The Life History of the Polychaetous Annelid *Neanthes caudata* (delle Chiaje), Including a Summary of Development in the Family Nereidae[1]

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THE STUDY OF REPRODUCTION, development, and life history of the polychaete family Nereidae has attracted considerable attention in the past. Stimulus for this interest undoubtably is due, in part, to the world-wide distribution of the family, the phenomenon of epitoky (=heteronereis), and the diverse reproductive patterns. A total of 20 species of nereids has been studied in the past; information about them has been summarized in Table 1. Reproduction and development of *Neanthes caudata* have been studied previously by Herpin (1923, 1924, 1926) at Cherbourg, France. He reared this species through the 24-segmented stage.

This is the first report of the species in the Pacific Ocean. Fauvel (1923) stated that it inhabited muddy and sandy bottoms in Europe, and recently Day (1953) reported it from South Africa. The first specimens from the Pacific were encountered in a suspended sediment bottle collector (adapted from Thorson, 1946) which had been exposed for a 28 day interval in the West Basin of Los Angeles Harbor in November–December 1953. Quantitative bottom surveys of Los Angeles—Long Beach Harbors were made during August 1951 (Anon., 1952), and again in January 1954, but *N. caudata* was not taken. However, *N. caudata* was taken at many stations in both harbors in the surveys made in June and November 1954. It is believed to have been recently introduced into the harbor, possibly by ships.

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MATERIALS AND METHODS

Culture Techniques

Living specimens were collected from sediment bottle collectors suspended for 28 days in the West Basin of Los Angeles Harbor. The techniques employed for culturing adults are in general similar to those utilized by the author for the adults of *Nereis grubei* (Kinberg) (Reish, 1953; 1954). Best results were obtained when the worms were placed in separate petri dishes. The worms were fed *Enteromorpha* sp., usually twice a week. This green alga was collected in quantities from estuaries in southern California. This alga was dried, and, prior to using, a small amount was soaked in sea water for a few minutes. Mud and sand, that had previously been dried, were substituted for *Enteromorpha* sp. with some success, but the use of the alga was favored because of the greater ease in observing the animal. The water in the petri dishes was changed at irregular intervals, usually once every two or three weeks.

Since the male incubates the fertilized eggs and larvae (Herpin, 1926), the developing worms were left undisturbed with the male until the larvae abandoned the parent tube. At this stage the larvae could be pipetted into separate petri dishes containing *Enteromorpha* sp. At first many larvae could be placed within the same dish, but as the worms grew they became cannibalistic and had to be separated.

A second method (Reish, 1953), but not as successful, was to place the bottom half of the petri dish containing a male and developing larvae into a one gallon aquarium. One liter of sea water was placed in the aquarium; the water was aerated by an aquarium stone connected to a compressed air system. Dried, ground *Enteromorpha* sp. was added twice a week. This technique was particularly useful for maintaining small larvae for a short period of time.

The Fighting Reaction

The sexes cannot be distinguished morphologically prior to the onset of sexual maturity. Females may be separated from immature females or males by the presence of developing ova in the coelom. Only by studying the reactions of sexually unknown specimens to known males or females could the males be distinguished. Herpin (1923; 1926) found that a female would readily accept a male but would fight off the introduction of a second female. These observations were confirmed by the author. Not only was it found that females would fight one another, but also a similar response occurred when two males were placed together. This behavior, which is termed the fighting reaction, is so definite that it was utilized to differentiate the sexes.

The fighting reaction is most pronounced when two worms of the same sex meet directly. Each proboscis is everted and the jaws extended to grasp the opposing animal. One such encounter lasts only a few seconds, but successive encounters may extend over an interval of several minutes. Termination of these fighting periods occurred when the worms became separated a few centimeters from one another. When one animal came in contact with any portion of the body of the second one other than its anterior end, it extended its jaws and attempted to grasp the worm. No injuries have been actually seen inflicted by this fighting, but when similar sized worms of the same sex were left together for a day, wounds were observed the next day. One or both of the animals lacked its posterior end, the remains of which appeared in fecal pellets. If the two worms were of the same sex but differed in size and were left together for a day, the larger worm usually will have eaten the smaller by the next day. This fighting reaction may account for the difficulty of culturing several worms within the same petri dish as discussed above.

A modification of this fighting reaction was observed in the male following egg-laying by the female. A male incubating eggs will frequently eat the spent female. A spent female will fight with a second female that has not yet laid her eggs. A male incubating eggs will fight with worms of either sex. After completion of the incubation period, the male will no longer fight with a female.

The basic behavior pattern appears to be an attraction to members of the opposite sex and a fighting reaction to members of the same sex. This pattern is altered in the male while incubating ova; he fights either sex. This behavior difference during the incubation period is apparently due to the presence of the eggs, although it was not the subject of any special investigation. Apparently there is no change in the behavior of the female during its life cycle.

Incubation of eggs is known to occur in *Micronereis variegata* (Rullier, 1954), *M. nanaimoensis* (Berkeley and Berkeley, 1953), *Platynereis massiliensis* (Hauenschild, 1951), *Laeonereis glauca* (Herpin, 1929), and *Cera-*

tonereis costae (Durchon, 1956), but it is not known whether or not this fighting reaction occurs in these species.

REPRODUCTION AND DEVELOPMENT

Sex Ratio

As reviewed by the author (1954), little is known concerning the sex ratio in the nereids. A ratio of one to one exists in *Nereis grubei* (Reish, 1954) on the basis of laboratory-reared specimens and field collections. Population studies showed a ratio of five males to four females in *Perinereis nuntia* var. *brevicirris* Grube (Takahasi, 1933), and 40 per cent males in *Nereis diversicolor* from South Baltic Sea (Bogucki, 1954) but only 10 per cent from the southern English coast (Dales, 1950).

Specimens of *N. caudata* were isolated into individual petri dishes shortly after they had left the parent tube. These worms were observed periodically for signs of egg formation. Those specimens which did not develop eggs were placed separately into a dish containing a female. The behavior of these worms was observed when they came in contact with one another. If the animals did not fight, then the unknown was considered a male. If the animals did fight, then the unknown was considered to be a female. The worms were then returned to separate petri dishes for further observations. No changes in the response to the fighting reaction were observed subsequently. A total of 170 specimens were isolated in this manner; they were offspring from six different matings. The results indicated a sex ratio of one to one; there were 88 females and 82 males.

Spawning

Spawning has never been observed in *N. caudata*. It has been described for several species of epitokal nereids (Reish, 1954) and in *Nereis diversicolor* (Bogucki, 1954). In *N. diversicolor*, a non-epitokal form, Bogucki found that the eggs are released through ruptures in the body wall, and that sperm may be discharged either through the nephridia or through ruptures in the body wall.

Some details concerning spawning behavior in *N. caudata* can be given, however. A series of 10 dishes, each containing a male and female, were observed at hourly intervals during the day (but not the week end) for a three-week period. Eight of the ten pairs spawned during the period. In one instance the female laid all her eggs between one hour observational periods. In a second instance a female was seen that had laid about one-half of her eggs. It is not known whether or not she was in the act of laying at the time of observation. She died three days later without laying any additional eggs. The remaining six pairs laid eggs either during the night or over the week end.

Freshly laid eggs of *N. caudata* were molded into a mucoid tube of one egg in thickness by the male. The male was undulating its body at all times. At first the eggs were free and easily withdrawn with a micropipette, but after the male had molded them into an egg tube, they became appressed and were difficult to remove with a micropipette. No gelatinous envelope (Hemplemann, 1911) surrounded the fertilization membrane as is typical for the epitokal nereids.

No sperm were observed in the water during placement of the eggs by the male. No dissections were made of these males. Periodic coelomic smears of the posterior part of known males did not reveal the presence of any bodies that could be definitely attributed to sperm or spermatic masses. Sperm was seen embedded within the space between the fertilization membrane and the developing ovum by Herpin (1926, fig. 115) and the author.

Fate of the Parents

Herpin (1923; 1926) stated that following completion of the larval incubation period, the male resumed its former life, and in one instance a male would reproduce a second time. The fate of the female was unknown except in one instance where Herpin noted that the male had eaten the female the day following egg-laying.

The observations of Herpin were confirmed, and the following additional details can be given. The female either died after egg-laying or was eaten by the male. This cannibalistic action by the male is believed to be incidental because the fate of the female was approximately equally divided between the two causes. One female lived a total of six days following egg-laying, but this was exceptional. Typically the female lives two or three days after laying her eggs before dying. The females ate *Enteromorpha* sp. until a day before egg-laying, but none of them resumed feeding after spawning.

After the larvae have left the tube of the parent, the male may also abandon the tube, but not necessarily. The male may reproduce and incubate larvae more than once. Many males have fertilized and incubated eggs two times and one male has successfully incubated eggs three times in the laboratory. How soon after completion of one incubation period the male can reproduce with a second female was not completely ascertained because of the lack of mature females at the critical time. The shortest period of time between two fertilization periods for one male was 27 days. The first eggs were fertilized on September 12, 1954, with all the larvae leaving the tube by September 22, 1954. The second female was placed with the male on October 4, 1954, with fertilization occurring October 8, 1954. *Neanthes caudata* is the only dioecious species of nereid known in which at least one of the sexes can reproduce a second time.

Number of Eggs

Little information on the number of eggs or larvae of nereids has been recorded in the literature. Smith (1950) stated that *Neanthes lighti* produced several hundred eggs but only 80 to 100 larvae were released. Rullier (1954) found that *Micronereis variegata* laid from 20 to 80 eggs in a gelatinous matrix. In *Nereis grubei* the author (unpublished data) found the number of eggs to vary from 1,000 to 49,000. The lower figures were generally for those animals reared in the laboratory, and the higher figures were from animals collected from nature.

The number of larvae of *N. caudata* hatching from the parent tube were counted rather than the eggs because of the greater ease in counting. This figure is believed to represent a close approximation of the actual number of eggs laid by the female since non-developing eggs were not seen. Only one count of larvae was made from a female collected from nature; a total of 481 larvae left the parent tube. Counts for seven laboratory-reared females ranged from 143 to 791, with a median of 365 larvae.

Fertilization and Early Development

The unfertilized ovum of *Neanthes caudata* is spherical and yellow (Fig. 1). Eggs from laboratory-reared females measured from 420 to 520 μ in diameter. The ova observed by Herpin (1926) were 600 μ in diameter, the largest size recorded for a nereid egg. No distinct cortical layer was observed.

The process of fertilization has not been observed either by Herpin or by the author. Eggs that had been laid within an hour al-

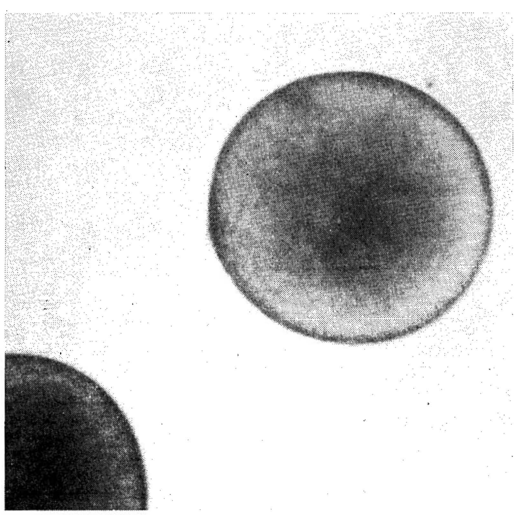

FIG. 1. Photomicrograph of an unfertilized egg of *Neanthes caudata*. Diameter, 425 μ.

ready possessed fertilization membranes. As stated above, sperm were observed embedded in the space within the fertilization membrane. Cleavage proceeded very slowly through the eight-cell stage. The cleavage pattern was spiral and similar to that described by E. B. Wilson (1892) for *Neanthes succinea* and *Platynereis dumerilii*. However, there was no further cleavage of the four yolky macromeres beyond this stage of development. These yolk cells will eventually become enclosed within the digestive tract and will be utilized for food (Figs. 2 to 7). These four cells can be seen until just prior to feeding.

Cleavage beyond the eight-cell stage was limited to the animal pole (Fig. 2, arrow). These cells come to surround the four macromeres by epibolic growth. The embryo was never ciliated, which is unique among the nereids.

The developing egg remained spherical until the seventh day when a slight elongation of the embryo was noted (Fig. 3). Longitudinal muscular movement appeared at this time. The course of growth from the elongation of the embryo through sexual maturity has been summarized in Table 2. Formation

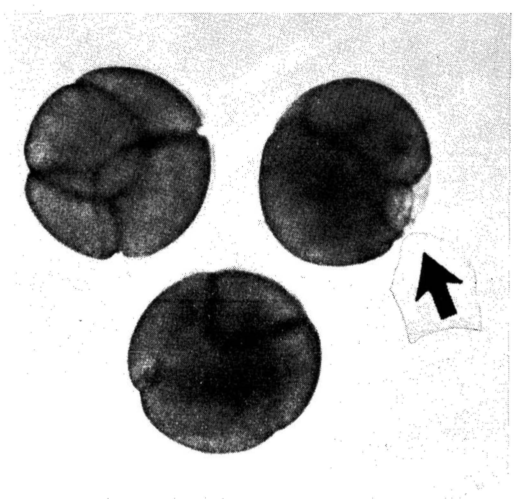

FIG. 2. Photomicrograph of developing embryos of about 18 hours in age showing the four macromeres. Arrow indicates site of cleaving micromeres. Diameter, 520 μ.

FIG. 3. Photomicrograph of an elongating embryo of seven days in age encased in egg capsule. Length, 520 μ.

of the three larval segments occurred at eight days. The anal cirri appeared as knobs at this time, but there were no indications of cephalic appendages (Fig. 4). Shortly thereafter the larvae hatched from the egg capsule.

During the ninth day the fourth larval setigerous segment, the first pair of peristomial tentacles, and the tentacles appeared. In addition, as many as four presumptive segments were often discernible as simple protuberances (Figs. 5 to 7). The four yolk-cells were still present, and because of their large size, they gave a humpback appearance to the larvae (Fig. 5). New segments were added rapidly until the animal had developed about 16 segments at 16 days (Figs. 5 to 8). The young worms, which have been crawling actively within the parent tube, begin to abandon the tube in the next few days. The larvae crawl about the petri dish, construct mucoid tubes, and begin to feed upon *Enteromorpha* sp. by 21 days. There is no true planktonic stage in *N. caudata*. However, if the young animals are disturbed, they abandon their tube and either crawl or swim away. This behavior may play an important role in the distribution of *N. caudata*, particularly within a bay or harbor. One specimen with 18 setigerous segments was taken in a plankton tow on October 21, 1954, in Los Angeles inner harbor. Further appearance of segments is indicated in Table 2.

The tentacles and first pair of peristomial tentacles appear as small knobs on the ninth day. The next two pairs of peristomial tentacles arise in the next two days (Fig. 5). The fourth pair was slow to appear; it did not form until the larva was 23 days of age and possessed 24 segments. The palpi were seen first at 10 days (Fig. 5) and became biarticulated a few days later.

The jaws were noticed when the larvae were 10 days old. They were colorless structures and consisted of only the terminal tooth. The first lateral tooth was added by the next day. Additional lateral teeth were formed rapidly; a larva 21 days old had 7 teeth. The tips of the jaws became dark brown at this time. Lateral movements of the jaws did not occur until the larvae had 15 segments, or just prior to leaving the parent tube.

Paragnaths were seen first on the maxillary ring at 14 days; they did not appear on the oral ring until 21 days. The paragnaths became dark brown at about 26 days when the animals possessed 32 segments. Figure 9 is a photomicrograph of the paragnaths of area I. A total of 37 paragnaths was observed in this specimen, which was a typical number for young worms. Adult worms reared in the laboratory had from 12 to 16 paragnaths present, indicating a loss in number with age. This was contrary to what was observed by the author (1954) in *Nereis grubei*, which showed little change, if any, with age.

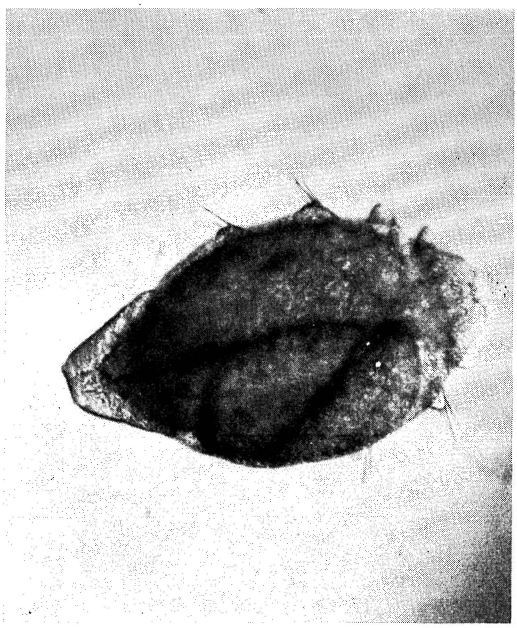

FIG. 4. Photomicrograph of a three-segmented larva of eight days in age. The anal cirri are beginning to develop as small knobs at the right side of the figure. Length, 750 μ.

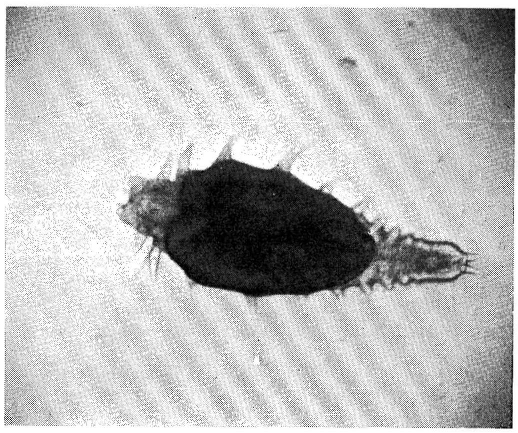

FIG. 5. Photomicrograph of five-setigerous segmented larva 10 days old. Shown in formation (from left to right) are the tentacles, palpi, two pairs of peristomial tentacles, five setigerous segments, four segments without setae, and one pair of anal cirri. Length, 1.1 mm.

The development of *N. caudata* collected at Cherbourg, France (Herpin, 1926), and Los Angeles Harbor, California, does not differ in morphological details, only in regard to time of appearance of structures. The three larval setigerous segments arose a day earlier at Cherbourg. This difference in one day continued until about 10 to 11 days when larvae from both localities possessed six larval segments. However, in the Los Angeles Harbor

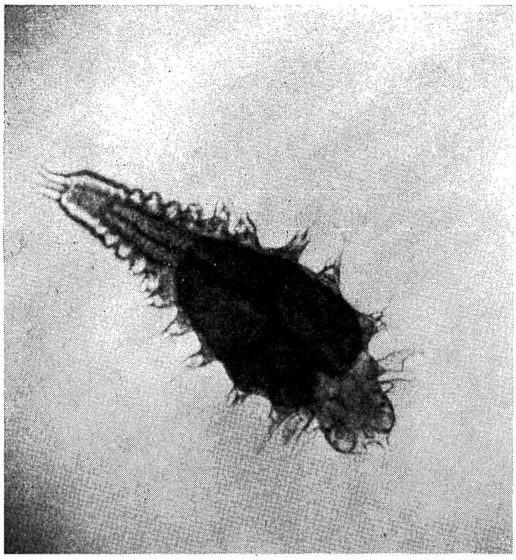

FIG. 6. Photomicrograph of seven-setigerous segmented larva 11 days old. Appendages as in Figure 5. Note the humpback appearance of the animals in Figures 5 and 6. Length, 1.1 mm.

material the 20-segmented stage was attained about eight days before the Cherbourg population.

Later Stages of Growth

Growth in the later stages of development in the nereids has been measured in three different ways. The use of segment number per unit of time has been employed most frequently (Banse, 1954; Bogucki, 1954; Dales, 1950; Hauenschild, 1951; Hemplemann, 1911; Herpin, 1926; Rullier, 1954; and D. P. Wilson, 1932). Body length was utilized by Bogucki (1954), Dales (1951), and Smidt (1951). The weight of the animal was determined periodically and correlated with metamorphosis and the appearance of genital products in *Nereis grubei* by the author (1954). With the former two methods, a sigmoid curve for growth was obtained. Similar results were attained for *N. grubei* when the number of segments per unit time was plotted (Fig. 8) using the data given by Reish (1954).

Growth in *Neanthes caudata* was followed by determining the number of segments present per unit time; the results have been summarized in Table 1 and plotted in Figure 8. The data are based on the growth of the offspring of one mating. Observations upon living specimens are difficult to make since they move about continually within their tube. The activity of these animals was slowed by placing the petri dish within an ice bath.

It is readily observable that growth in *N. caudata* differs from *Nereis grubei*. The appearance of the three larval setigerous segments lags in *N. caudata*, but the attainment of additional segments in *N. caudata* soon surpasses *Nereis grubei*. However, a plateau is reached at the time the larvae of *N. caudata* leave the parent tube and commence feeding at the 17- to 19-setigerous segment stage (Fig. 8; Table 1). Shortly thereafter a second growth spurt occurs which continued until the eggs were first discernible in the females at around the 55-segment stage. A few additional segments were added during the next 10 to 15 days. The maximum number of

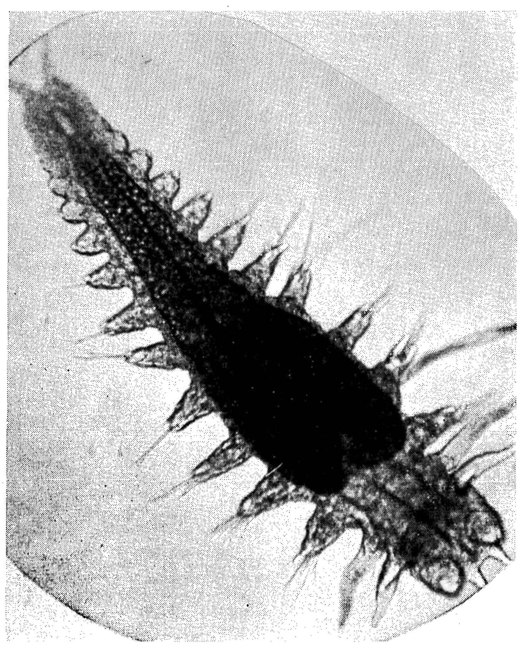

FIG. 7. Photomicrograph of eight-setigerous segmented larva 12 days old. Appendages as in Figure 5. Length, 1.2 mm.

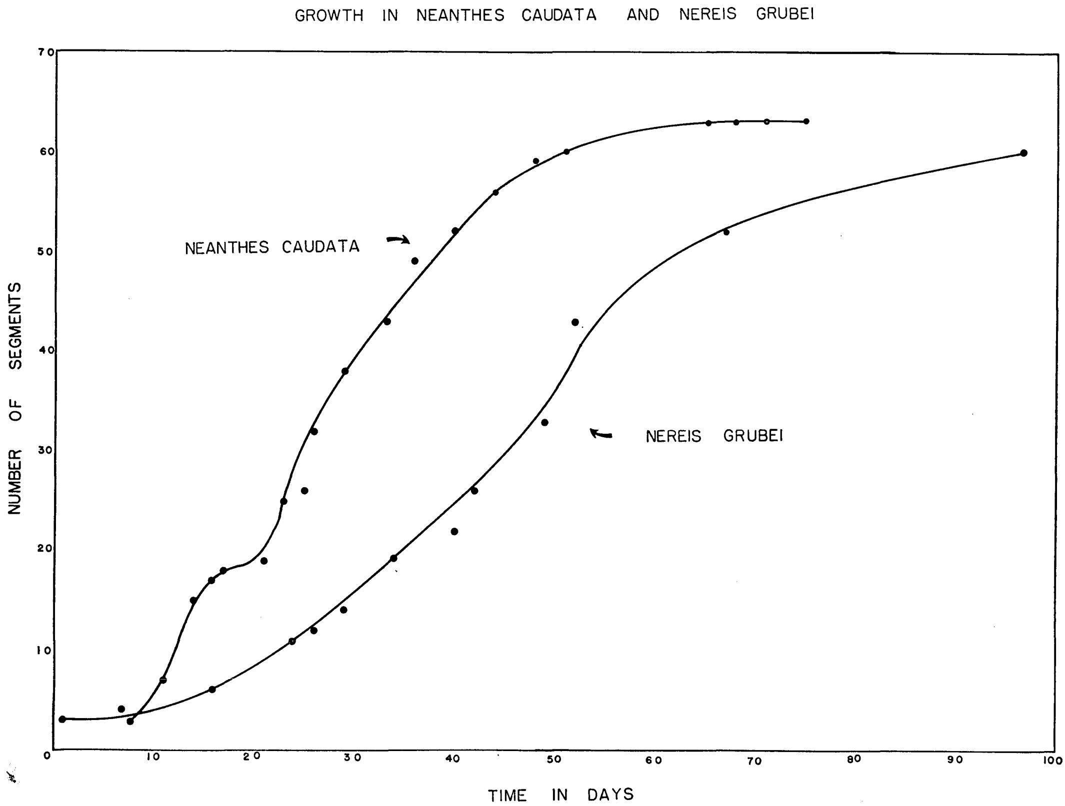

FIG. 8. Growth in *Neanthes caudata* and *Nereis grubei* as measured by the number of segments per unit time. Data for *Nereis grubei* taken from Reish (1954: 16).

segments were attained about 10 days before spawning. No sexual differences were noted with regard to the appearance or number of segments, and there was no indication that the males increase their number of segments between their first and second reproductive periods.

So far as is known, there seem to be two types of growth curves in the nereids when the appearance of segments is used as the unit of measurement. *Neanthes caudata* possesses a sigmoid growth curve with an interrupted plateau occurring at the onset of feeding. There is no initial prolonged phase after the appearance of the three larval segments in *N. caudata*, as is typical for the majority of nereids. It is possible that *N. lighti* is characterized by an interrupted growth curve. A similar initial spurt as in *N. caudata* was found when the data from Smith (1950) was plotted. Development of *N. lighti* was not followed after birth by Smith. As summarized in Table 1, several nereids incubate their young, but either data were not included or development was not continued far enough to ascertain whether or not these species possess a growth curve similar to *N. caudata.*

Sexual maturity was reached in 65 days (Table 2) with the female laying her eggs, and the male incubating them. The F_2 generation reproduced 148 days later, and the F_3 generation reproduced 203 days later. Five generations have completed their life cycle in the laboratory within a period of one year. No gross morphological differences between the different matings or generations were

TABLE 1

REVIEW OF REPRODUCTION AND DEVELOPMENT IN FAMILY NEREIDAE

SPECIES	METHOD OF REPRODUCTION	MAXIMUM STAGE REARED	REFERENCE
Ceratonereis costae......... (Grube)	Eggs laid in jelly mass in tube; eggs incubated by ♀	37 day old larva had 6 larval segments	Durchon, 1956
Micronereis nanaimoensis... Berkeley and Berkeley	Swarming and pairing but not epitokal; eggs laid in jelly mass with ♂ incubating	23 day old larvae possessed 3 larval segments	Berkeley and Berkeley, 1953
M. variegata Claparède...	As *M. nanaimoensis*	40 day old larvae possessed 6 segments	Rullier, 1954
Namanereis indica........ (Southern)	Protandric hermaphrodite	Preliminary note only	Aiyar, 1935
N. raneuensis............ (Feuerborn)	Hermaphroditic	4 day old larva possessed 3 larval segments	Feuerborn, 1932
Neanthes caudata......... (delle Chiaje)	Eggs laid in tube; eggs incubated by ♂	Sexual maturity in 2 months; ♂ reproduced more than once; ♀ reproduced only once	Reported herein
N. japonica (Izuka).......	Swarming but not epitokal	9 day old larva had 4 larval segments	Izuka, 1908; 1912
N. lighti Hartman........	Viviparity and probably self-fertilizing hermaphrodite	Parturation occurred at 3–4 weeks of larvae with up to 30 segments	Smith, 1950
N. succinea.............. (Frey and Leuckart)	Epitoky	60 day old larva had 17 segments	Banse, 1954
Nereis diversicolor......... Müller	Direct; population 40% ♂ in Baltic Sea and 10% ♂ on English coast	Sexual maturity reached in 10 months	Bogucki, 1954; Dales, 1950
N. grubei (Kinberg)......	Epitoky	Sexual maturity in 3.5 months; offspring all epitokal	Reish, 1954
N. irrorata (Malmgren)...	Epitoky	3 larval segments	Herpin, 1926
N. pelagica Linnaeus......	Epitoky	One year old specimen had 60 segments	D. P. Wilson, 1932
N. procera Ehlers.........	Epitoky	Reared to sexual maturity but no details given	Guberlet, 1934*b*
N. vexillosa Grube.......	Epitoky; eggs laid in jelly mass; no incubation	One specimen was 13 months old but not sexually mature at time of death	Johnson, 1943
Perinereis cultrifera........ (Grube)	Epitoky	45 day old larva had 7 segments	Herpin, 1926
P. marioni (Audouin and Milne-Edwards)	Epitoky	80 day old larva had 19 segments	Herpin, 1926
Platynereis bicanaliculata... (Baird)	Epitoky	Sexual maturity in 9 months; offspring all epitokal	Guberlet, 1934*a*
P. dumerilii (Audouin and Milne-Edwards)	Epitoky	Sexual maturity in 21 weeks; offspring all epitokal	Hauenschild, 1951
P. massiliensis........... (Moquin-Tandon)	Protandric hermaphrodite; ♂ incubates eggs	Sexual maturity; sperm present when worm had 17–25 segments; eggs present when worm had 41–47 segments	Hauenschild, 1951

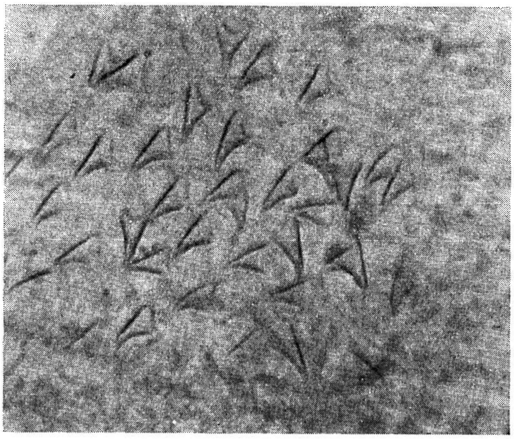

FIG. 9. Photomicrograph of colorless paragnaths on area I of a 17-segmented worm 17 days old. Dimensions top to bottom of area I, 70 μ.

TABLE 2
SEQUENCE OF EVENTS IN THE LIFE HISTORY OF *Neanthes caudata*

AGE IN DAYS	CHARACTERISTICS
7	Elongation of egg; muscular movement; length 0.52 mm.
8	Appearance of three larval segments; anal cirri; hatching from egg capsule; length 0.62 mm.
9	Four larval segments; tentacles; one pair of peristomial tentacles; length 1.0 mm.
10	Five larval segments; two pairs of peristomial tentacles; early palpi; jaws with terminal tooth only; length 1.1 mm.
11	Seven larval segments; three pairs of peristomial tentacles.
13	Animals with 12 adult segments; setae of first larval segment drop out, segment becomes peristomium; jaws with four lateral teeth; length 1.4 mm.
14	Animals with 14 segments; jaws with five lateral teeth; paragnaths on maxillary ring only.
16	Animals with 16 segments; jaws with six lateral teeth.
21	Animals with 18 segments; jaws with seven lateral teeth; jaws becoming dark brown at tips; paragnaths present on oral ring; worms have left parent tube and have built own mucoid tube; length 4.0 mm.
23	Animals with 24 segments; four pairs of peristomial tentacles; feeding; length 6.0 mm.
26	Animals with 32 segments; paragnaths getting dark brown.
33	Animals with 42 segments.
36	Animals with 48 segments.
40	Animals with 51 segments.
44	Animals with 55 segments; eggs observed in coelom.
65	Female lays eggs with male incubating.
92	Male fertilized eggs from second female.
148	F_2 generation reproduced.
203	F_3 generation reproduced.

noted; however, a statistical analysis of the offspring was not the subject of any special study.

DISCUSSION

A review of the literature on nereid development (summarized in Table 1, which gives the method of reproduction, the maximum stage to which the species has been reared, and the most recent reference) shows many different reproductive methods but apparently only two patterns of development. The most common method of reproduction is through epitoky. In this method the worms abandon their tubes or burrows at maturity and the sexual elements are emptied directly into the water, where fertilization and development ensue. These ova give rise to planktogenic larvae (Hemplemann, 1911). Both male and female die after spawning. This form of reproduction has been observed and studied in *Neanthes succinea*, *Nereis grubei*, *N. irrorata*, *N. pelagica*, *N. procera*, *N. vexillosa*, *Perinereis cultrifera*, *P. marioni*, *Platynereis bicanaliculata*, and *P. dumerilii*. *Nereis vexillosa* deviates slightly from the pattern in that the eggs are laid in a gelatinous egg mass, rather than singly.

Swarming, without epitoky, followed by pairing and egg-laying, has been observed in *Micronereis variegata*, *M. nanaimoensis*, and *Neanthes japonica*. In the two species of *Micronereis*, the female lays the eggs in a gelatinous mass on the substrate and incubates them until the larvae emerge from the matrix. Fertilization takes place in the water mass in *N. japonica*.

The female of *Ceratonereis costae* lays her eggs in a gelatinous matrix within her tube. Neither epitoky nor swarming precedes egg-laying in the population in Algeria. The eggs are incubated by the female (Durchon, 1956).

The larvae of *Nereis diversicolor* and *Neanthes lighti* resemble those species given above, but differ in their site of development. This proceeds on the substrate in *N. diversicolor* (Dales, 1950) and in the coelom of viviparous *N. lighti* (Smith, 1950).

Only two of the species studied have eggs with a large amount of yolk, giving rise to nereidogenic larvae. In both of these species, the male incubates the eggs within a mucoid tube, a ciliated embryonic stage is lacking, there is no larval planktonic stage, and the adults do not undergo metamorphosis into epitoky prior to sexual maturity. One of these two species, *Platynereis massiliensis*, has been studied by Hauenschild (1951) who found it to be a protandric hermaphrodite. The other is *Neanthes caudata*, whose life history is discussed in this paper.

It certainly appears from this summary that the method of reproduction and development of *Neanthes caudata* is unusual among the nereids. But only a few species have been studied and there is too little information available as yet to make any positive statement on this subject. As no correlation is apparent between genera and mode of reproduction, the life history of each species must be worked out before any authoritative conclusions can be reached.

SUMMARY

1. Reproduction and development in the polychaete family Nereidae was reviewed and summarized in Table. 1.
2. *Neanthes caudata* was reported from the Pacific Ocean for the first time. It was taken from suspended sediment bottle collectors and from the bottom of Los Angeles–Long Beach Harbors.
3. Techniques for rearing *N. caudata* through sexual maturity were described.
4. Males and females are attracted to one another, whereas individuals of the same sex fight with one another. This behavior is altered in the male while he is incubating the developing ova; he fights either sex.
5. A sex ratio of one to one was found in laboratory-reared specimens.
6. Spawning was not seen. The female died or was eaten by the male following egg-laying. The male incubated the eggs within its mucoid tube. The male may reproduce more than once.
7. The ova ranged in size from 420 to 520 μ in diameter. Fertilization was not observed. Cleavage proceeded very slowly. The four macromeres did not undergo further cleavage beyond the eight-cell stage. The micromeres continued to divide and gradually surrounded the macromeres by epibolic growth. The embryo was not ciliated. The three larval segments with setae appeared at eight days. The larvae left the parent tube at 21 days. Feeding commenced shortly thereafter. Sexual maturity was reached in both sexes in 65 days. The F_2 generation reproduced 83 days later and the F_3 generation 65 days later still. The sequence in the life history was summarized in Table 2.
8. *Neanthes caudata* was characterized by a sigmoid growth curve with an interrupted plateau, when the number of segments was used as a measure of growth. The interrupted plateau was correlated with the onset of feeding.

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