Proceedings - Cambridge Philosophical Society
Cambridge [etc.], Cambridge Philosophical Society [etc.],
https://www.biodiversitylibrary.org/bibliography/39008

v.17-18 (1913-1916): https://www.biodiversitylibrary.org/item/96059

Article/Chapter Title: The swarming of Odontosyllis
Author(s): Frank Potts
Subject(s): Annelida, reproduction
Page(s): Page 193, Page 194, Page 195, Page 196, Page 197, Page 198, Page 199, Page 200

This page intentionally left blank.

The Swarming of Odontosyllis. By F. A. Potts, M.A., Trinity Hall.

[*Read* 10 February 1913.]

Throughout the months of June and July in 1911 I had frequent occasion to take and examine dredgings from the sea bottom outside the harbour of Nanaimo, British Columbia. The bottom deposits there are of a peculiar character, consisting largely of the debris of dead Hexactinellid sponges. The long interwoven spicules form a matted mass which furnishes a secure retreat for many species of Polychaet worms. One of the most abundant and interesting of these is a species of Syllid which proved to be *Odontosyllis phosphorea* described by Moore* in 1909. During the whole period the worms of this species contained reproductive products. The females were of a bright red colour due to the eggs, while the males showed the natural yellow colour and transverse markings of the species. Both sexes were very irritable under handling and broke up entirely when attempts were made to fix them with sublimate solutions or alcohol, and at the same time an intense phosphorescence was produced.

No appearance of the mature worms at the surface was noticed during these months, though a close lookout for phenomena of this kind was maintained. On August 15th, however, Professor McMurrich of Toronto informed me that he had observed just before sunset hundreds of small worms swimming on the surface of the sea in Departure Bay, a shallow inlet adjacent to the grounds described above. Examination of a number of these which had been brought into the laboratory showed me that they belonged to the species found so abundantly amongst the sponge debris.

The next night Professor McMurrich and myself followed the phenomenon as closely as possible. Sunset was about seven o'clock, and half an hour or more before isolated individuals began to appear. At first these were mostly males, but as the numbers increased so did the proportion of females to males until there was approximate equality. On their appearance from the depths the individuals of both sexes swam round and round in circles with swift undulatory movements. A short time after, the movements became slower, finally ceasing, and during spasmodic flexures of the whole body the eggs and spermatozoa were discharged. Then the spent individuals sank slowly beneath the surface. No approximation of the two sexes was observed to take place, but my impression was that each individual sought the surface without fixed plan or

* J. Percy Moore, *Proc. Acad. Nat. Sci.*, Philadelphia, vol. lxi. 1909, p. 327.

direction, rid itself of its contents as quickly as might be, and then lost no time in descending to its accustomed habitat. The phenomenon continued till the light had nearly faded, but by then there were only very occasional individuals to be seen, so that probably the whole period of swarming is less than an hour.

On the following day I left Nanaimo, but I was afterwards told that, though a few individuals were seen on the surface on that night and the next, there were nothing like the numbers of the two preceding nights.

The accompanying map shows the distribution of *O. phosphorea* in the neighbourhood of Nanaimo. In explanation of the small area assigned to the swarming worms, it must be noticed that the short time did not allow a complete investigation of their distribution, but doubtless future observers will be able to map out the area more completely. One fact is quite clear; that the worms, in seeking the surface, migrate inshore in considerable numbers, for I never, in the course of many dredgings, found a single example of *Odontosyllis* in Departure Bay itself.

Recently Professor McMurrich has been kind enough to send me very interesting information which establishes the periodic appearance of the swarms of *Odontosyllis*. The weather was very unfavourable in 1912 and there had been a great deal of rain just before August 18th. On that night, however, the weather was fine, and on going out at 7.30 p.m. Professor McMurrich found *Odontosyllis* swarming at the surface as in the year before. Dr Fraser again observed the phenomenon on the two or three evenings following.

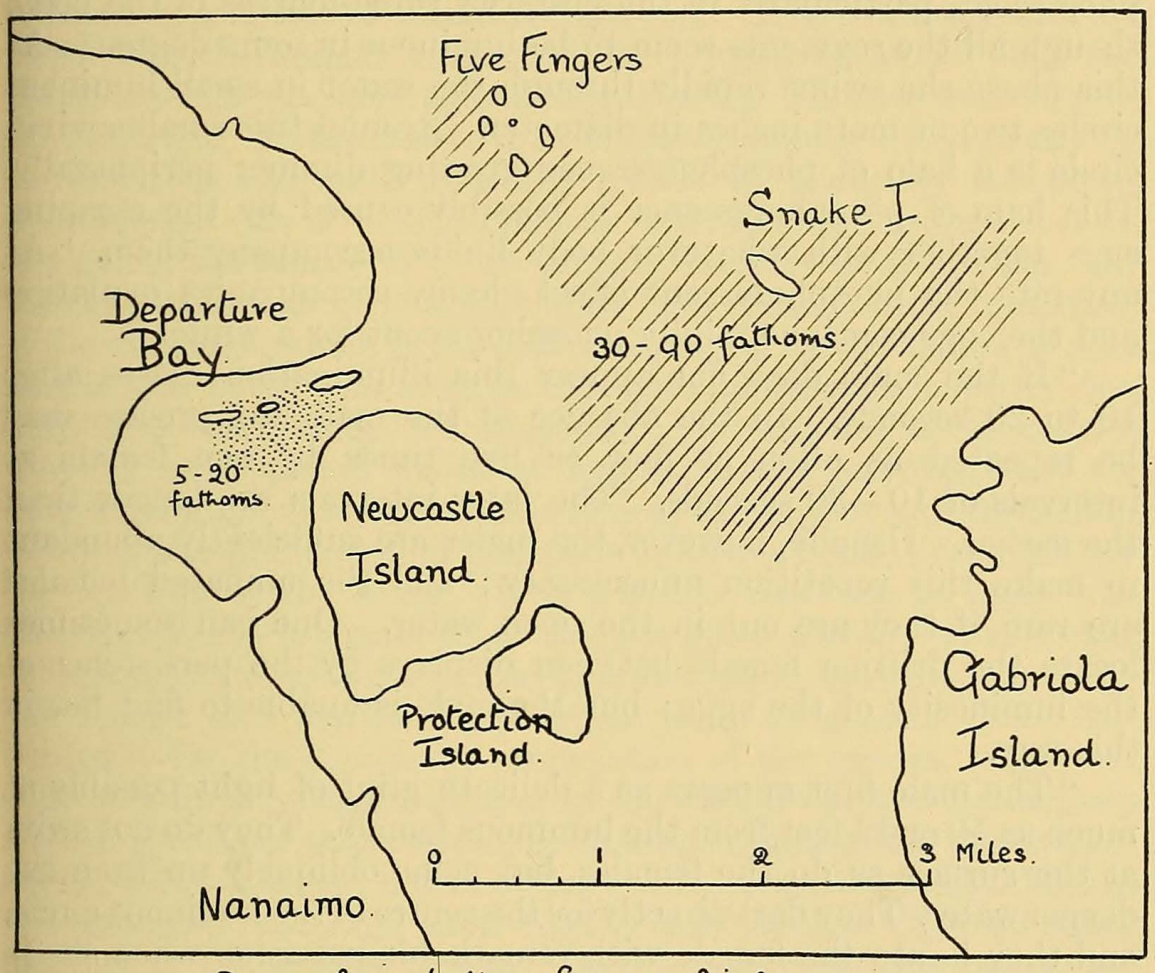
It seems certain, then, that the swarming of *Odontosyllis phosphorea* takes place at Nanaimo at approximately the same date every year. In 1912 it occurred three days later than in 1911, but this may possibly have been due to the unfavourable weather. In 1911 swarming took place during the last quarter of the moon and in 1912 at the beginning of the first quarter. In both cases the tide was full or just falling. The close proximity of the Dominion Government Biological Station will allow of a close watch being kept on the circumstances of the appearance from year to year, and I trust that the scanty data which I give here will soon be supplemented. In particular I hope that enquiry will be made as to whether swarming takes place at any other period of the year*.

For some time I supposed that the phenomenon witnessed at Nanaimo had not been previously described in *Odontosyllis*, and it

* In the original description by Moore (*loc. cit.*) he states that the type specimens were labelled "Phosphorescent annelids caught at surface; Avalon Bay, Catalina Island, evening, April 11, 1904." This fixes a date for the swarming of this species in California.

was with great interest that I discovered and read a paper by Galloway and Welch* on very similar phenomena in an Atlantic species *Odontosyllis enopla*. In the summer of 1904 this species was observed to appear in the surface waters of Harrington Sound, Bermudas, in considerable numbers and with striking regularity. The following dates of appearance are chronicled:

July 3—7 reaching a maximum on the 4th,
July 29—31 „ „ „ „ 30th,
August 23 (no further details),



Distribution of O. phosphorea.

so that there appears to be an interval of approximately 26 days. On the two first occasions when they were carefully observed they appeared each day within fifteen minutes of the same time just at twilight. The daily period of swarming lasted from 20—30 minutes. "Only a few appeared at first each evening. The numbers gradually

* *Trans. Amer. Micr. Soc.*, vol. xxx. 1911, pp. 13–39.

increased to a maximum when scores might be seen at once. The display waned somewhat more suddenly than it waxed.

"The males and females differ considerably in size, the females often being twice as long as the males....Both sexes are distinctly phosphorescent—the female with strong and more continuous glow and the male with sharper intermittent flashes.

"In mating the females, which are clearly swimming at the surface of the water before they begin to be phosphorescent, show first as a dim glow. Quite suddenly she becomes acutely phosphorescent, particularly in the posterior three-fourths of the body, though all the segments seem to be luminous in some degree. At this phase she swims rapidly through the water in small luminous circles two or more inches in diameter. Around this smaller vivid circle is a halo of phosphorescence growing dimmer peripherally. This halo of phosphorescence is possibly caused by the escaping eggs together with whatever body fluids accompany them. At any rate the phosphorescent effect closely accompanies ovulation and the eggs continue mildly phosphorescent for a while.

"If the male does not appear this illumination ceases after 10 to 20 seconds. In the absence of the male the process may be repeated as often as four or five times by one female at intervals of 10—30 seconds. The later intervals are longer than the earlier. Usually, however, the males are sufficiently abundant to make this repetition unnecessary; and the unmated females are rare, if they are out in the open water. One can sometimes locate the drifting female between displays by the persistence of the luminosity of the eggs; but the male is unable to find her in this way.

"The male first appears as a delicate glint of light possibly as much as 10 or 15 feet from the luminous female. They do not swim at the surface as do the females, but come obliquely up from the deeper water. They dart directly for the centre of the luminous circle, and they locate the female with remarkable precision when she is in the active stage of phosphorescence. If, however, she ceases to be actively phosphorescent before he covers the distance he is uncertain and apparently ceases swimming, as he certainly ceases being luminous, until she becomes phosphorescent again. When her position becomes defined he quickly approaches her, and they rotate together in somewhat wider circles, scattering eggs and sperm in the water. The period is somewhat longer on the average than when the female is rotating alone; but it, too, is of short duration.

"So far as could be observed the phosphorescent display is not repeated by either individual after mating. Very shortly the worms cease to be luminous and are lost."

This is, I submit, a very remarkable account. In its general

aspects the swarming in this species resembles that in *O. phosphorea*, *i.e.* in the appearance of great numbers of individuals at the surface of the sea at definite times of the year and at a definite period of the day in the neighbourhood of sunset. But the divergencies in the habits of the two species are very interesting. While *O. phosphorea* first reaches the surface well before sunset, *O. enopla* is not seen till dusk has fallen. In this latter species, moreover, the phosphorescence, which is characteristic of most species of this genus, is developed to a most extraordinary extent and is adapted to serve as a means of sexual recognition. This is almost without parallel in the animal kingdom. It is, however, stated that the function of the phosphorescent organs in the Fireflies is to attract the other sex. In the case of the common glow-worm it is generally allowed that the male finds the female by means of her phosphorescence. Mr J. C. F. Fryer has told me of a Lampyrid beetle in Ceylon, the female of which actually remains in deep holes, but that she emits a most powerful light from organs on the underside of the abdomen, which is the better displayed by the flexion of that part of the body. As soon as the male approaches, however, the light dies down as in *Odontosyllis*. The account of *O. enopla*, which I have quoted above at length, shows, however, that we have among much lower animals almost as complex a phenomenon in which the production of phosphorescence is equally essential for the meeting of the sexes. It is possible, however, to make one criticism of the interpretation which is given above. This is that an arrangement to secure close approximation between the male and female of a marine worm would seem in general to be unnecessary for the successful propagation of the species. There is none such in *O. phosphorea*, and in the case of our two commonest British species of *Odontosyllis*, *O. ctenostoma* and *gibba*, the heterosyllids seem to occur, not in swarms, but as scattered individuals, and probably discharge their eggs or spermatozoa when no other member of the species is near. In the only reference respecting the pelagic occurrence of these species that I am able to find Gravely* says: "The brown *Odontosyllis* (*i.e. O. gibba*) is frequently seen in the adult condition—occasionally accompanied by *O. ctenostoma* and sexual specimens of *Autolytus* and *Myrianida*—swimming at the surface of the sea at the mouth of Port Erin Bay and further out towards the Calf on calm evenings during July." This passage, I think, clearly points to an irregular and sporadic occurrence.

If there are these considerable differences in the reproductive habits of the different species there must, I think, be equivalent physiological differences in the reproductive cells of the species. One would expect, from the elaborate devices practised by *O. enopla* to ensure fertilisation, that the independent life of the eggs and

* *Q. J. M. S.*, vol. LIII. p. 600.

spermatozoa of that species was very brief and that fertilisation must take place very shortly after dehiscence, while probably in *O. gibba* and *O. ctenostoma* the genital products can survive for a much longer time in sea-water.

In the literature of swarming amongst Annelids a majority of the observations refer to the genus *Nereis* and show a great diversity of reproductive habits. Hempelmann*, who has investigated the case of *N. dumerilii* very thoroughly, found that at Naples heteronereid forms occurred at the surface of the sea from 1st October, 1908—15th May, 1909. From 15th May, 1909—15th August, 1909 there were no heteronereids. The mature worms appear at the surface indifferently in the day or the night and usually occur not as swarms but scattered individuals which discharge their eggs or spermatozoa when no other heteronereid is near. But on one occasion at least, on May 2nd, 1908, there was seen in the Bay of Naples a great swarm of *N. dumerilii* and *N. coccinea.*

Similarly attention has been lavished on the heteronereids which are seen off the east coast of England. Sorby† was accustomed to observe the phenomena in the summer throughout a long series of years. On several occasions he saw immense numbers of heteronereids on the surface. The date, time and place of occasion of these are indicated in the following table:—

23 May, 1885.	*N. dumerilii.*	In the evening at the mouth of the Colne.
16 July, 1898.	„ „	At 5 o'clock in the morning at the mouth of the Stour and Orwell, the sea being covered with millions of worms.
11 May, 1882.	*N. longissima.*	In the evening near Sheerness.
24 May, 1889.	„ „	At the mouth of the Orwell.
9 September, 1889.	„ „	In the evening at Queenborough.

In twenty years Sorby only saw five such great swarms of nereids. He does not state that he ever observed isolated heteronereids on the surface of the sea, and for this reason the record of these English occurrences is lamentably incomplete. But his observations go to establish several facts which Hempelmann's more thorough, but less extended, investigations give no clue to, viz.:—

* "Zur Naturgeschichte von *Nereis dumerilii*," *Zoologica*, Bd. xxv. Heft 62, 1911, pp. 92 ff.

† Sorby, *Journ. Linn. Soc.*, London, vol. xxix. 1906.

(1) that these great swarms of nereids are only seen rarely;

(2) that they occur at almost any time of the day (at early morning, at midday* or in the evening) and nearly any period of the summer;

(3) that the date of swarming has no definite relation to the full moon.

On the whole I think we are justified in stating that in *N. dumerilii* and probably other species the swarming habit is not fixed. Hempelmann has noticed a slight correlation between the appearance of the heteronereids and the phases of the moon, but this is by no means marked. There is no doubt from Hempelmann's observations that the ascent of the sexually mature worms is due to a combination of causes which act throughout a long period and whose efficacy fluctuates considerably.

Enough has been said to indicate the irregularity in period and time of the swarming of *Nereis dumerilii* and other associated forms. There is, however, at least one good case in the genus where an absolute periodicity has been established. I refer to *N.* (*Ceratocephale*) *osawai* of Japan†, the heteronereids of which regularly issue forth four times in the year in the months October and November, in 3—4 day periods. Their date of appearance is absolutely fixed for the days following the new moon. Their presence on the surface is limited to from one to two hours in the evening, but the time of appearance is by no means so definitely fixed as in the case of *Odontosyllis phosphorea* and *enopla* (sunset). They appear in fact well after sunset and often after moonset, so that the immediate stimulus would appear to be independent of the action of light.

Other cases might be quoted, but I think my main contention, the diversity of swarming habits in *Nereis*, is sufficiently proved.

The phenomenon of swarming, at least in its final form, does appear to be of a definitely adaptive nature. The object is the fertilisation of the maximum number of eggs, and this is gained by the simultaneous emission of eggs and spermatozoa from a crowded mass of male and female individuals. Galloway and Welch found in *O. enopla* that of eggs collected in connection with the swarming worms from 45—80 °/₀ were already fertilised. In the case of the Atlantic Palolo worms, which turn the clear blue waters of the Tortugas into a thick milky mass with their eggs and spermatozoa, it is difficult to imagine how any of the eggs escape fertilisation. Yet Professor Mayer tells me that the

* Mr William Brockett in the month of June, 1910, collected a rather large number of heteronereids off Mersea Island on the Essex coast between midday and two o'clock in the afternoon.

† Izuka, "Observations on the Japanese Palolo *Ceratocephale osawai*," *Journ. Coll. Sc.*, Tokio, T. xxxvi. 1903.

eggs laid by females on the borders of the swarm are certainly not developed.

How, then, does it come about that a species like *N. dumerilii*, the heteronereids of which become sexually mature at any time within a widely extended period, and in which the swarming habit is very indefinitely developed, is able to maintain its great numbers and wide distribution. Not only is there no arrangement to ensure the simultaneous swarming of the sexes, but it has frequently been observed in this and related species that large swarms consist of a single sex*. Under these circumstances there must be an enormous waste.

There is, however, one obvious explanation. *N. dumerilii* is a polymorphic species, and according to the results of von Wistinghausen and Hempelmann all individuals have more than one period of sexual maturity. When they first reach a certain length the female lays eggs, within the tube she normally inhabits, to the number of 1000 or more. These are generally fertilised in the most economical manner by the male, who creeps into the tube and spreads his sperm over the eggs. It would seem probable that this is the method most responsible for the maintenance of the species, the production of sexually ripe heteronereids at a later period of life being a subsidiary (possibly incipient or degenerate) phenomenon.

These comments on swarming in *Odontosyllis* and *Nereis* are only intended to illustrate the diversity in the habit existing among related forms. I have not attempted to discuss the thorny question of the part played by external stimuli or the possibility of an inherited rhythm in the organism.

Note. Since writing the above I have had access to a paper by Lillie and Just (*Biol. Bull.*, Feb. 1913) on the breeding habits of *Nereis limbata*. In this species swarming takes place quite regularly in four runs during the summer corresponding to the lunar cycles in the months June, July, August, September, occurring on many successive nights shortly after sunset and lasting little longer than an hour. This is, then, an advanced case of the swarming habit, but the great interest lies in the fact that the female produces a substance which acts on the male causing the emission of sperm. It will be of great interest to see whether the distribution of this phenomenon is at all general or whether it is a peculiar development of the swarming habit to ensure fertilisation, like the mating relations in *Odontosyllis enopla*.

* Cf. Sorby, Hempelmann, *loc. cit.*