of collection were considered to have been reproductive in the field. Reproductive individuals were separated out and examined for stolon type, stolon segment number, oocyte size in females, and number of regenerating posterior segments. The larval development was followed by periodically anesthetizing larvae in 7.3 percent $MgCl_2$ and observing with a compound microscope.

Scanning Electron Microscopy

Some larvae were placed on 0.45-μm millipore or 0.1-μm nucleopore filters, covered with another filter, put in a filter holder, treated with 1500 NF[3] units/ml ASW ovine hyaluronidase for 30 min (Atwood, Crawford, and Braybrook 1975) to remove mucus, and fixed in 2.5 percent glutaraldehyde in 0.2 *M* phosphate buffer containing 0.14 *M* NaCl (pH 7.4). The specimens were then rinsed in 0.2 *M* phosphate buffer with 0.3 *M* NaCl (pH 7.4) and postfixed in 2.0 percent OsO_4 in 1.25 percent $NaHCO_3$ (pH 7.5) (Cloney and Florey 1968). Larvae were then dehydrated through increasing concentrations of ethanol, placed in an Omar SPC 900 critical-point device and critical-point dried in CO_2 (Anderson 1951). After coating with gold in a Technics V sputtering device, the specimens were examined with an ETEC Ul Autoscan scanning electron microscope (SEM).

[3]NF = National Formulary.

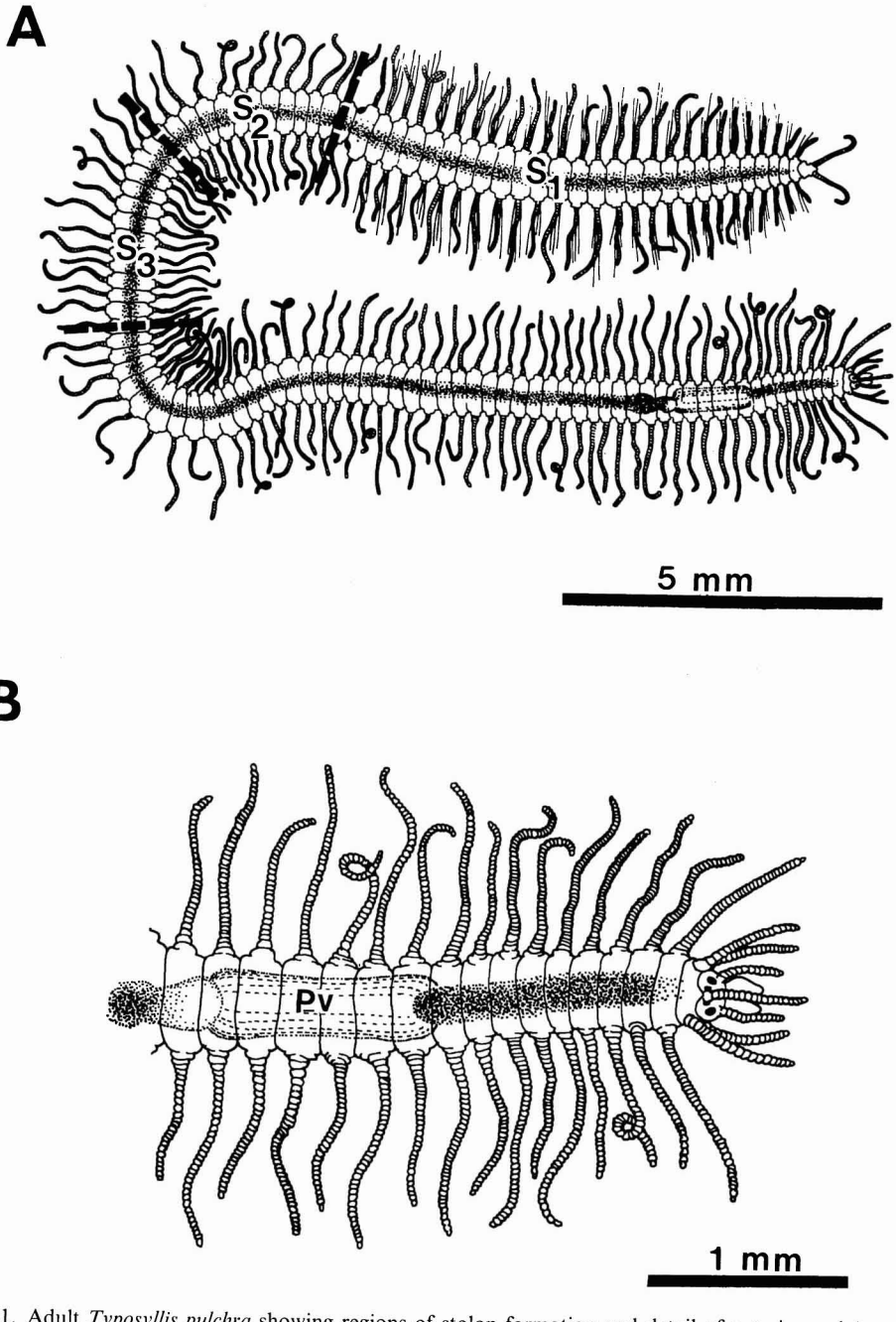

FIGURE 1. Adult *Typosyllis pulchra* showing regions of stolon formation and detail of anterior end (parapodia not shown). *A*, adult *T. pulchra* (S_1, segments involved in forming the first stolon; S_2, segments involved in forming the second stolon; S_3, segments involved in forming the third stolon); *B*, detail of anterior end (Pv, proventriculus).

RESULTS

Description and Life Cycle

Adult *Typosyllis pulchra* have 76–110 setigers and are 15–25 mm long and 0.5 mm wide, excluding parapodia and setae (Figure 1*A*). Although Clallam Bay specimens fit the general descriptions of Berkeley and Berkeley (1948) and Banse (1972), they differ consistently in some characteristics (Figure 1*B*). For instance, the proventriculus begins in setigers 9–11 and extends through 5–7 segments (rarely 8, Figure 1*B*); Banse indicates it is 8 or 9 segments long. The dorsal cirri are slender and alternately long and short. Long cirri on midbody segments have 35–40 annuli, considerably fewer than the 50–70 recorded by Berkeley and Berkeley. Banse (1972) concludes that the "heavily pigmented papilla" of Berkeley and Berkeley is a small but distinct occipital flap. However, in Clallam Bay animals the pigmentation may be almost completely lacking. Living specimens vary from the "chocolate brown" seen by Berkeley and Berkeley through green-brown, bright green, blue-green, and yellowish brown. Such variability occurs even within the laboratory-reared offspring of a single pair of animals.

Adults occur in the field throughout the year, although the percentage of adults and the number of reproductive individuals fluctuate. Between December and August only adult individuals were found in the samples. Reproductive animals were first seen in late January and were found until July. Early in the reproductive season, stolonizing worms comprise 10–20 percent of the collected adults; the percentage gradually increases through the spring until May and June when reproductive animals make up 40–60 percent of a collection. Animals collected after July were never reproductive in the field, and adults collected in August and September showed high mortality when maintained in the laboratory. The number of animals collected, as well as the percentage of adults, declines from late summer through October. The scarcity of worms in the fall is believed to be due to the higher proportion of small, immature animals (less than 50 segments, or 10 mm), many of which were probably overlooked during sorting. Water temperature in the field reached a low of 8°C in December. The water temperature gradually began to increase in early March and reached a high of 12°C in late July and August before beginning its decline. During the peak reproductive period, water temperature was about 10°C.

Stolon Formation

Stolonization can first be recognized by a posterior color change—to blue or purple in females and to white or light pink in males—due to the accumulation of gametes. Stolons consist of 22–30 setigers and have a chaetosyllis head type (Malaquin 1893, Schroeder and Hermans 1975) (Figures 1*A*, 2). The latter consists of a prostomial cleft, two pairs of eyes, a single pair of antennae, and a single pair of tentacular cirri. Laboratory-produced and field-collected stolons are similar in size.

In the laboratory, mature animals reproduce by the sequential production of three or four stolons during consecutive 30-day periods at 10°C. Ten days after the release of the previous stolon, gametes can again be seen in the 10–12 posteriormost segments; these segments will be incorporated into the newly forming stolon. Within 5 days of the first appearance of gametes, two pairs of eye spots form on a segment near the anterior end of the sequence of gamete-bearing segments. The segment bearing the eye spots will become the head of the stolon. Between day 15 and day 25, the stolon changes little externally. Shortly after day 25, bundles of capillary swimming setae erupt from the notopodia of each stolon segment except the head and the 3–4 terminal segments. These bundles of about 20 setae attain their full length (3 mm) within 48 hr. Soon thereafter the stolon commences swimming movements, which are independent of the stock. It eventually breaks free, swims to the surface, and spawns.

Before stolonization is complete, the stock begins to regenerate new posterior segments.

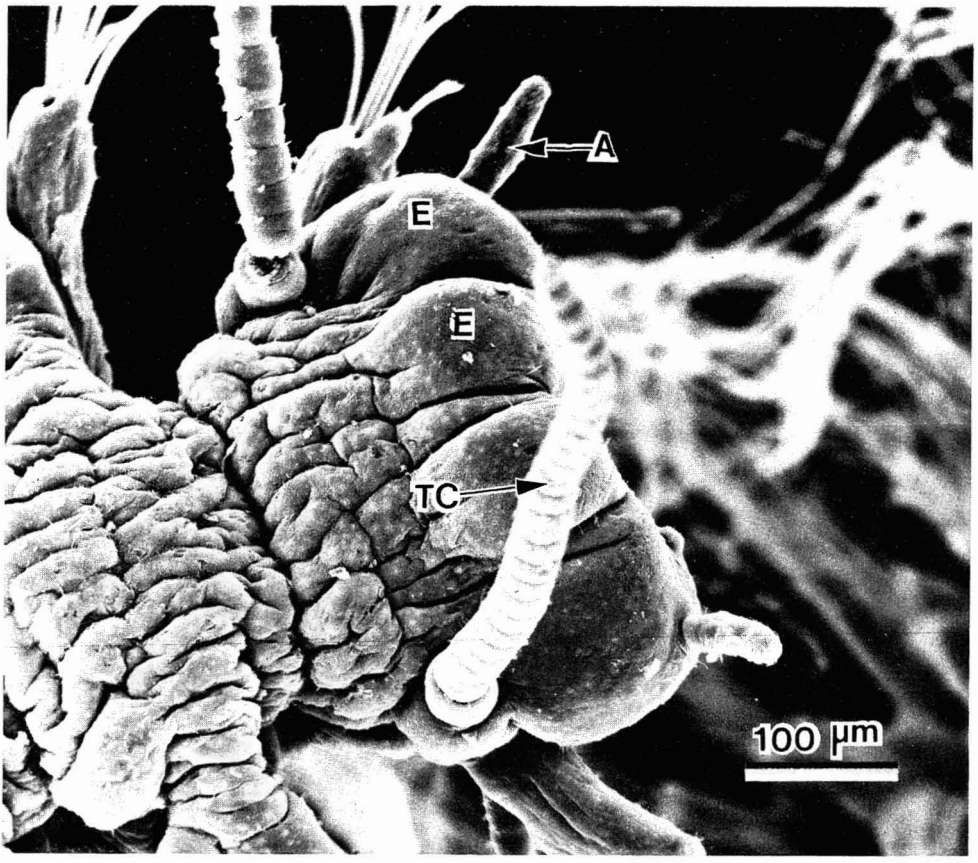

FIGURE 2. Scanning electron micrograph of stolon chaetosyllis head (A, antenna; E, eye; Tc, tentacular cirrus).

Immediately after stolon separation, four or five newly formed segments can be seen at the posterior end of the stock. In all, about ten segments are regenerated. This means the worm must use additional stock segments to form the subsequent stolon (average, 25 ± 3 segments, Figure 1*A*).

Culture Results

Animals that were determined to be reproductive in the field could be kept in their reproductive condition by either the short-day, low-temperature cycle or the long-day, high-temperature cycle. However, the short-day regime neither brought nonreproductive winter animals to maturity nor did it maintian reproductivity in the laboratory cultures. The long-day cycle (18L/6D) is similar to natural light conditions in the field during the late spring peak reproductive period; at 10°C, it proved suitable for raising larvae and maintaining reproductive worms. Nonreproductive adults (determined by size) taken from the field and subjected to these conditions often became reproductive even if collected in the late fall or winter. Once animals had become reproductive, they would remain so for at least two consecutive stolonizations.

The step increase following the initiation of the light seemed to stimulate stolon release. Most stolons were found to separate, swim, and spawn soon after the end of the dawning period, but detailed records were not kept. Although a few stolons would

begin swimming later in the day, none were found to separate and swim during the dusk or dark portions of the cycle.

The artificial lunar cycle produced no recognizable synchronization of stolon release or spawning. Both field-collected and laboratory-reared animals appeared to spawn randomly. This apparent randomness may be an artifact of the relatively small number of animals in the laboratory at any one time. Usually, no more than two or three animals spawned on any one day, and reproduction was evenly spread over the entire month.

Potential food items were placed on the bottom of the culture dishes, and responses were recorded. A positive response was recorded when an animal approached the food, everted its proboscis, and the proventriculus exhibited a pumping movement. The results are summarized in Table 1.

TABLE 1

FOOD AND FEEDING RESPONSE

FOOD	RESPONSE
Dunaliella tertiolecta (Chlorophyta)	−*
Phaeodactylum tricornutum (Diatomacae)	−*
Tubularia sp. (Hydrozoa)	−
Garveia sp. (Hydrozoa)	−
Artemia (adults, frozen) (Crustacea)	+
Mytilus californianus (Bivalvia)	−
Powdered alfalfa	−
Tetramin®	+
Tetra® squid flakes	+
Spinach (frozen)	−

*Although no positive feeding response was observed, some larvae were raised through adulthood on this alga.

A number of animals were raised solely on the two algae; however, these cultures always contained a number of protozoa and occasionally some other small animals that could also have served as food items. After the initial testing, cultures were generally fed on a combination of *Dunaliella*, *Phaeodactylum*, *Artmeia*, and both Tetra® products.

This light–temperature regime and feeding schedule allowed the maintenance of adults and the culture of larvae. Worms were successively raised from larvae through three generations. The third generation did not reproduce as expected, however, and the cultures eventually died out.

Spawning and Fertilization

Spawning takes place near the water surface, usually within the first hour after stolon release. There is no obvious mating behavior such as has been observed in *Autolytus* (Gidholm 1965). Both male and female gametes are shed through nephridiopores at the base of each parapodium. Freshly spawned oocytes float on the surface for about 24 hr if they remain unfertilized. A similar observation was made by Herpin (1925) for *Syllis amica*. Fertilization also appears to take place at the surface, but early cleavage stages are always found on the bottom of the culture bowls. It appears that the eggs sink soon after fertilization.

Cleavage through Gastrulation

Fertilization produces a very thin fertilization membrane. Within 15 min, two polar bodies are released; they remain within the fertilization membrane for a time. No polar bodies were ever observed attached to the embryo after the four-cell stage. Cleavage is spiral, holoblastic, and unequal. Polar lobe formation, reported in some syllids (Schneider 1914, Allen 1964), was never observed. Early blastulae are found as soon as 4 hr after fertilization, spinning on the bottom of the culture dishes. An equatorial band of cilia penetrates the fertilization membrane; hatching does not occur. Gastrulation is by epiboly and occurs within the next 4 hr.

Trochophore

The first trochophore larvae can be observed after 24 hr and are nearly spherical (90×100 μm). They have a long apical tuft, a telotroch composed of several short cilia, and a single pair of eye spots. The eyes are reddish, bean-shaped structures located on the dorso-lateral surface midway between the prototroch and the apical tuft. Just an-

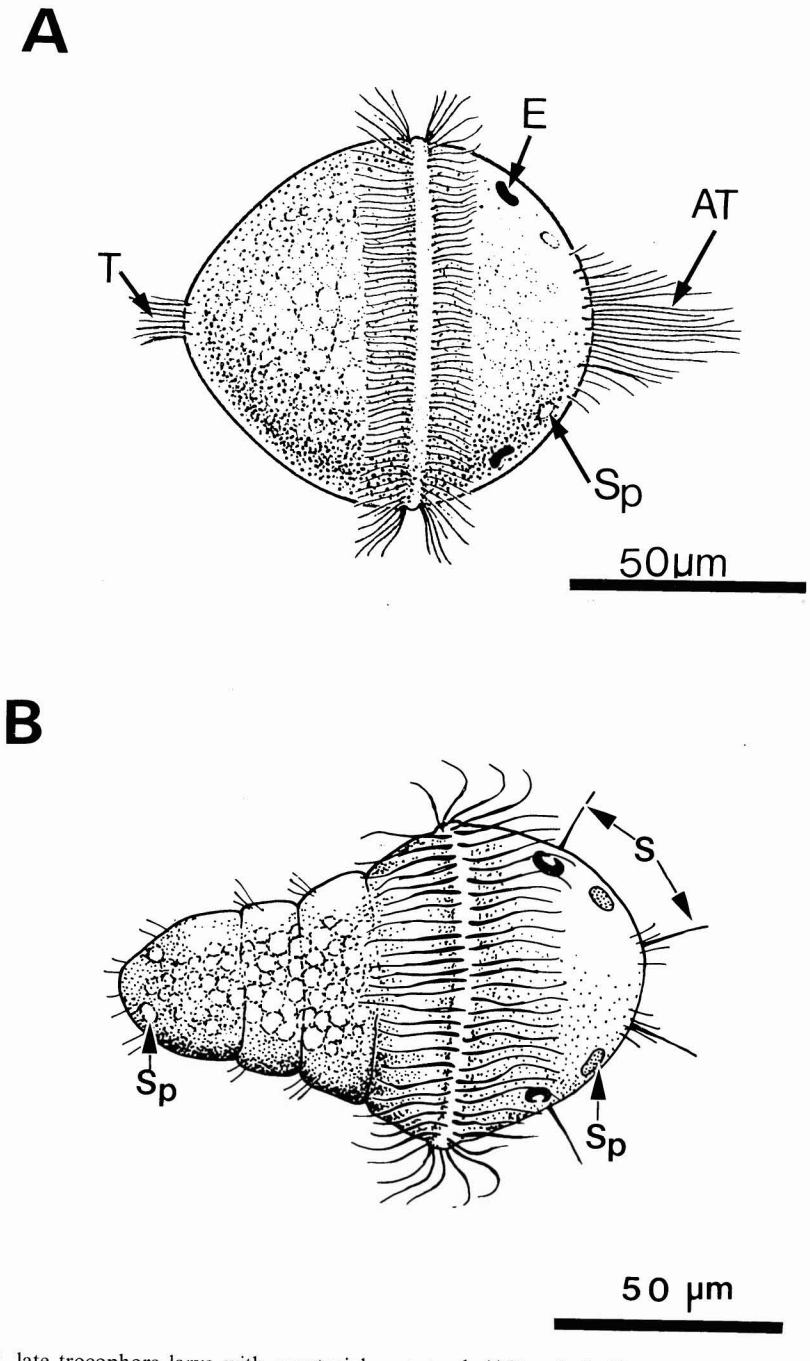

FIGURE 3. *A*, late trocophore larva with equatorial prototroch (AT, apical ciliary tuft; E, eye spot; Sp, light-colored spot; T, telotroch); *B*, metatrochophore larva (S, spinelike protrusion; Sp, light-colored spots).

terior to the eyes is a pair of light-colored spots in the area that eventually gives rise to the lateral antennae (Figure 3*A*).

During the next 24 hr, the larvae elongate slightly and taper at the posterior end, prior to segment formation and initiation of the metatrochophore stage.

Metatrochophore

The slightly more elongate (115 μm) metatrochophore can be recognized by a posterior segment separating the episphere and pygidium. The apical tuft becomes a diffuse band of cilia bordering the anterior end of the episphere. Within this apical band there are also two spinelike projections, which have been regarded as tactile by Herpin (1925). The prototroch is still prominent; it divides the episphere transversely into approximately equal halves. Eventually, the anterior half will develop into the prostomium, while the posterior half of the episphere will become the peristomium. Posteriorly the pygidial segment has some short cilia, two spines, and two light-colored spots. The latter are similar in size and shape to those anterior to the eyes. The pygidial cirri arise near these spots. The mouth is a transverse slitlike opening, surrounded by cilia, and located in the center of the ventral surface of the episphere. At this stage the pharynx and the gut are well developed, but there is no indication that the larvae have begun to feed. A great deal of yolk is still present. The neurotroch is a 20-μm wide ventral band of cilia that extends posteriorly from the mouth to near the end of the pygidium.

The metatrochophore adds a second segment and settles within 75 hr of fertilization, when it is about 130 μm long (Figure 3*B*). The apical cilia are more diffuse, and a second pair of spinelike protrusions projects laterally (one near each eye). Although the prototroch is still present, the gliding motion exhibited by these larvae is due to the neurotroch. Each segment has two or three spines that protrude in a posterolateral direction.

During the subsequent 48 hr, the larvae reach 200 μm in length and change shape. Both these changes are due in part to the narrowing of the episphere, which may be due in part to yolk consumption. The larvae now appear to have a head and neck. The prototroch has disappeared, and only a few cilia project laterally in the region of the eyes. Several additional spines have also appeared in place of the apical cilia, as well as along the lateral portion of the head and neck region. By this time the purplish yolk has disappeared; the larvae are translucent. The pharynx is 60 μm long and occupies most of the head and neck region; movements of this organ indicate that the animal begins feeding at this time. Two budlike caudal cirri are now present on the pygidium.

Setigerous Larvae

The first setigerous larva (Figure 4) is about 300 μm long and appears early in the third week. The first pair of parapodia appears as fleshy lateral outgrowths from the second larval segment following the episphere. Each parapod is supported by a blunt aciculum and contains a single simple notoseta (Figure 5). Soon afterward, one compound seta appears in each parapodium, followed shortly thereafter by a second (Figures 5, 6). Two lateral antennal buds now appear on the head region. In addition, the median antenna is beginning to form between the eyes. Toward the end of the third week the second pair of eyes forms. They are smaller than, and posterior and medial to, the first pair. The caudal cirri are not quite 35 μm long.

By the fourth week another segment with parapodia is added, and both median and lateral antennae elongate. At the end of the fourth week parapodia form on segment one and a fourth segment begins to appear. In the fifth week larvae are 375 μm long and have four well-developed eyes, a median antenna with five or six articles, and lateral antennae with one complete article. The episphere cannot be differentiated into an anterior prostomium and a posterior peristomium. The peristomium forms in the neck

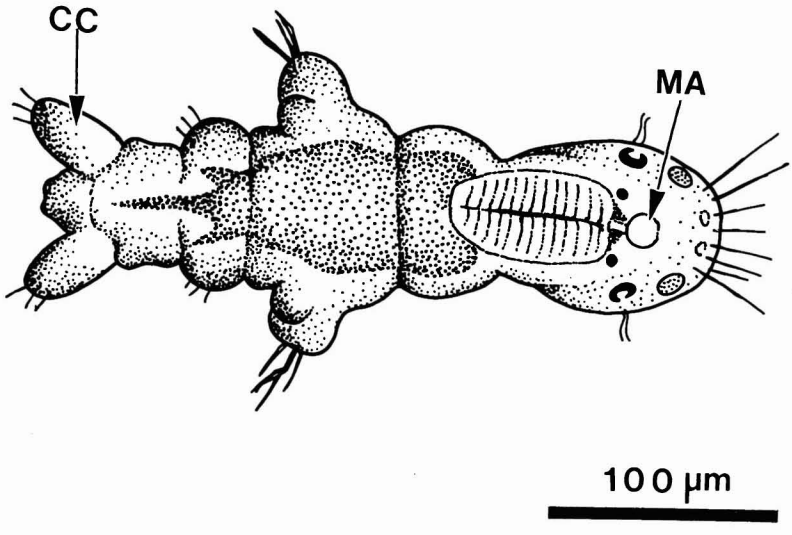

FIGURE 4. One setiger larva (CC, caudal cirrus; MA, median antenna).

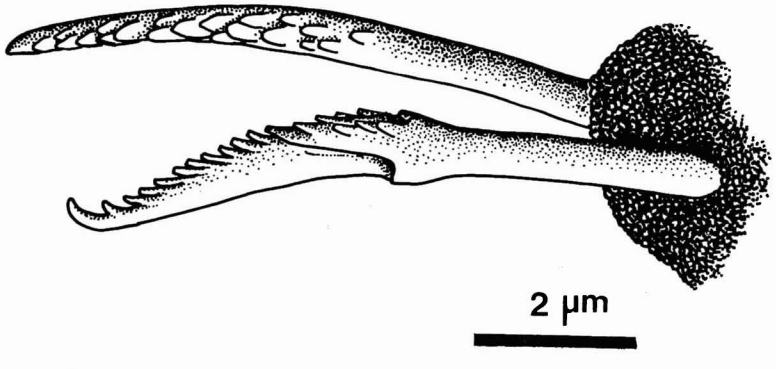

FIGURE 5. Illustration of larval setae on parapod of a one setiger larva.

region and becomes a presetigerous segment with a pair of tentacular cirri. The next three segments have well-developed parapodia (although those of segment one are smaller) and setae, and the better-developed parapodia have rudiments of dorsal cirri. Segment four is beginning parapodium formation, but setae are absent. The caudal cirri include two articles (Figure 7).

By the eighth week the larvae consists of 6–10 setigers and begin to resemble adults. The more anterior setigers are well developed and their dorsal cirri have up to ten articles. The median antenna has eight or ten articles, and the lateral antennae have up to six. A second pair of tentacular cirri has formed on the peristomium, and the first has two to three articles. The prostomium has developed small palps. Growth proceeds by the addition of segments at the posterior until the adult number of 80–100 segments is reached in 6–9 months, at which time animals become sexually mature.

DISCUSSION

Reproduction

Correlation of field observations and laboratory cultures makes possible the prediction

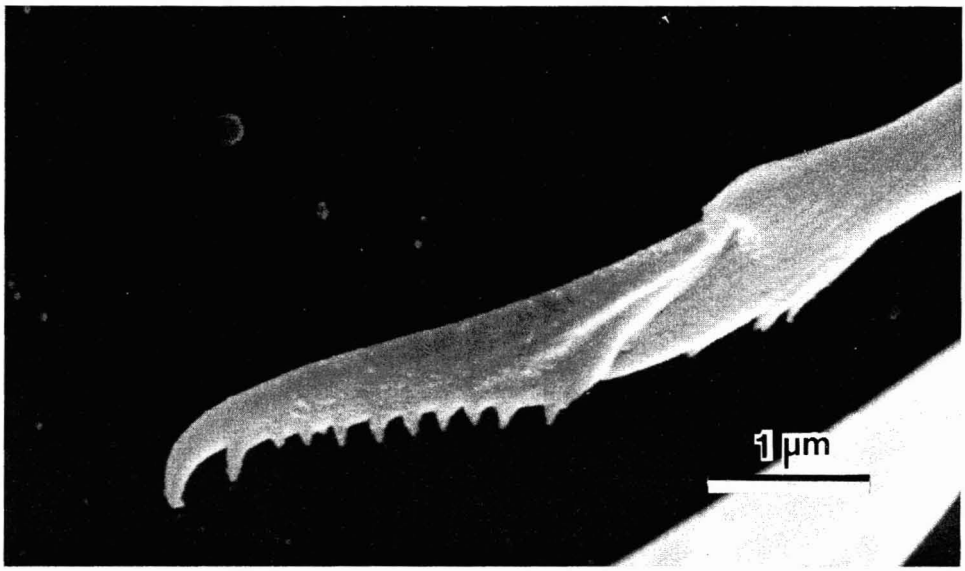

FIGURE 6. Scanning electron micrograph of larval compound seta.

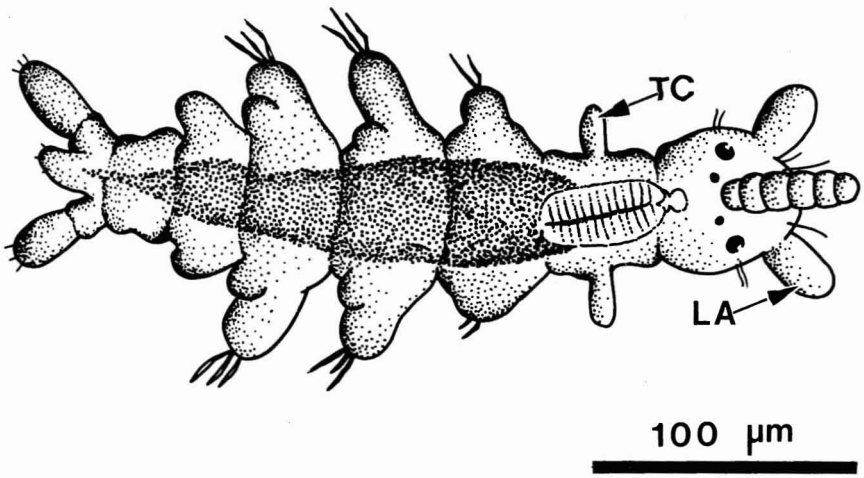

FIGURE 7. Three-setiger larva (LA, lateral antenna; TC, tentacular cirrus).

of an annual history for *Typosyllis pulchra*. Most larvae are spawned in the spring and, after a short period of swimming, settle, metamorphose, and develop into adults during the subsequent 8 months. Once maturity is reached, the adult produces stolons during three or four consecutive 30-day periods. After the final spawning, the adults die.

Although a number of polychaetes have been reported to breed all year (Schroeder and Hermans 1975), most have a distinct reproductive season. Synchronization of reproduction within this short reproductive season has been correlated with a number of environmental factors, including a spring plankton bloom (Thorson 1946, Barnes 1963), temperature (Orton 1920, Okada 1941, Dales 1950, Bhaud 1967, 1972), the

lunar cycle (Clark and Hess 1940, Korringa 1947, 1957, Hauenschild 1960, Hauenschild, Fischer, and Hoffman 1968), and salinity (Aiyar 1931, 1933, Smith 1964, Åkesson 1970).

Temperature has been shown to influence maturation in several polychaetes. Durchon (1959) has shown that stolonization and gametogenesis in *Syllis amica* can be induced if worms are maintained for a month at temperatures higher than those in the field. Higher laboratory temperatures have also been shown to accelerate maturation in *Glycera dibranchiata* (Simpson 1962) and *Hydroides dianthus* (Turner and Hanks 1960, Leone 1970). The effects of day length are still virtually unknown. Sarvala (1971) indicates that spawning of *Antinoella sarsi* at different localities corresponds to the breakup of arctic ice, which varies light and temperature. However, Sarvala feels that light intensity or day length is more important than temperature. Garwood (unpublished, from Olive and Clark 1978) has found that moderately long days accelerate the growth of vitellogenic oocytes while long days inhibit vitellogenesis in *Harmothoë imbricata*. Early oocytes seem not to be affected. Franke (1979) has shown that both day length and temperature affect stolon production in *Typosyllis prolifera*. The largest number of stolons is produced under conditions of high temperature (20°C) and long (18-hr) days. Decreasing temperature (to 12°C) or shortening day length (to 10 hr) reduces stolon formation about 50 percent; low temperatures and short days inhibit reproduction.

Temperature and day length were not changed independently for *Typosyllis pulchra*. However, winter animals would become reproductive when maintained at higher temperature (10°C) and long days (16 hr). Stolons and gametes can first be seen in the field population during late January, before water temperature begins to rise. Peak reproduction is not reached until both day length and temperature have increased. This situation is similar to that of *T. prolifera* (Franke 1979). Increasing day length may be responsible for initiating the reproductive season, but higher temperature may be needed to support peak reproduction. This response to increasing day length appears to be very sensitive; animals respond to very slight changes in day length.

While temperature and day length may regulate breeding season, the proximate causes for synchronized spawning are thought to be, in some cases, lunar or tidal cycles. The laboratory population of *Typosyllis pulchra* released stolons and spawned in the early morning hours of the artificial light cycle. Changes in light intensity, which occur at dawn and dusk, induced swimming in stolons of *Autolytus edwardsi* (Gidholm 1969). No response to the change in light intensity at dusk was observed in *T. pulchra*; most started swimming at dawn. Changes in light intensity may also be implicated in the swarming of the epigamous eusylline syllids *Pionosyllis lamelligera* and *Eusyllis blomstrandi*. These swarms seemed to be influenced by the presence of direct sunlight; they disappeared when the sun was obscured by a cloud (Herpin 1925).

Typosyllis prolifera can be entrained to an artificial lunar cycle. Animals spawned throughout the month, but the greatest number of worms spawned just prior to the artificial full moon (Franke 1979). However, no more than 10 percent of this laboratory population spawned on a given day. If a similar response were given by *T. pulchra*, it may have gone unobserved because of the small number of animals kept in the laboratory. Lunar synchronization of spawning thus cannot be discounted.

Larval Development

Larval development in *Typosyllis pulchra* is similar to that in other syllids, especially the Syllinae (Malaquin 1893, Herpin 1925, Cazaux 1969, Franke 1979). The differences relate primarily to the timing and duration of larval stages, the precocious development of cephalic structures, and the sequence of parapodium formation. Differences in the timing of larval development are probably related to the temperatures at which larvae were raised.

Although the larvae of the *Typosyllis pulchra* swim, it is not known whether the larvae actually contribute to the plankton. No syllid larva is known to have an extended phase of pelagic development. Extensive sampling by Thorson (1946) and Bhaud (1972) has shown few syllids to be present in the plankton.

The development of cilia, which precedes the swimming larval phase, appears to be related to the reproductive strategy of the subfamily. All Syllinae and most Eusyllinae fertilize eggs in the sea and have a relatively long swimming phase; larvae develop cilia early during development. In *Typosyllis pulchra*, cilia develop during the blastula stage; other Syllinae develop cilia at least prior to the trochophore stage (Malaquin 1893, Herpin 1925, Cazaux 1969). The Exogoninae and some Eusyllinae [e.g., *Parapionosyllis gestans* (Cazaux 1969)], which brood their young until some setigerous segments form, have neither cilia nor a swimming phase. In contrast, *T. prolifera* larvae are ciliated but lack a swimming phase; early development takes place within an extraembryonic membrane (Franke 1979). Allen (1964) indicates that the precocious development of larval cilia in *Autolytus fasciatus*, when compared to other autolytids, represents a probable swimming stage.

Larval cilia also seem to be responsible for the formation of certain larval structures. Spinelike processes, found in the apical ciliary band of *Typosyllis pulchra* and many other syllids (Malaquin 1893, Herpin 1925, Okada 1930, Dales 1950, Allen 1964, Cazaux 1969), are not found in the exogonines. Allen (1964) indicates that these structures in *Autolytus fasciatus* are tufts of cilia.

Development of head structures in *Typosyllis pulchra* is somewhat precocious. The median antenna, the lateral antennae, and the second pair of eyes differentiate in the first setigerous larva. These structures are already well developed by the three- and four-setiger stage, when they are first appearing in other Syllinae (Cazaux 1969).

Although segments in the presetigerous metatrochophore larva apparently develop in a normal sequence, in *Typosyllis pulchra* the parapodia develop in an unusual sequence. As with *Syllis amica* (Herpin 1925) and *T. variegata* (Cazaux 1969), the first pair of parapodia forms on the second segment behind the episphere. In *T. pulchra* this happens prior to external signs of peristomium formation. This is different from *T. prolifera*, where Franke (1979) shows the first setigerous larva with parapodia on the first postepisphere segment. In *T. pulchra* an additional segment forms and develops parapodia before parapodia develop in the first postepisphere segment. Neither Herpin nor Cazaux make clear the fate of the first postepisphere segment. In *S. amica* and *T. variegata* this larval segment may give rise to the peristomium. Cazaux clearly shows the best-developed parapodia immediately posterior to the peristomial segment in older setigerous larvae. The episphere of *T. pulchra* gives rise to both prostomium and peristomium, while all the setigerous segments originate from the former hyposphere. This indicates a fundamental difference between the peristomium and the setigerous segments.

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