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Reproductive longevity in two species of polychaetous annelids

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Abstract

Polychaetes reproduce many different ways. Regardless of the method of reproduction very little is known on how long an individual, which reproduces multiple times, can live. In attempt to answer this question two species of laboratory reared polychaetes, *Neanthes arenaceodentata* and *Dinophilus gyrociliatus*, were selected for this study. The female *N. arenaceodentata* lays her eggs in a tube, then dies. The male incubates the embryos for 21–25 days and is capable of reproducing again. One male spawned nine times, but the eggs were not fertilized the eighth and ninth time. He lived 13 months. *D. gyrociliatus* is a minute species which lays two sizes of eggs within a capsule. The smaller ovum develops into a male, fertilizes the larger sized female ova within the capsule, and then dies. The maximum number of capsules and female ova occurred during the first three egg layings then decreased. The oldest worm reproduced 11 times and lived 63 days. Morphological changes with age were noted in both species.

Key words: ova production, life history, aging, feeding, abnormalities, *Neanthes arenaceodentata, Dinophilus gyrociliatus*

Introduction

Polychaetes reproduce in a variety of ways (see review by Giangrande 1997). Many species reproduce once then die such as epitokal nereids (Reish 1954). Others develop reproductive stolons at the posterior end which break off, swim to the surface, release their gametes, and die. However, the parent survives and continues to live to produce additional stolons. This is a common method in syllids (Heacox 1980). Hermaphroditism occurs in many polychaete families, for example, serpulids (Qiu & Qian 1998). *Eurythoe complanata* (Pallas) can reproduce sexually or by fragmentation with each part capable of forming a head and a tail (Kudenov 1974; Reish et al. 1989). While a considerable amount is known on the different modes of reproduction in polychaetes, very little is known on how many times an individual can reproduce and how long it can live. *Capitella* sp. individuals are known to reproduce five times in their lifetime (Qian & Chia 1992); *Ophryotrocha diadema* Åkesson reproduces many times (Åkesson 1982), and *Polydora cornuta* (Bosc) can reproduce multiple times (Rice et al. 2008); however, no mention was made of aging in these species other than the decline in reproductive rate.

The purpose of this study was to determine how many times an individual polychaete can reproduce and if the individual worm shows any morphological changes due to aging. For this study we selected two species of polychaetes which have been raised in laboratory cultures for many generations: *Neanthes arenaceodentata* (Moore, 1903) and *Dinophilus gyrociliatus* Schmidt, 1857.

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Materials and methods

Both species used in this study were taken from laboratory populations maintained for many generations. Both were collected from estuarine waters in Southern California. Six living specimens of *Neanthes arenaceodentata* were collected by DJR from Los Angeles Harbor in 1964. All worms used in this study were derived from this population. It is estimated that they have undergone approximately 200 generations in the laboratory. *Dinophilus gyrociliatus* was collected in 2004 from Alamitos Bay in Long Beach. Since this species has a 7–10 day life cycle, it is estimated that it has undergone hundreds of generations in the laboratory.

To set up the experiment, many small juvenile *Neanthes* were placed in individual dishes and fed the green alga *Enteromorpha* sp. as needed. When developing ova were observed within the coelom, she was paired with a worm of unknown sex using the fighting reaction as the criterion (Reish & Alosi 1968). Males fight males; females fight females. A total of 25 pairs were established, but three pairs died prior to reproduction, resulting in 22 pairs used in this experiment. Sexually paired worms were placed in a gallon jar with 2500 ml seawater with aeration provided. Worms were examined three times a week for deposition of ova. After spawning, the female is either eaten by the male or leaves the tube and dies within a day or two. She is unable to survive and reproduce a second time. Males incubate the fertilized ova for 21−25 days; however, as a convenience in counting offspring, the non-feeding young were removed and counted at 16−18 days. A second female with developing ova was then placed with the male and established in a gallon jar. This procedure was continued until the male died.

Hermaphroditic *Dinophilus* lays a small number of ova of two sizes in a capsule at an approximate ratio of three large to one small ovum (Reish & Pernet 2009). The larger ones develop into females and the smaller ones into males. The male fertilizes the females within the capsule, then dies. The female emerges from the capsule and commences feeding on powdered Tetramin©. Young worms were isolated into individual stender dishes as soon as they emerged from the capsule. These worms were used in the experiment. A total of 22 worms were used in this experiment. Worms were examined three to four times a week for capsule deposition. The adult was removed when capsules were observed, and it was placed in a clean dish with food. The number of capsules and female ova was counted; since the male ova were so small and difficult to be certain of the number, these ova were not included in the results.

The data for both species were analyzed statistically using the first reproductive period as the base. The range, mean, and standard deviation were calculated and recorded.

Results

Neanthes arenaceodentata

The data are summarized in Tables 1 and 2 with reference to the spawning period as to the number of juveniles produced and the growth of the male *Neanthes*, respectively. There was a slight reduction in the number of successful spawnings and incubations after the second spawning (22 to 19) with a noticeable decline between the fourth and fifth spawning period (22 to 12). The mean number of juveniles ranged from 316 to 348 through the first four reproductive periods, and was lower at the fifth period. The mean number of juveniles was higher for the sixth period, but this figure was based on the results of two worms. One male was able to spawn three times after the sixth period, but the juveniles only developed one additional time (Table 1). As noted in Table 1, there was a large difference in the range and standard deviation in the number of juveniles produced. In four cases, the male failed to successfully incubate the developing worms. Based on previous experience, it is not uncommon for the male to eat the embryos. However, these four males were able to produce juveniles when placed with the new female. One male was able to incubate young successfully through seven reproductive periods but was unable to do so with the ova from the eighth and ninth female. The ova were not fertilized.

TABLE l. Reproduction and number of juveniles produced per spawning period in *Neanthes arenaceodentata* (based on 22 males).

Spawning Period	Number Spawned	Mean No. Juveniles	Range ± S.D. of Juveniles
1	22	319	2−568 ± 168
2	22	316	104−578 ± 149
3	19	348	17−856 ± 200
4	17	331	101−607 ± 190
5	12	250	3−514 ± 147
6	2	365	343−387
7	1	328	—
8	1	*	—
9	1	*	—

*Eggs may not have been fertilized.

Growth of the male, as measured by wet body weight, is indicated in Table 2. The weight of the male continued to increase with each reproductive period through the sixth one from a mean weight of 67 to 155 mg wet weight. There was a reduction in weight in the four remaining males at the seventh reproductive period. The sole surviving male at the eighth and ninth period lost additional weight.

TABLE 2. Growth of male *Neanthes arenaceodentata* by spawning period (in mg wet weight).

Spawning Period	Number of Males	Mean Weight	Range ± S.D.
1	22	67	43−90 ± 12
2	19*	67	50−110 ± 17
3	20	98	53−130 ± 33
4	20	113	72−198 ± 24
5	17	123	70−192 ± 43
6	13	155	72−350 ± 85
7	4	110	57−150 ± 29
8	1	75	—
9	1	92	—

*One male was not weighed.

Dinophilus gyrociliatus

The results are summarized according to the number of capsules laid and number of female eggs per reproductive period in Table 3. The first capsules were laid 5 days after the worm emerged from the capsule. The mean number of capsules varied between two and three through the first four capsule reproductive periods, then decreased. Only one capsule was laid by the sole surviving worm at the eleventh reproductive period. The mean number of female eggs increased through the first three reproductive periods (14.2 to 19.9). There was a decline in number at the fourth reproductive period and a sharp decline thereafter. The average life span was 43 days, and one worm lived 63 days. The longest living worm laid 20 capsules with 106 female eggs.

TABLE 3. Reproduction, number of capsules, and female ova laid per spawning period in *Dinophilus gyrociliatus*.

Spawning Period	No. of Worms	Mean No. Capsules	Range ± S.D. Capsules	Mean No. Female Ova	Range ±S.D. Female Ova
1	20	3.05	2−5 ± 1.1	14.2	6−28 ± 7.3
2	20	2.3	1−3 ± 0.6	16.2	9−25 ± 4.5
3	20	3.35	1−4 ± 2.8	19.9	3−37 ± 8.2
4	20	2.3	1−4 ± 1.1	11.8	3−31 ± 7.9
5	18	1.4	1−3 ± 0.6	6.2	1−25 ± 6.5
6	17	1.8	1−5 ± 1.1	4.4	1−43 ± 10.4
7	17	2.0	1−5 ± 1.2	4.2	1−18 ± 4.3
8	11	1.3	1−4 ± 0.9	3.6	1−10 ± 3.0
9	9	1.6	1−3 ± 1.3	4.4	1−11 ± 3.7
10	5	1.0	1 ± 0	3.4	1−3 ± 2.7

Discussion

These two species of polychaetes differ widely in their method of reproduction, the number of eggs laid, and their length of life; however, there were similarities. There was an increase in the number of eggs laid after the initial deposition in both species and also an increase in the number of capsules laid in *Dinophilus*. A peak in reproductive output per individual was reached at the third reproductive period with both species. *Ophryotrocha diadema* is a simultaneous hermaphrodite that is capable of laying many capsules containing fertilized eggs (Åkesson 1976). Beginning with mature worms, *O. diadema* reproductive output was similar for four weeks, then declined. The population of *Capitella* sp. used by Qian & Chia (1992) are self-fertilizing hermaphrodites which lay their eggs within a tube. The number of eggs laid was similar through the first three reproductive periods, then declined. Interestingly, the egg size decreased after the first laying; egg volume was not determined in *O. diadema* or the two species studied herein. In summary, the effect of aging on reproduction was similar in these four species possessing different modes of reproduction: there was a peak of reproductive output in three of the four species, except *O. diadema*, and a decline in all four thereafter. In only *N. arenaceodentata* and *D. gyrociliatus* did the experiment extend to death. *D. gyrociliatus* continued to reproduce until death. However, *N. arenaceodentata* was able to live but apparently unable to fertilize the eggs laid by the last two females.

During the course of this study, we noted changes in the appearance of both species with age. Many morphological modifications were noted at the anterior end of *Neanthes*. By the time the male had completed the second reproductive period, the two eyes on each side were enlarged and by the fourth or fifth reproductive period they became fused. This enlargement did not correspond to eye changes present in epitokal nereids. Dark pigment, in contrast to the tan body color, was noted at the fourth reproductive period, especially on the ventral side around the mouth. Pigmentation extended laterally and dorsally and extended to the prostomium, peristomium, and the first setiger. In some males, the distal end of the palpi and peristomial cirri were shortened and distorted. Males continued to feed on algae through the seventh spawning period. The one male that lived beyond this time did not eat. It is not known if these morphological changes had any effect on the ability of the one surviving male to feed. It is unknown if the male inability to fertilize the eggs at the eight and ninth laying was because of declining health or lack of sperm.

Distortion of the body shape was the only morphological change observed in *Dinophilus.* The posterior half of the worm became bulged after several egg layings, which apparently was due to the accumulation of eggs in the coelom. While capsule formation and egg laying continued throughout the life of the worm, both male and female eggs were laid free of a capsule initially at the fourth laying period and increased with subsequent layings. Neither the male nor female eggs developed. It is not known if the male egg contained sperm.

The possible explanation given by Qian & Chia (1992) for the decrease in egg size and number may be the result of depletion of the adult's resources for reproduction in the fourth and fifth eggs layings. They also noted that the body size of *Capitella* sp. decreased with age. No such change was noted in *Dinophilus.* The situation is different with *Neanthes* since only the male survives. It continued to increase in weight through the sixth egg laying, but lost weight after this time when it was no longer able to feed. Whether the inability to fertilize the eggs was due to the lack of spermatogenesis or the poor condition of the sperm is unknown.

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