Reference: *Biol. Bull.*, **149**: 109–127. (August, 1975)

REPRODUCTION AND LARVAL DEVELOPMENT OF *PSEUDOPOLYDORA PAUCIBRANCHIATA* (OKUDA) AND *PSEUDOPOLYDORA KEMPI* (SOUTHERN) (POLYCHAETA: SPIONIDAE)[1]

JAMES A. BLAKE AND KEITH H. WOODWICK

Pacific Marine Station, University of the Pacific, Dillon Beach, California 94929, and Biology Department, California State University, Fresno, Fresno, California 93740

Pseudopolydora paucibranchiata was described originally by Okuda (1937) from Onomichi, Hiroshima Prefecture, Japan. Since this find in the western Pacific it has been reported a number of times from the eastern Pacific. The earliest eastern Pacific report was as *Polydora* (?) n. sp. from Los Angeles-Long Beach Harbors, California (Los Angeles R.W.P.C.B., 1952). *Pseudopolydora paucibranchiata* was then identified by Reish (1954, 1955, 1959a, 1961a) and Barnard (1958) in surveys of pollution-related organisms in Los Angeles-Long Beach Harbor. Reish reported the species from Newport Bay (1959b) and from Alamitos Bay (1961b, 1963) in California. The species was overlooked, however, by Hartman (1969).

Pseudopolydora kempi was described by Southern (1921) from a brackish water lake in India. The original description was supplemented by Okuda (1937) who found the species in Japan. Imajima and Hartman (1964) designated the Japanese form as a new subspecies, *P. kempi japonica* and regarded the size, length of the caruncle, and number of branchial pairs as being characters of sufficient difference to warrant subspecific designation. The species was first reported from California by Blake (1966) and Reish and Barnard (1967) from Morro Bay. Light (1969) named a new subspecies, *P. kempi californica*, based on three specimens taken near Bolinas. A major distinction of *P. kempi californica* from *P. kempi japonica* was considered to be the absence of a nuchal tentacle in the former. Light also figured a rather unusual pygidium.

Pseudopolydora paucibranchiata and *P. kempi* are both common in sandy-mud sediments in bays and estuaries of central and northern California. The authors have collected *P. paucibranchiata* at Santa Barbara, Elkhorn Slough and Tomales Bay. *Pseudopolydora kempi* was found on mud flats in Morro Bay and was common at Lawson's Landing and Walker Creek in Tomales Bay where it occurred on sand and mud flats.

This paper describes the reproduction and larval development of *P. paucibranchiata* and *P. kempi*, with comments on developmental patterns of *P. antennata* Claparède and *P. pulchra* Carazzi. Some additional information on natural history is also provided. Systematics of *P. kempi* is reviewed in light of larval adult morphology, and a possible route of species introduction from Japan is suggested.

[1] This research was supported in part by N.S.F. Grant GB-1264 to Keith H. Woodwick and N.S.F. Grant GA-30900 (Oceanography Section) to James A. Blake. Contribution Number 46 from the Pacific Marine Station, Dillon Beach, California.

Methods and Materials

In the Tomales Bay studies, tubes containing adult worms were collected from sediments at Lawson's Flat and from the Walker Creek Delta. Tubes were opened and egg capsules were removed and examined under the dissecting microscope in the laboratory at the Pacific Marine Station. The stage of development of larvae within the capsules was determined and larvae were freed from the capsules for study.

Plankton samples were taken from the dock at Lawson's Landing, located near the mouth of Tomales Bay. During 1971–72 (September–August) samples were taken each week just before high tide. Polychaete larvae were removed from the sample and sorted to species.

Larvae were cultured in filtered sea water in Stender dishes. Water was changed every two days. Pure cultures of *Dunaliella tertiolecta* and *Phaeodactylum tricornutum* were fed to the larvae. Constant temperatures were maintained in modified refrigerators and beverage coolers. Temperatures unless otherwise stated were at 17° C.

Worms collected by the second author at Morro Bay and Elkhorn Slough were transported to California State University, Fresno, where they were sorted and maintained in an air conditioned laboratory at 21° C. Larvae were removed from egg capsules, placed in culture dishes and observed. Larvae were fed a dried *Chlorella* powder.

It was decided to combine information and prepare a single paper from the two studies. Initial observations on larvae were compared and differences noted and discussed. For the most part, observed differences proved to be matters of interpretation and not actual differences due to studying different populations. Possible discrepancies were checked against actual specimens. In this manner we believe an accurate picture of larval morphology has been constructed.

Both authors used Zeiss optics with bright field and phase contrast. Nomarski phase interference was available to the first author. Line drawings were made from an initial observation and subsequently compared with other individuals at the same stage of development.

Pseudopolydora paucibranchiata (Okuda)

Reproduction

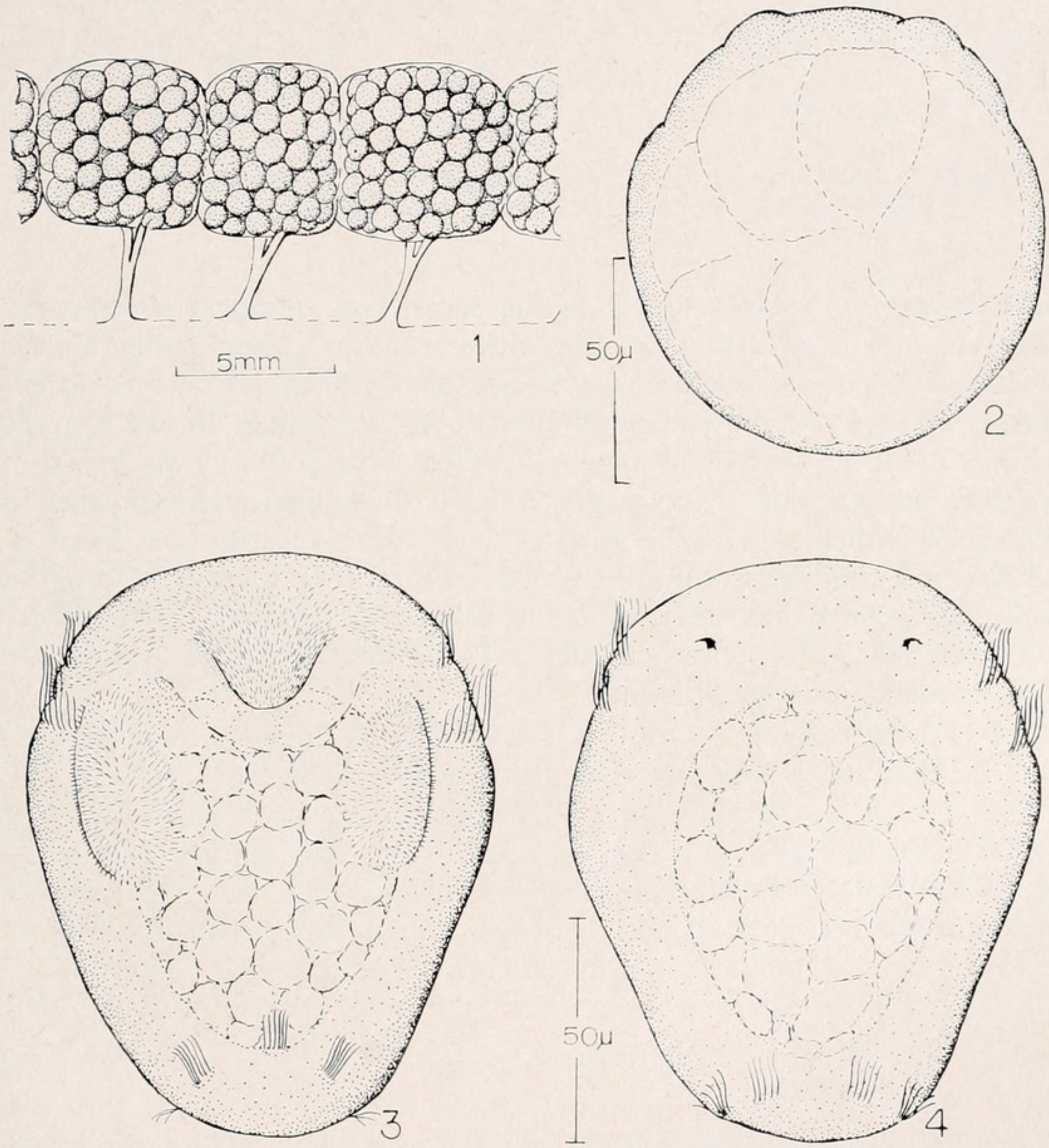
Although a year-round population study was not attempted, sexually mature adults were found in February and March (Elkhorn Slough) and from February to July (Tomales Bay). Egg capsules, however, have been taken in every month of the year in Tomales Bay. Pelagic larvae have been identified in Tomales Bay in each month except for January and February. The highest numbers of *P. paucibranchiata* planktonic larvae were encountered from July through October. Considering that larvae and egg capsules occur throughout most of the year, paucity of mature adults is undoubtedly an artifact of limited benthic collecting.

One mature male of about 45 setigers had testes and sperm present from setiger 24 through setiger 37. Another specimen with 60 setigers measured 12.0 mm, had branchiae on setigers 7–21, ripe gametes in setigers 21–45 and immature testes in setigers 46–60. A female of 42 setigers had branchiae on 7–16 and oocytes in setigers 15–30.

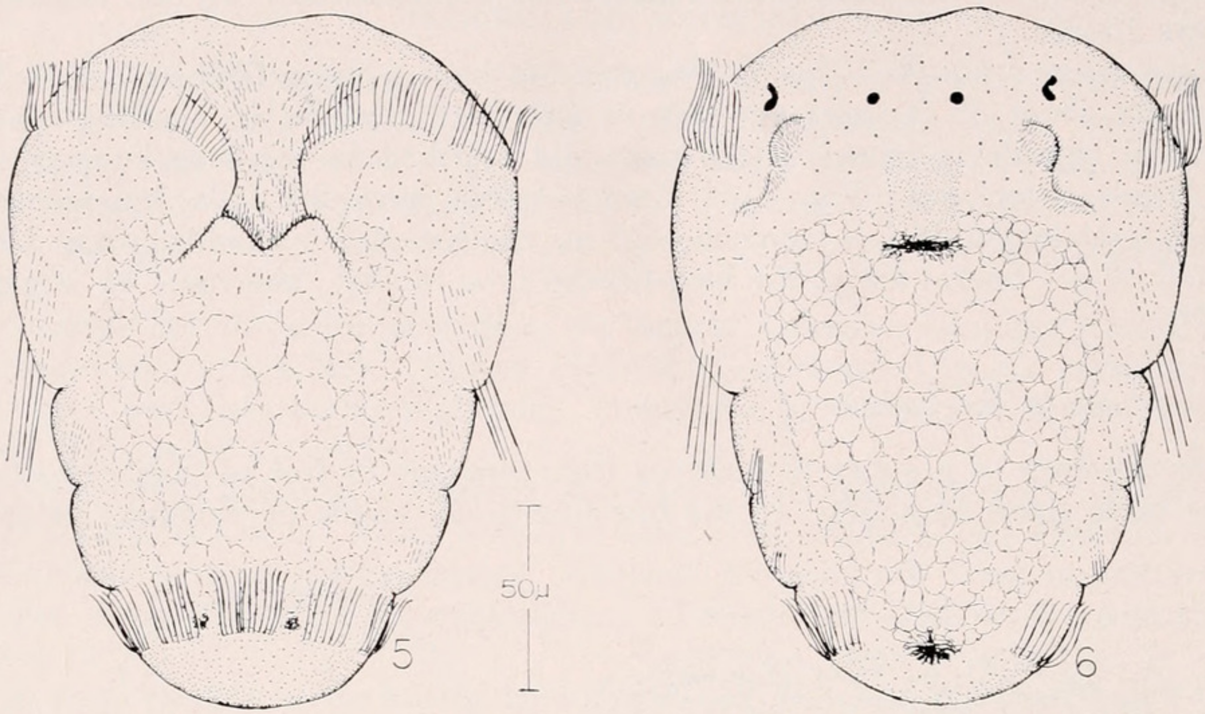
Eggs range from 96–105 μ in diameter but have a mean diameter of 96.2 μ. There are about 35–50 eggs per capsule and 7–10 capsules in a string. Each individual capsule is joined to the next and attached to the tube by two thin cytoplasmic extensions (Fig. 1). Mature sperm have the following measurements; total length 56.1 μ, acrosome 2.1 μ, nucleus 10.8 μ, middle piece 3.2 μ, and tail 40 μ. Sperm are of the long-headed type termed "aberrant" by Franzen (1956).

Development in the capsule

Development of a series of embryos from cleavage to free moving pre-setiger larvae takes about 24 hours. In the first five to six hours, development proceeds



FIGURES 1–4. *Pseudopolydora paucibranchiata:* 1) egg capsules; 2) early undifferentiated embryo removed from capsule; 3) pre-setiger larva in ventral view; 4) pre-setiger larva in dorsal view.

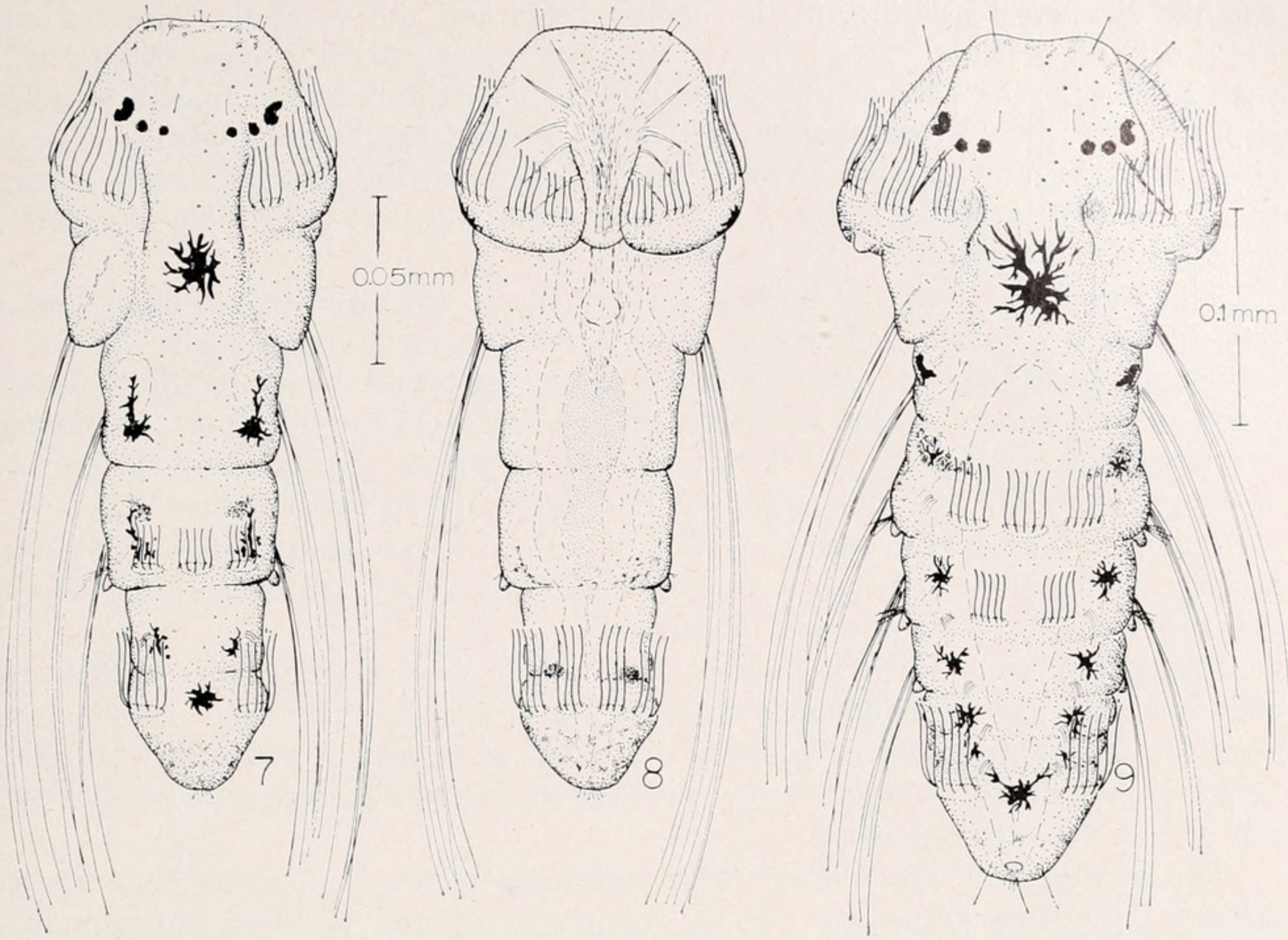


FIGURES 5-6. *Pseudopolydora paucibranchiata:* 5) early 3-setiger larva in ventral view; 6) early 3-setiger larva in dorsal view.

to a ciliated larva that rotates slowly in the sac. The youngest embryo removed from a capsule measured 102 μ at the widest point. Large yolky macromeres surrounded by micromeres are the only noticeable features. There is no evidence of ciliation (Fig. 2). At the end of 24 hours, the pre-setiger larvae are 130 μ in length (Figs. 3–4). The central region is filled with yolk. Two broad ventral ciliated patches are present. The prototroch has developed and is formed of two ciliated bands on either side of the anterior end. The anteriormost band is transitory but the posterior band continues to develop and is retained throughout the larval life. The mouth has developed and is heavily ciliated. The telotroch is a ring of seven isolated patches of cilia. There are two eyes located dorsally. There is no evidence of segmentation.

EARLY 3-SETIGER LARVAE (*Figs. 5–6*). Another 24 hours is required for development of the first three setigerous segments when the larvae measure 190 μ in length. The central yolk mass is prominent but the larvae have feeble swimming abilities when released from the egg capsules. The two ventral ciliated patches are gone. The prototroch has continued to develop and now ventrally merges with the cilia of the vestibule which has deepened. A broad neurotroch is forming posterior to the mouth. Cilia of the telotroch have lengthened. There is a dorsal gap in the telotroch. Four eyes are present; the inner pair is rounded; while the lateral pair is cup-shaped. Two ciliated areas on either side of the head represent presumptive nuchal ciliation.

There are two dorsal median chromatophores. One is located at about the level of setiger 1, while the second is on the anal segment. Two small patches of iridescent pigment occur ventrally on the anal segment. Dark pigment in the gullet is visible in dorsal view.



FIGURES 7–9. *Pseudopolydora paucibranchiata:* 7) pelagic 3-setiger larva in dorsal view; 8) pelagic 3-setiger larva in ventral view, posterior setae omitted; 9) pelagic 5-setiger larva in dorsal view.

Development in the plankton

Larvae emerge from the capsule with three fully developed setigers. Upon release from the capsule, larvae swim rapidly toward the surface and a light source, demonstrating a strong photopositive response. Soon their movement is more random with returns to the bottom of the culture dish to sweep it with their vestibule though the gut is as yet not complete. As they touch the bottom they flex their bodies and extend their setae, especially those of setiger 1.

PELAGIC 3-SETIGER LARVAE (*Figs. 7–8*). The hatching 3-setiger larvae range from 245–272 μ in length with a mean of 250 μ. The head is the widest part of the larva at 121 μ, with setiger 1 intermediate in width (95 μ), and the remainder of the trunk narrow (68 μ). The prostomium is definite in form only at the anterior end where it is broad with a slight medial indentation. The peristomium flares laterally and the lateral lips turn ventrally to the developing vestibule which although heavily ciliated has not opened to the yolk of the central intestine. The posterior end of the intestine is still separated from the anal tube of the pygidium. The anal tube is heavily ciliated. Later the vestibule and anal canal open to the yolky intestine and the feeding process moves food into and through the gut.

On the dorsal surface of the head there is a medial crescent of four small round eyes and an anterolateral pair of cup-shaped eyes. The prototroch is made up of five patches of cilia on each half of the head with the longest cilia in the lateral cells and the shortest bordering on the nuchal ridge and the vestibule. Nuchal cilia are short and difficult to see. The telotroch is formed of six groups of long cilia, with a dorsal gap. Stiff tactile cilia are present on the prostomium and posterior end. Nototrochs first develop on setiger 3. Lateral bundles of grasping cilia are also present. A neurotroch extends posteriorly from the ciliated mouth opening to the posterior border of setiger 1 and in some specimens to the middle of setiger 2. There is no ciliated pit.

The pigmented areas all appear dark to black with transmitted light, but in reflected light separate yellow and black areas can be differentiated. A pair of yellow iridescent pigment spots (reflected light) are found dorsolaterally on setiger 3 and ventromedially on the anal segment; paired spots are found on the extreme lateral surface of setiger 2 and dorsolateral on setiger 3. Spots occur on the sides of the peristomium. Granular rust-colored pigment is found on setiger 2.

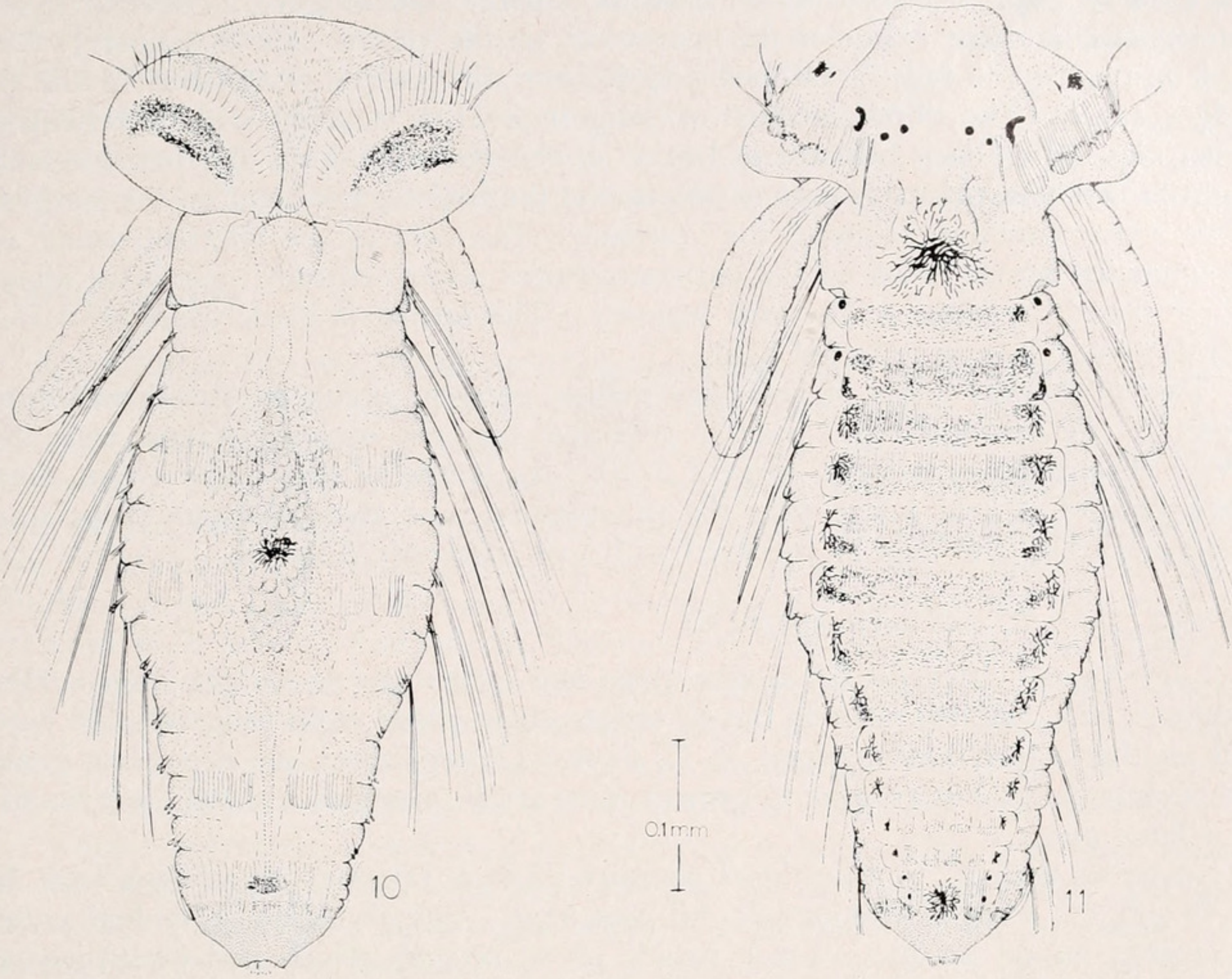
The larval setae are serrate. Those of setiger 1 extend beyond the pygidium and are about 200 μ in length. In setigers 2 and 3 they are successively shorter but still reach to the pygidium or beyond.

Pelagic 5 to 6-setiger larvae (*Fig. 9*). A five-setiger larva with two additional segments developing is about 375 μ in length. The head is wider than the body, measuring 163 μ, while at the level of setiger 3 the width is 100 μ. Setiger 1 is noticeably narrower than the head and from that setiger the body tapers gently to a rounded pygidium.

The prostomium has definite form anteriorly where it is wider than its less distinct tapered posterior end which reaches to setiger 1. The prostomium is gently notched anteriorly and is stippled with brown pigment. The peristomium flares laterally, due to elaboration of the lips of the vestibule. Palps are short; their development begins at about the 5-setiger stage. There are three pairs of eyes organized into two posteromedial pairs nearly in line and round in shape. An anterolateral pair is cup-shaped. Cilia of the prototroch are well-developed and very active. There is also a pair of stiff tactile cilia on the leading edge of the prostomium. The telotroch is made up of long active cilia forming a dorsally incomplete ring of six separate groups of cilia.

Nototrochs first appear on setiger 3 and continue on succeeding setigers. Grasping cilia occur on setigers 3–7. Gastrotrochs are found on setiger 5. The posterior end is stippled with brown pigment like the prostomium and bears three tactile cilia, two lateral and one medial. In addition to reddish-brown pigment on the anterior and posterior ends the other two types of larval pigment are also represented. Reflective yellow pigment is found in small rounded spots on the anterodorsal surface of the lateral oral flare of the peristomium and dorsolaterally on setiger 3 and as paired spots on the pygidium. Black pigment is represented dorsomedially by a large dendritic chromatophore on setiger 1 and a smaller one on the anterior margin of the anal segment. The black pigment also occurs in paired small black patches on the posterior margin of the peristomium and paired dorsolaterally on segments 2–6 and on successive segments as they develop. The gut has a yellow-green color due to ingested food, especially in the anterior part of the intestine.

Setal sacs of setiger 1 are large and the larval setae extend to near the posterior end. Setae of setiger 2 reach to the anal segment and each succeeding



FIGURES 10–11. *Pseudopolydora paucibranchiata:* 10) pelagic 13-setiger larva in ventral view: 11) pelagic 13-setiger larva in dorsal view.

segment has shorter setae. Notopodial lobes are distinguishable on setigers 3, 4 and 5. Stiff sensory cilia are associated with the lobes.

Larvae swim near the surface of the water and edge of the dish but regularly move to the bottom. There they maneuver in loop-the-loop fashion scraping their oral area along the bottom in an effective feeding activity. They tend to swim with posterior end bent down and the long larval setae angled upward.

Larvae with eight setigers remain near the bottom with greater regularity and they also often swim ventral side up.

PELAGIC 13-SETIGER LARVAE (*Figs. 10–11*). A 13-setiger larva measures 640 μ in length and is fusiform. The head width is greatly increased by expansion of the lateral lips of the vestibule. Palps arise from the dorsolateral region of the peristomium. Each palp has a ventral ciliated groove. The six eyes are similar in arrangement to those of the 6-setiger stage. A nuchal ridge is present with areas of rapidly beating cilia on either side. The prototroch is well-developed with several long tactile cilia emerging from various locations. Nototrochs begin on setiger 3 and continue on posterior setigers. Setiger 3 has four patches, setigers 4–8 have six patches and setigers thereafter have four again. Gastrotrochs occur on setigers 3, 5, 7, and 11. Those on setiger 3 are small and often lost at this stage. There are four patches on setiger 3 and six on 5, 7, and 11. The telotroch, which is composed of several patches of cilia, encircles the anal segment, but has a dorsal gap. The neurotroch extends halfway into setiger 1. Several small patches of cilia occur lateral to the neurotroch on the ventral side of setiger 1.

The pigment is fully developed and follows the pattern established in the 6-setiger stage. The dorsal surface of setigers 2–11 is covered with a reticulate green pigment. Black pigment is heavy on the ventral side of the peristomium. Light brown, non-reflective pigment occurs on the anal segment and on the margins of the peristomium and lips of the vestibule. The cilia of the telotroch occur in unpigmented areas. Two medial chromatophores occur ventrally; one is on about setiger 6 and the other on the anal segment. The former is black while the latter is iridescent yellow in reflected light.

Two prominent areas of reflective yellow pigment occur on the dorsolateral aspect of the peristomium. Similar reflective pigment occurs dorsally with the lateral chromatophores from setigers 3–10. As larvae of this stage swim, their posterior end is held lower than the prostomium, and their elongate palps trail posteroventrally and may be recurved with tips anteriorly directed.

Settling, growth, and metamorphosis

Larvae settle after the 13-setiger stage and before the 18-setiger stage. One specimen which settled prior to the 17-setiger stage added eight setigers in 15 days and another added nine setigers in 37 days. Growth rates are dependent upon temperature. Studies relative to growth rates are in progress and will be reported in a later paper.

Juveniles with 23 to 26 setigers measured 2.8 to 3.0 mm. Specimens with 46 to 49 setigers were approximately 5.0 mm long. The youngest individual noted to possess sexual products was a female of 42 setigers which had branchiae on setigers 7–16 and oocytes in setigers 15–30. The largest individual reared beyond settling was 12.0 mm in length and 60 setigerous segments. This specimen had branchiae on setigers 7–21 and mature gametes in setigers 21–45.

Metamorphosis is accompanied by loss of larval setae, pigment and most ciliary bands. The head becomes elongated and the palps are directed forward; they grow rapidly and acquire regularly spaced pigment spots along their length. The spots are conspicuous and appear yellow by reflected light. They are largest distally and decrease in size towards base. As the juveniles grow there is a regular increase in the number of spots on the palps as well as an increase in the number of branchiae.

Table I

Relationship of palpal pigment spots and number of branchial pairs to segments in Pseudopolydora paucibranchiata *adults.*

Number of segments	Number of pigment spots on palps	Setigers with branchiae
18	1	7–9
22	3	7–10
23	5	7–11
27	8	7–12
42	10	7–16
49	12	7–18

By counting the number of palpal pigment spots and the number of gills it is possible to estimate the size of the worm. Since the palps and the anterior end of the animal regularly protrude from the tubes which they occupy one can make counts without having to remove the worm from the tube and, thus, alter its behavior pattern. It is also possible to determine more closely the size of incomplete worms by utilizing the palp pigment and/or branchial counts (see Table I).

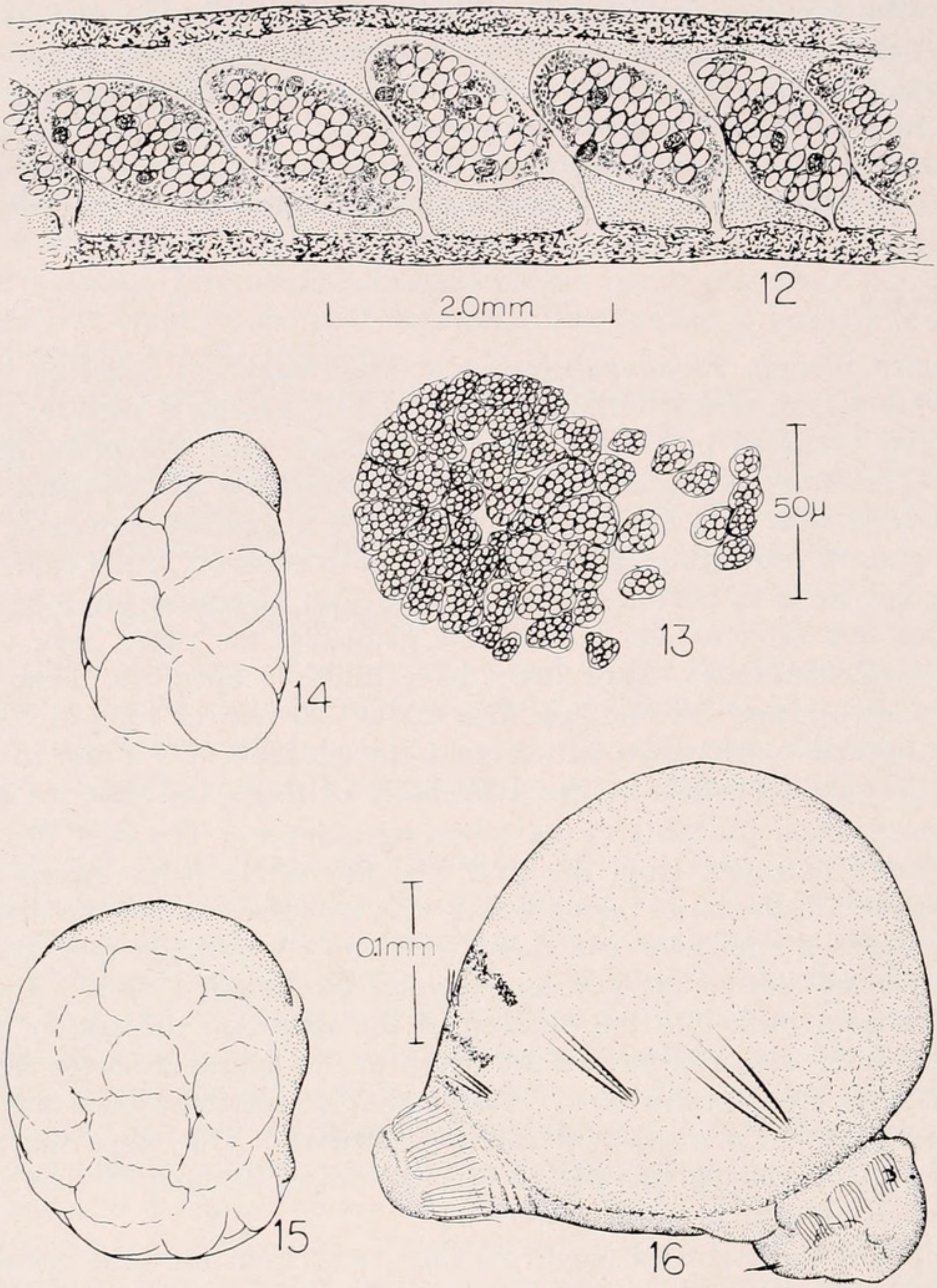
Natural history

In Elkhorn Slough, *Pseudopolydora paucibranchiata* was collected in association with *Phoronopsis viridis* Hilton and *Streblospio benedicti* Webster in a sandy habitat. They occurred in a zone lower intertidally than *Boccardia proboscidea* Hartman. The tubes of *Pseudopolydora paucibranchiata* are constructed of silt and/or fine sand with firm inner walls which have a spiraled pattern of construction. This pattern provides greater strength, and in addition, if the tube is broken, the broken end tends to curl and close off the tube. Because the tubes are constructed with fine sand or silt as they are available, the tubes have alternating sections of wall materials. Most tubes have multiple openings. Tube construction may be very rapid, for one specimen added 2.0 mm of tube in 5.0 minutes but a more normal construction pattern was the addition of 9.0 mm in 12 hours. The rate is in part dependent on the availability of foods and tube materials.

Tube construction proceeds in the following manner. The first three setigers of the body are extended from the tube and the active palps sweep silt along the ciliary groove to the basal region where it is gathered around the mouth. The worm then bends the anterior end down over the edge of the tube and touches it with the ventral side of the peristomium and the mouth region. The anterior end is then drawn back into the opening of the tube and the silt in the mouth area is added with a smooth downward sweep of the mouth from the new section towards the inner lining of the tube. This process is repeated around the periphery of the tube lip both clockwise and counterclockwise. The palps move massive amounts of silt and during this period of observation 2.0 mm of tube were constructed in 5.0 minutes as noted above.

Fecal strands are deposited about 5.0 mm away from the tube opening. The strands, measuring 2.0 mm or longer, regularly break up into elongate pellets having an undulating conformation easily distinguishable from the straight rod-like fecal pellets of an associated polychaete, *Streblospio benedicti.* Fecal strands are not deposited external to tube by extending the pygidium but are moved from tube entrance by the palps.

One adult in a silt tube was placed in a dish with half the substratum of silt and the other half of fine sand. At 0.0 hours the posterior half of the worm was in the tube and the anterior extended. Twenty minutes later it had left the tube and was crawling in the sand; at 30 minutes, 90 minutes, and 16 hours it was still in the sand. At 40 hours it had produced a sand tube, but with the newest section made of silt; the tube was 20.0 mm long. At the end of $4\frac{3}{4}$ days the tube was mainly silt and measured nearly 40.0 mm. The adults may construct the original and basal portion of the tube from sand but then in processing silt in feeding they add to the tube mainly from the silt debris.



FIGURES 12–16. *Pseudopolydora kempi:* 12) egg capsules in tube with contained embryos, nurse eggs and fragmented nurse egg granules; 13) nurse egg in the process of fragmenting into discrete granules; 14 and 15) early embryos prior to engulfing yolk granules; 16) encapsulated 3-setiger embryo after eating nurse egg granules and beginning morphological differentiation.

Pseudopolydora kempi (Southern)

Reproduction

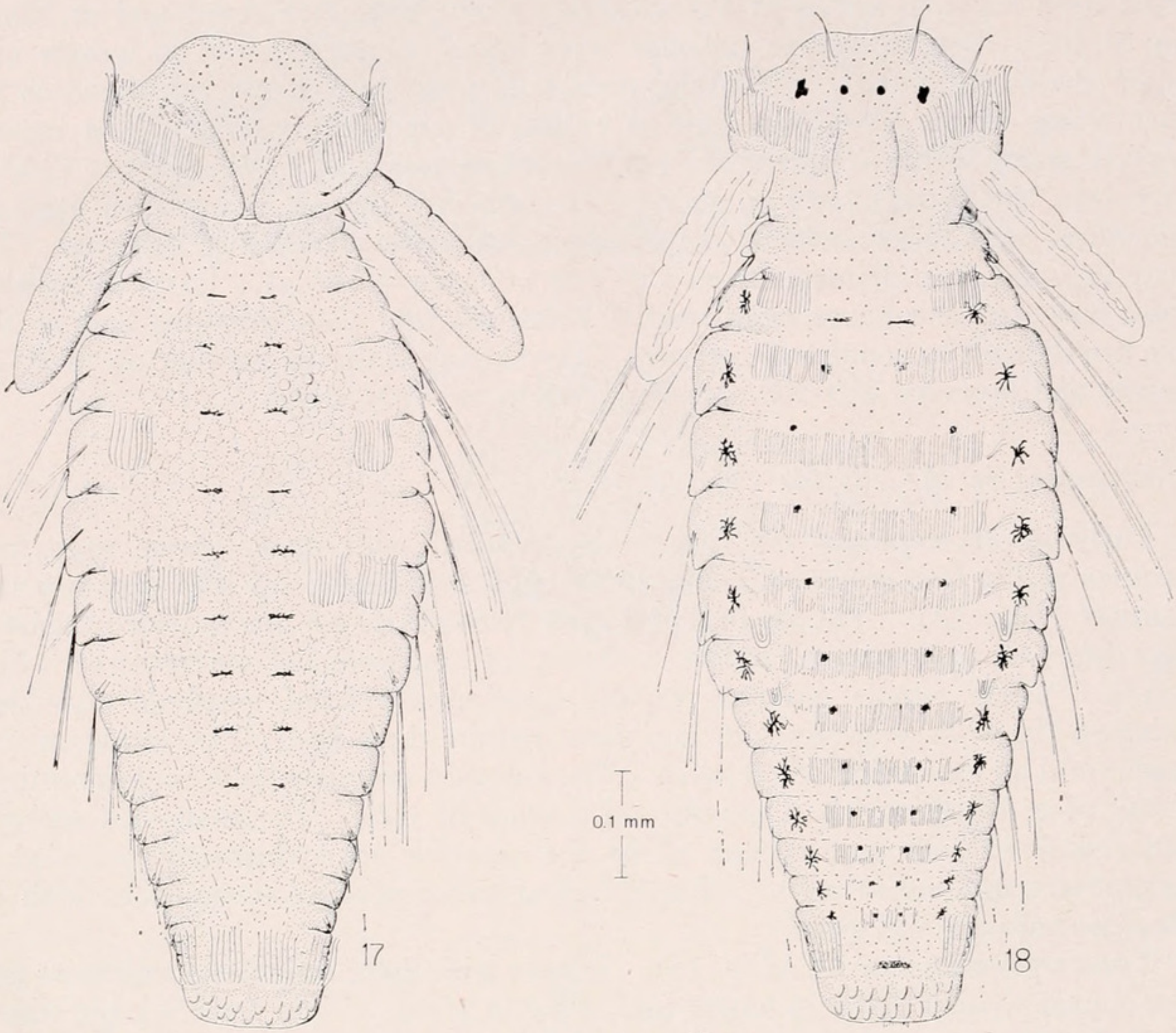
Although a year-round population study was not attempted, mature males were taken mid-February at Morro Bay and in October and November in Tomales Bay. Mature sperm have the following measurements: total length 57.5 μ, acrosome 0.8 μ, nucleus 7.5 μ, middle piece 4.6 μ, and tail 44.6 μ. Egg capsules were collected from tubes of adults in Tomales Bay from August to April and at Morro Bay in July. Ten to sixteen capsules were found joined together in loosely connected chains (Fig. 12). Each egg capsule is pear-shaped and connected to the inner lining of the tube by a thin extension of capsular material. The capsule shape is nearly identical to that of *P. antennata* as described by Rasmussen (1973). There are 15–20 capsules in a string. In each capsule the majority of eggs are unfertilized and serve as food (nurse eggs) for a few developing embryos. The nurse eggs range in diameter from 150–200 μ (mean = 165 μ). Early in development, however, the nurse eggs readily break up into yolk granules and at that time are difficult to count and measure. Developing embryos number up to 20 per capsule and measure 270–300 μ in diameter at an early stage.

Development in the capsule

Early in development the capsule is crowded with intact nurse eggs, yolk granules and a few embryos. The nurse eggs soon break up into separate yolk granules (Fig. 13). The earliest embryos removed from the capsule consist of large internal macromeres and a covering of unpigmented micromeres (Figs. 14–15). These simple embryos rapidly develop a ciliated vestibule and begin to ingest the yolk granules, storing them within their body. Ingestion is continued until all extrinsic yolk is taken. The embryos are essentially undifferentiated at this time, being merely a mouth and a mass of yolk. The distended embryos with contained yolk now occupy all of the capsular space formerly occupied by the embryos and nurse cells. Morphological differentiation commences with development of cilia and setae.

Three-setiger larvae (*Fig. 16*). Larvae with three setigerous segments measure approximately 300 μ in length and 270 μ in width. They have a large ciliated vestibule, several patches of prototrochal cilia, and a telotroch. Three sets of serrate larval setae on each side mark the location of future segments. Ventral cilia are present at the level of setiger 1. Nototroch cilia are visible at about setiger 3. Several areas of black granular pigment are present dorsally near the posterior end of the larva. The pygidial area appears golden brown in transmitted light. Encumbered by the enormous yolk supply the larvae were incapable of swimming when released from the capsule at this stage.

Eight-setiger larvae. Larvae with eight setigerous segments have a well-developed prostomial-peristomial region which is gently rounded in shape. There is a pair of tactile cilia, one on each side of the midline, which project anteriorly from the leading edge of the larvae. The palps resemble elongate knobs. There are two pairs of eye spots in contrast to the 6–7-setiger stage which has only a single central pair. Dorsal pigment consists of two lateral rows of spots and two central rows on setigers 3, 4, 5, and 6. There is diffuse central pigment on setiger 7 and a well-developed dorsomedial pigment spot on the anterior margin of the anal segment. The larva is somewhat enlarged in its middle segments and the contained yolk mass has an hour glass shape. The yolk may bulge the body and distort segmental lines. Long larval setae project from the first four or five setigers. Those of the first setiger are longest and reach to about setiger 6 or 7. Setae on setigers 6 and 7 are very short. The posterior end of the body is gently tapered in shape and the anal segment is rounded.



FIGURES 17–18. *Pseudopolydora kempi:* 17) pelagic 15-setiger larva in ventral view; 18) pelagic 15-setiger larva in dorsal view.

TEN TO 11-SETIGER LARVAE. At this stage the larval form is generally elongate with a tapered posterior end and a rounded anal segment. The anterior end is squared off medially and the four eyes are aligned nearly straight across the body just anterior to the palpal bases. The central pair are smaller and round; the lateral pair are larger and polymorphic. The palps are more elongate than in preceding stages and reach to the midline of setiger 2. The four rows of dorsal pigment are formed by spots on setigers 3, 4, 5, 6, 7, and 8. The spots are less distinct and pigment is diffusely distributed dorsomedially on setigers 9 and 10. The anal segment is pigmented as before. There is a pair of large pigment spots ventrally placed in the vestibular region. Larval setae are present. The modified fifth setiger is not specialized at this stage.

TWELVE TO 13-SETIGER LARVAE. Larvae are brooded in the capsule until they have at least 12 setigers. During this period the larvae are distended with yolk and until release they subsist entirely on yolk. The digestive tract is not complete posteriorly until the very end of the brooding period. The length of time spent in the capsule probably depends on the number of nurse cells originally available.

At about the 12-setiger stage and release from the capsule, larval setae are lost and short adult notosetae form on anterior setigers. Neuropodial lobes also form at this stage. These larvae when freed from the capsule may swim actively for hours or several days or may move directly to the bottom and spend most of the time slowly moving along the bottom and feeding on silt and other debris in the laboratory culture dishes. They also fed on less successful, decomposing larvae present in the dishes but this may be unnatural laboratory-influenced behavior.

A larva artificially released from a capsule at the 12-setiger stage developed the thirteenth setiger in 48 hours. It had four rows of dorsal pigment on setigers 3–9, two rows on setigers 10–12, and a single median pigment spot on setiger 13. Also noticeable at this stage are the two rows of ventral pigment on setigers 2–8.

Development in the plankton

PELAGIC 15-SETIGER LARVAE (*Figs. 17–18*). Large pelagic larvae were encountered in Tomales Bay plankton in March 1970 but they were never as abundant as *Pseudopolydora paucibranchiata* larvae. Pelagic larvae of *P. kempi* at this stage measure 850–900 μ in length. Their body is somewhat expanded centrally producing an overall modified fusiform shape. The prototroch extends ventrally to near the lips of the vestibule and dorsally covers about two thirds of the head. The low nuchal ridge is surrounded on each side by a few short nuchal cilia. A short neurotroch extends posteriorly into setiger 1. Four tactile cilia arise from the head, two located in front of the eyes and two located laterally near the prototroch. Palps reach into setiger 4. There are four eyes; a round inner pair and an irregular shaped lateral pair. Parapodial lobes are well-developed. Serrate larval setae may still be present on each segment including setiger 5. Gastrotrochs occur on setiger 5 (two patches) and setiger 7 (four patches). Nototrochs begin on setiger 3 and continue on succeeding setigers. Nototrochs of setigers 3 and 4 do not extend all of the way across the segment. Grasping cilia begin on setiger 5. The telotroch is formed of six discrete patches of cilia separated by a dorsal gap. The anal segment has golden brown pigment as does the prostomium. The anal segment also contains glandular structures. Branchial buds occur on setigers 7 and 8. The dorsal pigment consists of two lateral rows of branching chromatophores which begin on setiger 3 and continue on succeeding segments. There are also two central rows of pigment spots which are more granular in nature. These usually begin on setiger 3 but may not appear until setigers 4 or 5. There is a centrally located black pigment spot on the dorsal surface of the pygidium. Ventral pigment begins on setiger 2 and consists of paired bars on the posterior border of each segment. Some irregular areas of black pigment occur above and below the prototrochal cilia on the ventral side of the larva. The anterior margin of the prostomium and the posterior end have considerable golden brown pigment. The gut is packed with oily globules and digestive residue of phytoplankton. The anal segment bears gland-like papillae on its surface.

Growth, settling and metamorphosis

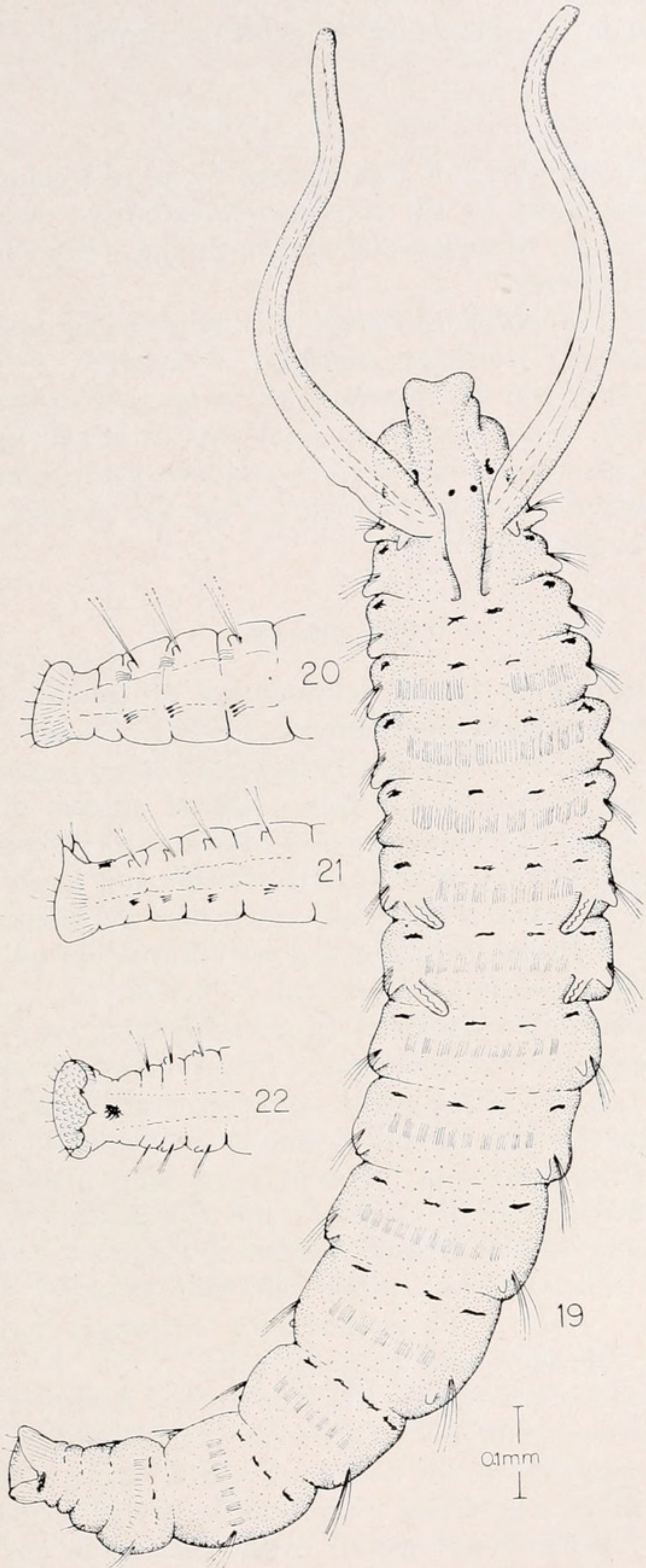
One larval specimen released from an egg capsule and observed regularly over several days in a laboratory culture dish was maintained at about 21° C. It was at 10 setigers on day 1, 12 setigers on day 2, and 14–15 setigers on day 3.

A 12–13 setiger larva freed artificially from a capsule collected at Morro Bay was placed in a culture dish of sea water with silt from the adult habitat. The larva immediately accumulated silt on its body and crawled through the silt, abandoning all swimming activities. In the next 72 hours its settling activities included tube construction. The dorsal body pigmentation was somewhat reduced but the basic pattern was retained. In 24 more hours the golden brown anterior pigment had become more noticeable. Palps elongated, became prehensile and reached about two-fifths the way back along the body.

Young adults placed in culture dishes containing sand, mud, and silt from the habitat produced extensive tubes with as many as six or seven openings. The tubes were of silt and mucous with an outer covering of coarser sand grains. The adults were secretive compared with *P. pacibranchiata* and rarely appeared at the tube openings. They extended the palps only to feed or dispose of fecal materials. Adults have white spots on the palps. The spots are numerous and irregularly arranged. One large adult collected at Morro Bay had 50 segments and measured about 13.0 mm.

Metamorphosis of the pelagic larva into a benthic juvenile involves loss or modification of larval organs and development or elaboration of other organs which have not been functional during the larval phase. Chief among the latter structures are the palps which do not process food during larval life but become the main organ of feeding during benthic life. In a settled 12-setiger specimen the palps, even in a slightly contracted state, reach to setiger 8. In conjunction with development of the palps there is a marked elongation of the prostomium and peristomium and loss of larval cilia. A 16-setiger juvenile is figured (Fig. 19). The prostomium projects anteriorly and is clearly bifurcate; posteriorly it reaches to the position of setiger 1 or the middle of setiger 2. The eyes have assumed a more typical adult arrangement, with a closely spaced oval posterior pair and a larger anterior pair, irregularly shaped and widely separated. Most of the larval pigmentation is retained in the juveniles. As juveniles grow, however, the lateral pigment bands on the anterior segments elaborate and spread down the sides of the segments. The strong anterior bands remain and become part of the adult pattern, but other pigment disappears. Lateral pigment may develop in setigers 1 and 2. Larval setae have been lost and adult setae are present in all but the incipient setigers of a 12-setiger stage. Setiger 5 is not highly specialized but the internal formation of spines can be discerned. Hooded hooks are present in setigers 8, 9, 10, and 11. The digestive tract is complete and the interface of esophagus and intestine is located at the anterior margin of setiger 6. Numerous sensory cirri are distributed on the palpal and pygidial surfaces. Changes in the pygidium are of interest. Immediately following metamorphosis the pygidium is a simple cup-shaped structure similar to that of *P. paucibranchiata* and many species of *Polydora* (Fig. 20). With continued growth, however, two dorsal elevations or projections appear on the previously simple pygidium (Figs. 21–22).

A metamorphosing form with 19 setigers and three incipient segments taken in August at Morro Bay had a caruncle which reached to the middle of setiger 3. Eyes were as before and no nuchal tentacle was observed. Palps reached to setiger 11. Five modified setae were present on each side of setiger 5. Branchiae began



FIGURES 19–22. *Pseudopolydora kempi:* 19) benthic juvenile with 16 setigers; 20) pygidial structure of newly settled juvenile in lateral view; 21 and 22) pygidial structure of older juvenile in lateral (21) and dorsal (22) views; 20–22) not to scale.

on setiger 7, were full size on 8 and 9, were small on 10 and 11. Numerous other juveniles were taken in mid-December in a benthic sample.

Natural history

In natural habitat members of this species form rust-colored tubes. Adults maintained in the laboratory in silt constructed extensive dendritically arranged tubes with as many as six or seven different openings. Branched tubes were not observed in the field, however.

In Morro Bay, *Pseudopolydora kempi* was collected in association with *Boccardia hamata* (Webster), *Polydora nuchalis* Woodwick, *Streblospio benedicti, Armandia brevis* Moore, and *Hemipodus californiensis* Hartman.

In Tomales Bay, *P. kempi* occurs on tidal flats in mixed sand-mud sediments The species is often associated with *Pseudopolydora paucibranchiata, Hemipodus borealis* Johnson, *Capitella capitata* Fabricius, *Pygospio elegans* Claparède, *Eteone dilatae* Hartman, and *Armandia brevis.*

Discussion

Information pertaining to larval development of spionid polychaetes is extensive and has been reviewed by Hannerz (1956), Simon (1967) and Blake (1969). Most larval studies of this family have concerned organisms from Europe or from the east coast of North America. Larval studies of species from the west coast of North America include those of Hartman (1940, 1941) on *Boccardia proboscidea,* Woodwick (1960) on *Polydora nuchalis* and Dean and Blake (1966) on *Boccardia hamata.* To date there is little published information on reproductive habits of any species of *Pseudopolydora* and no information on the larva development of *Pseudopolydora paucibranchiata* and *P. kempi.*

Pseudopolydora paucibranchiata and *P. kempi* exhibit very different modes of early development and brood protection. *Pseudopolydora paucibranchiata* has small eggs (96–105 μ), no nurse cells, larvae emerge from the capsule at the 3-setiger stage and spend a long period of time in the plankton. This pattern, with a short period of brood protection followed by a long planktotrophic period is typical for most related species of *Polydora* and *Boccardia* (Wilson, 1928; Dean and Blake, 1966; Blake, 1969). Seven species of *Polydora* and one of *Boccardia* have, however, been shown to have nurse cells and to spend little or no time in the plankton (Blake, 1969). *Pseudopolydora antennata* has been shown by Rasmussen (1973) to develop without nurse cells.

The nurse cell feeding pattern of *Pseudopolydora kempi* is very unusual but similar to that of another spionid, *Pygospio elegans* (Hannerz, 1956; Rasmussen, 1973). Within a single capsule the many nurse cells are fragile and immediately disintegrate into small yolk granules. The few embryos develop a vestibule and engulf the granules. When these are all eaten, the larvae are greatly distended with the enormous yolk supply which they utilize during growth and development in the capsule. The nurse cell feeding pattern of *Pseudopolydora kempi* differs markedly from that of *Polydora quadrilobata* Jacobi described by Blake (1969). In *P. quadrilobata* the nurse cells remain intact until they are engulfed whole by the larvae, which do not feed until about the 4-setiger stage. They con-

TABLE II

Patterns and distribution of pigmentation in four species of Pseudopolydora.
(– *indicates pigment absent;* + *indicates chromatophore present*).

	Antennata[1]	Kempi	Paucibranchiata	Pulchra[1,2]
Number of eyes (12 to 13 setigers)	6	4	6	4
Pigment				
Dorsal median pigment spots				
Anterior	+	–	+	+
Pygidium	+	+ (small)	+	+
Number dorsal rows	2	4	2	4
Anterior dorsal pigment pattern				
Prostomium	–	–	–	+
Setiger 1	+	–	+	++++
Setiger 2	–	–	+ +	++++
Setiger 3	–	++++	+ +	++++
Setiger 4	+ +	++++	+ +	++++
Setiger 5	+ +	++++	+ +	++++
Ventral segmental pigment pattern	++ (between setigers 1–2 only)	++ (setigers 2–10)	+ (setiger 6)	–
Reflective yellow	absent	absent	present	present
Dorsal dispersed green	absent	absent	present	present
Palp pigment	absent	spots numerous irregular white	spots regular reflective yellow	bands black and green
Approximate size: (13 setiger stage)	860 μ	750 μ	640 μ	1450 μ

[1] Data from Hannerz (1956).
[2] Data from Rullier (1963).

tinue feeding on nurse cells until all are eaten; then, the larvae leave the capsule. A similar pattern occurs in *Polydora hoplura* Claparède (Wilson 1928), *P. nuchalis* (Woodwick, 1960) and *Boccardia proboscidea* (Hartman, 1940, 1941; Woodwick, unpublished).

The morphology of *Pseudopolydora paucibranchiata* and of *P. kempi* larvae can be compared with that of *P. antennata* larvae described by Hannerz (1956) and *Pseudopolydora pulchra* larvae described by Casanova (1952), Rullier (1963) and Hannerz (1956). Pigmentation appears to be the most useful characteristic and is emphasized in Table II, although no groupings or special relationships of species are evident from the pigmentation patterns delineated. One striking alternative characteristic is the comparatively large size of *P. pulchra* larvae.

The characteristics noted in Table II for larvae of *P. antennata* and *P. pulchra* were taken from Hannerz (1956). It is of interest to note, however that there is apparent variation in the pigment among the published descriptions of *P. pulchra* larvae.

California adult specimens of *P. kempi* collected by us agree with descriptions given by Okuda (1937) for the same species in Japan. They have a well-developed nuchal tentacle and the peculiar pygidium with two dorsal lappets. These observations are based on specimens collected from Morro Bay, San Francisco Bay, Bolinas Lagoon, Tomales Bay and Bodega Harbor. The specimens collected by Light (1969), however, were said to lack a nuchal tentacle and to have a different pygidial structure.

In order to shed some light on this apparent anomaly, one of us (JAB) examined the type material of *P. kempi californica* deposited in the California Academy of Sciences. The type material consists of the holotype which is badly preserved and two paratypes, each of which is fragmented and incomplete. All three specimens lacked the nuchal tentacle. The second paratype, however, had a small circular scar just posterior to the second pair of eyes which suggests that the nuchal tentacle was broken off. The first paratype was damaged in the same area and an irregular slit marked the possible site of a nuchal tentacle. A pygidium was present only on the holotype, but was so badly preserved and contracted that its true structure was impossible to determine.

Based on our observations of living *P. kempi* adults and juveniles and upon examination of the type collection of *P. kempi californica* Light we conclude that California specimens agree well enough with descriptions from Japan to preclude the necessity of the subspecies name *californica*. This conclusion is further supported by Carlton (1975) who suggests that *P. kempi, P. paucibranchiata* and many other California marine invertebrates may have been introduced from Japan.

Summary

1. The larval development of *Pseudopolydora paucibranchiata* (Okuda) and *P. kempi* (Southern) is described. Both species occur in tidal flats of California bays and estuaries.

2. Adult females of *P. paucibranchiata* deposit eggs in capsules which are attached to the inner lining of their tubes. All eggs are fertilized. Larvae develop in the capsules until they have 3 setigerous segments at which time they enter the plankton. After development of 13–17 setigers they begin to settle out of the plankton and assume a benthic life.

3. Eggs of *P. kempi* are also deposited in capsules, but in this case only a small percentage are fertilized. The unfertilized eggs fragment into separate yolk granules and are eaten by the developing embryos. After all yolk is devoured the larvae continue their development sustained by this stored food reserve. They remain in the capsule until they have about 15 setigers. They remain in the plankton only a short time before settling and taking up a benthic life.

LITERATURE CITED

Barnard, J. L., 1958. Amphipod crustaceans as fouling organisms in Los Angeles-Long Beach Harbors, with reference to the influence of seawater turbidity. *Calif. Fish Game,* **44**: 161–170.

Blake, J. A., 1966. On *Boccardia hamata* (Webster), new combination (Polychaeta, Spionidae). *Bull. S. Calif. Acad. Sci.,* **65**: 176–184.

Blake, J. A., 1969. Reproduction and larval development of *Polydora* from northern New England (Polychaeta: Spionidae). *Ophelia,* **7**: 1–63.

Carlton, J. A., 1975. Introduced intertidal invertebrates. Pages 17–25 in R. I. Smith and

J. A. Carlton, Eds., *Light's Manual, Intertidal Invertebrates of the Central California Coast.* Berkeley, U. C. Press.

Casanova, L., 1952. Sur le développement de *Polydora antennata* (Claparède). *Arch. Zool. Exp. Gen.,* **89**: 95–101.

Dean, D., and J. A. Blake, 1966. Life history of *Boccardia hamata* (Webster) on the east and west coasts of North America. *Biol. Bull.,* **130**: 316–330.

Franzen, A., 1956. On spermiogenesis, morphology of the spermatozoon, and biology of fertilization among invertebrates. *Zool. Bidr. Uppsala,* **31**: 355–482.

Hannerz, L., 1956. Larval development of the polychaete families Spionidae Sars, Disomidae Mesnil and Poecilochaetidae n. fam. in the Gullmar Fjord (Sweden). *Zool. Bidr. Uppsala,* **31**: 1–204.

Hartman, O., 1940. *Boccardia proboscidea,* a new species of spionid worm from California. *J. Wash. Acad. Sci.,* **30**: 382–387.

Hartman, O., 1940. *Boccardia proboscidea,* a new species of spionid worm from California. *J. Wash. Acad. Sci.,* **30**: 382–387.

Hartman, O., 1941. Some contributions to the biology and life history of Spionidae from California: with keys to species and genera and descriptions of two new forms. *Allan Hancock Pac. Exped.,* **7**: 287–324.

Hartman, O., 1969. *Atlas of the sedentariate polychaetous annelids from California.* Allan Hancock Foundation, University of Southern California, 812 pp.

Imajima, M., and O. Hartman, 1964. The polychaetous annelids of Japan. Part II. *Allan Hancock Found. Publ. Occ. Pap.,* **26**: 239–452.

Light, W. J., 1969. *Polydora narica,* new species, and *Pseudopolydora kempi californica,* new subspecies, two new spionids (Annelida: Polychaeta) from central California. *Proc. Calif. Acad. Sci.,* **36**: 531–550.

Los Angeles, Regional Water Pollution Control Board, 1952. Los Angeles-Long Beach Harbor Pollution Survey. *Report to Los Angeles Regional Water Pollution Control Board,* **4**: 1–43.

Okuda, S., 1937. Spioniform polychaetes from Japan. *J. Fac. Sci. Hokkaido Imp. Univ., Ser. VI Zool.,* **5**: 217–254.

Rasmussen, E., 1973. Systematics and ecology of the Isefjord marine fauna (Denmark). *Ophelia,* **11**: 1–504.

Reish, D. J., 1954. Polychaetous annelids as associates and predators of the crustacean wood borer, *Limnoria. Wasmann J. Biol.,* **12**: 223–226.

Reish, D. J., 1955. The relation of polychaetous annelids to harbor pollution. *Public Health Rep.,* **70**: 1168–1174.

Reish, D. J., 1959a. An ecological study of pollution in Los Angeles-Long Beach Harbors, California. *Allan Hancock Found. Publ. Occ. Pap.,* **22**: 1–119.

Reish, D. J., 1959b. Ecology of Amphipoda and Polychaeta of Newport Bay, California. *Allan Hancock Found. Publ. Occ. Pap.,* **21**: 1–106.

Reish, D. J., 1961a. The use of the sediment bottle collector for monitoring polluted marine waters. *Calif. Fish Game,* **47**: 261–272.

Reish, D. J., 1961b. A study of benthic fauna in a recently constructed boat harbor in southern California. *Ecology,* **42**: 84–91.

Reish, D. J., 1963. Further studies on the benthic fauna in a recently constructed boat harbor in southern California. *Bull. S. Calif. Acad. Sci.,* **62**: 23–32.

Reish, D. J., and J. L. Barnard, 1967. The benthic Polychaeta and Amphipoda of Morro Bay, California. *Proc. U. S. Nat. Mus.,* **120**(3565): 1–26.

Rullier, F., 1963. Développement de *Polydora* (*Carazzia*) *antennata* (Claparède) var. *pulchra* Carazzi. *Cah. Biol. Mar.,* **4**: 233–250.

Simon, J. L., 1967. Reproduction and larval development of *Spio setosa. Bull. Mar. Sci.,* **17**: 398–431.

Southern, R., 1921. Fauna of the Chilka Lake. Polychaeta of the Chilka Lake and also of fresh and brackish waters in other parts of India. *Mem. Indian Mus.,* **5**: 563–659.

Wilson, D. P., 1928. The larvae of *Polydora ciliata* Johnston and *Polydora hoplura* Claparède. *J. Mar. Biol. Ass. U. K.,* **15**: 567–603.

Woodwick, K. H., 1960. Early larval development of *Polydora nuchalis* Woodwick, a spionid polychaete. *Pac. Sci.,* **14**: 122–128.