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THE SPAWNING OF *ARENICOLA MARINA* (L).

I. THE BREEDING SEASON

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(Text-figs 1 and 2)

As a result of work by Pirlot (1933), Newell (1948), Smidt (1951) and Duncan (1953) it has become accepted that on European coasts the lugworm has a restricted breeding season occurring only in the autumn. Previously, several workers had stated that this species also spawns in the spring. Kyle (1896) reported that at St Andrews spawning took place between January and March and again between July and September. Similarly, Gamble and Ashworth (1898) and Ashworth (1904) found that on the Lancashire coast the laminarian variety spawned in the spring, although the littoral variety spawned during late summer.

Pirlot (1933), Newell (1948) and Duncan (1953) also suggest that there is some relationship between the onset of spawning and a particular phase of the tidal cycle. Thus, Pirlot (1933) observed spawning during three seasons on the Belgian coast; on each occasion there was a 2-day spawning crisis falling on either full or new moon spring tides. He suggested that the onset of spawning is influenced by the moon acting through tides. Newell (1948), in a comprehensive review of the life history, found that at Whitstable, although spawning started during springs, the peak of spawning occurred during neaps. Duncan (1953) collected data from many areas around the British Isles and, with the exception of St Andrews, again found that the peak of spawning took place during neap tides. Duncan also noted that spawning occurred later in the year on the west coast of Britain and in Ireland than on the east coast of Britain, and suggested that in any one area spawning takes place at about the same time each year.

In the present paper, the relationships between environmental conditions and the onset of the breeding season are analysed in greater detail and the possibility of a spring breeding season re-examined.

Lugworms were collected at intervals during the years 1949–53 at St Andrews, and 1953–57 (excluding 1956) at Dublin. Mr E. Latham of the Marine Laboratory, Millport, supplied worms from Fairlie Sands and Kames Bay during the spring of 1958.

The terms *laminarian* and *littoral* are used here merely to indicate whether the worms were collected at a low level (L.W.N.T.—L.W.S.T.—laminarian) or high level (H.W.N.T.–L.W.N.T.—littoral) on the shore. Both littoral and laminarian forms were obtained at St Andrews; while near Dublin, littoral forms were collected at Booterstown, and laminarian forms at Seapoint. The worms supplied from Millport were laminarian forms.

The earlier part of this work was carried out at the Gatty Marine Laboratory, St Andrews. Grateful acknowledgement is made to Dr J. M. Dodd for help and advice, and to the Carnegie Trust for a grant in aid of research. The author is also indebted to the Meteorological Office of the Air Ministry, Edinburgh, for sea temperature records from the Bell Rock Lighthouse, off St Andrews, and air temperatures from the R.A.F. station, Leuchars near St Andrews. The Meteorological Service, Department of Industry and Commerce, Dublin, kindly supplied air temperature records from Dublin Airport (Collinstown).

THE SPRING BREEDING SEASON

The opportunity was afforded at St Andrews to re-examine, in the same area, the work of Kyle (1896) who reported the spawning of *Arenicola marina* in the spring. Lugworms were collected during February, March and April in each year from 1949 to 1953. None of the worms examined contained genital products, and there was no evidence of spawning taking place.

As regards Millport, the author is indebted to Dr J. D. Robertson of the University of Glasgow and Mr E. Latham of the Millport Marine Station for the following observations (personal communications). Robertson states that he received '*Arenicola* with near-ripe eggs and sperm' from Millport on 30 March 1956 and on 19 March 1957. Latham agreed that 'around Easter spring tides *Arenicola* collected from Fairlie Sands were ripe', but he also mentioned that specimens from Kames Bay spawned later in the year. As a result of these observations, samples were obtained from Millport at approximately monthly intervals in the spring of 1958. On 10 March, fourteen specimens were obtained from Kames Bay. None of these contained genital products. In contrast, fourteen specimens collected from Fairlie Sands on the same date all contained genital products. Of these, five females contained eggs approaching maturity (average diameter 100–180 μ) while three females contained 'mature' eggs (average diameter 180–190 μ). Three males contained sperm cells approaching maturity (40–80 % in morulae) while three were immature (0–40 % in morulae). The stage in development of the sexual products of males can be estimated by counting the relative numbers of rosettes and morulae (sperm plates) in thin films of coelomic fluid. Morulae gradually replace rosettes as spawning approaches. Newell (1948) describes the stages in the development of the germ cells in the body cavity.

In the further collection of twenty-seven worms from Fairlie Sands on 9 April, twenty-one contained genital products approaching maturity or were mature. There was one immature specimen and five specimens which were thought to be spent. Spent females contained a few residual eggs, irregular in size; spent males contained a few morulae. In both sexes, there was an unusual amount of dark granular material in the body fluid.

There was a marked change in a sample obtained on 19 May (Table 1). Of twenty-five worms, eighteen were spent, only three contained genital products approaching maturity or 'mature' while four specimens were immature. This pattern was repeated in a sample obtained on 3 June, except for an increase in the number of immature specimens (Table 1).

TABLE 1. SAMPLES FROM FAIRLIE SANDS, MILLPORT, DURING SPRING OF 1958

Date	No. of worms	Immature[1]	Approaching maturity[2]	'Mature'[3]	Spent or no genital products
10. iii. 58	14	3	8	3	0
9. iv. 58	27	1	14	7	5
19. v. 58	25	4	1	2	18
3. vi. 58	30	12	2	0	16

[1] Gametocytes or eggs: 40–100 μ. Sperm: 0–40 % morulae.
[2] Eggs 100–180 μ. Sperm: 40–80 % morulae.
[3] Eggs 180–190 μ. Sperm 80–100 % morulae.

TABLE 2. DEVIATIONS IN ANNULATION AND SEGMENT NUMBER AMONG SPECIMENS OF *ARENICOLA MARINA* FROM FAIRLIE SANDS, MILLPORT

	Annulation formula[1]		Chaetigerous segments		
No. of specimens	i. 2, ii. 3, iii. 4	i. 2, ii. 2 or 2½, iii. 4	Incomplete 19	Complete 19	Incomplete 20
96	90	6	6	85	5
Percentage	93·75	6·25	6·25	88·5	5·25

[1] See Wells, 1957.

The specimens from Fairlie Sands were examined anatomically. All were large (trunk = 19 cm average length), dark worms and were collected from the laminarian zone. This suggests that they might belong to the spring-spawning 'laminarian variety' defined by Gamble & Ashworth (1898) and Ashworth (1904). However, a very large proportion of the worms from Fairlie Sands displayed the annulation of the first chaetigerous segments described for their 'littoral variety', i.e. i. 2, ii. 3, iii. 4 (formula after Wells, 1957, see also Table 2).

No evidence was thus found to support Kyle's (1896) report of a spring breeding season at St Andrews. However, there is no doubt that a large proportion of the laminarian population on Fairlie Sands, Millport, spawns in the spring (mainly between 9 April and 19 May in 1958). The immediate appearance of immature worms (containing gametocytes) after the spring breeding season at Fairlie Sands suggests that at least a proportion of this population spawns again later in the year. In view of the fact that Gamble & Ashworth (1898) and Ashworth (1904) gave accurate accounts of oviposition when describing a spring spawning among lugworms on the Lancashire coast, it is surprising that little credence has been given to their work in recent years. Although Duncan (1953) reported autumn breeding among nearby populations (Wales, Isle of Man), this does not invalidate their observations. As shown above, the Fairlie Sands population probably breeds both in spring and autumn, while the adjacent Kames Bay population breeds only in the autumn. It may well be then, that at least on the west coast of Britain, there are isolated spring-spawning populations other than that described here. In common with worms from all other areas studied in recent years (Wells, 1957; Brewster, unpublished), the vast majority of the worms from Fairlie Sands display the characters of the 'littoral variety' as defined by Gamble & Ashworth (1898). It appears, therefore, that the occurrence of a spring spawning at Millport is unrelated to varietal differences.

Southward & Southward (1958) have recently reviewed breeding in the Arenicolidae. The belief that *A. marina* spawned only in the autumn led them to suggest that this species conforms to Orton's (1920) dictum that species towards the southern limits of their distribution should breed only in the colder months of the year. Despite the account of a spring breeding season given here, this statement is still largely true. It is significant that the spring-spawning population at Millport is laminarian in situation. It is suggested that the higher temperatures experienced by these forms, due to their greater coverage by the tide, permits gamete formation to go forward during the winter. If this is true, it might be expected that spring spawning would be common among laminarian populations. However, the larval stages of *A. marina* are found in the surface sand towards the upper reaches of the shore (Newell, 1948). It is unlikely that the larvae of a cold-water species would be able to survive the high summer temperatures experienced in this habitat, particularly towards the southern limits of its distribution. This hypothesis would account for the possibility of gamete production during the winter and at the same time the rarity of spring-spawning populations in Britain. It may be that, due to local factors, larvae of *A. marina* find an unusually sheltered habitat on Fairlie Sands.

THE AUTUMN BREEDING SEASON

The percentages of worms containing genital products in the collections made at St Andrews and Dublin during late September, October and November are given in Tables 3 and 4 and shown against minimum air temperatures and tidal conditions in Figs. 1 and 2. The air temperatures given are the lowest *at low tide* in periods of 5 days. When spawning was not observed on the shore the appearance of spent worms in the collections, i.e. a decrease in the percentage of worms containing genital products, indicated that breeding was taking place.

St Andrews

The date on which spawning commenced was most accurately determined in 1951 and 1952. A few sperm puddles were observed on the shore on 29 and 31 October 1951. It was evident that spawning had just commenced as few of the worms collected on these dates were spent (Table 3). The peak of spawning occurred on 1 and 2 November and spawning continued up to

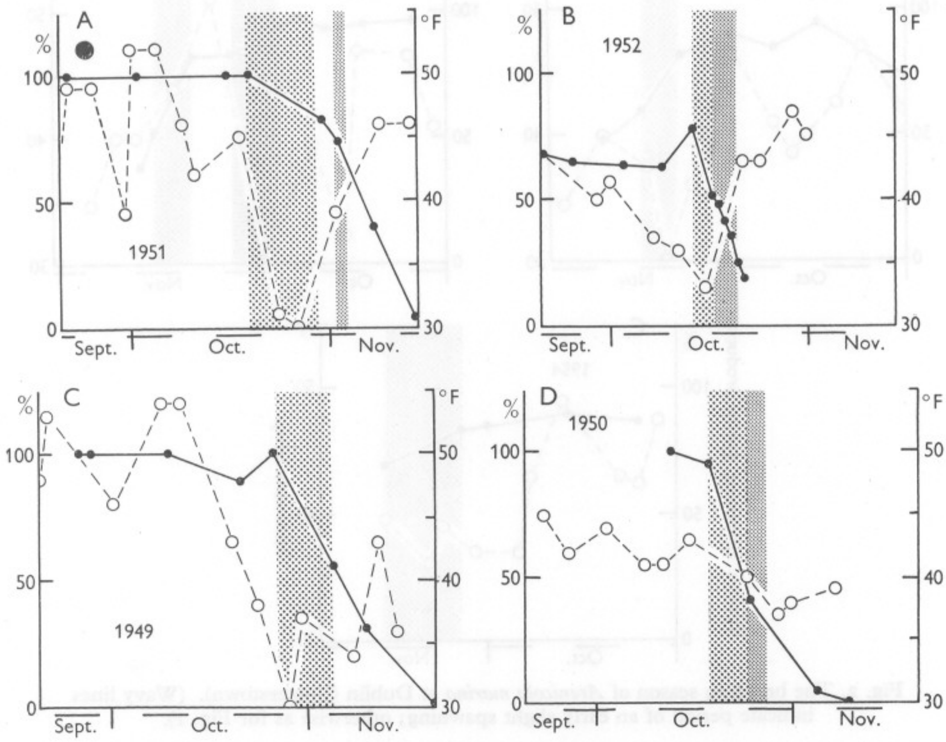

Fig. 1. The breeding season of *Arenicola marina* at St Andrews related to minimum air temperatures and tidal conditions. ○- -○, minimum air temperatures (° F); ●——●, percentage of worms containing genital products; Large stippling, period during which spawning commenced; fine stippling, time at which peak of spawning was observed on the shore. A double line on the abscissa indicates a spring tide period.

14 November, when less than 5% contained genital products (Fig. 1A). In 1952, 527 worms were collected between 7 and 14 October; there was no evidence of a drop in the percentage containing genital products (Table 3) and no sign of spawning on the shore. On the 16th to 19th inclusive, sperm puddles appeared all over the shore (the peak) and the percentage of mature worms decreased sharply. Spawning activity had very much decreased by the 20th and 21st.

The breeding seasons in these years were similar in that (*a*) they commenced towards the end of a period of neap tides, (*b*) the peak was mainly during the succeeding full moon springs, and (*c*) the beginning of spawning coincided with a sharp fall in minimum air temperatures; this being the first drop to the seasonal minimum in each year (Fig. 1 A, B).

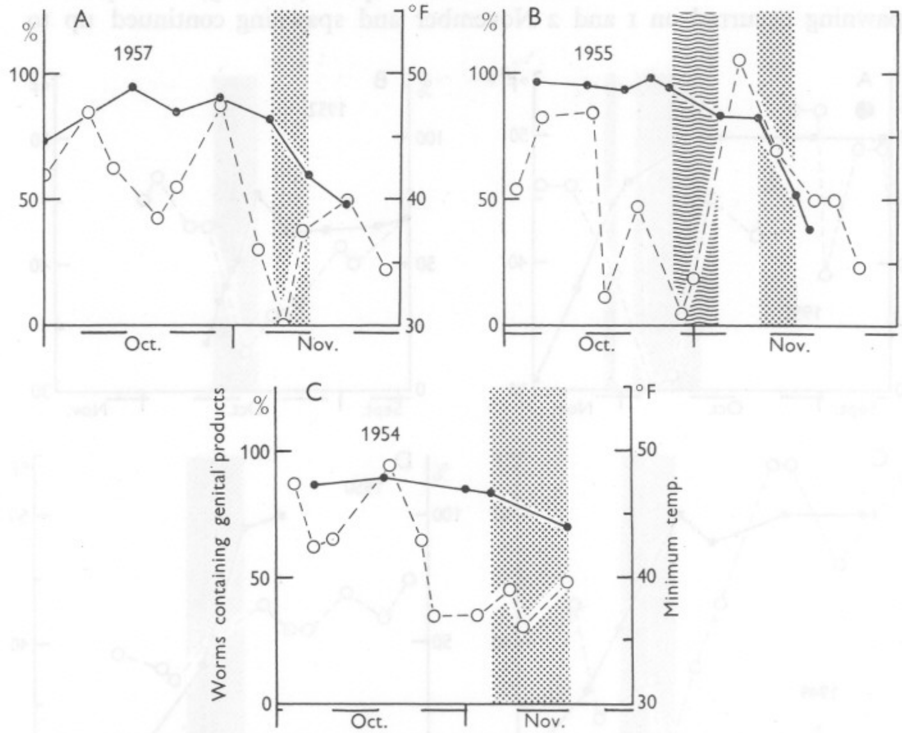

Fig. 2. The breeding season of *Arenicola marina* at Dublin (Booterstown). (Wavy lines indicate period of an early slight spawning; otherwise as for Fig. 1).

The seasons differed in relation to weather conditions. In 1951, spawning began in calm weather but storms developed during the peak. In 1952, the weather was calm throughout.

In 1949, collections were smaller and observations were made less frequently. Spawning was not observed, but collection data show that it commenced between 24 October and 3 November, i.e. probably during neap tides (Fig. 1 C). Spawning again coincided with a sharp fall in minimum temperatures. In 1950, collections were made principally from a laminarian population, and it was this population which was observed spawning on the shore. Spawning appears to have commenced between 18 and 24 October (neaps) and the peak was observed on the 24th to 26th inclusive (springs). These data support the tidal relationships observed in 1949, 1951 and 1952. While there was a gradual fall in minimum air temperatures prior to spawning (Fig. 1 D) there was no sharp decrease similar to that observed in the other years mentioned. The spawning of laminarian forms will be discussed as a special case below.

In 1949 the breeding season was characterized by intermittent storms, while in the following year it was calm at first but stormy later in the season.

TABLE 3. RECORDS OF COLLECTIONS AT ST ANDREWS

The 1949–51 records are compounded from two populations which differ in the percentage of the total population normally containing genital products in the summer. This percentage is therefore in each case treated as 100 % and any fall in the number of worms containing genital products is percentaged accordingly. The 1952 figures are from a single population and actual percentages are given.

	Date	Total worms examined	Percentage containing genital products	Spawning observed
1949	26–28. ix.	54	100	—
	9. x.	9	100	—
	20, 21. x.	75	89	—
	24–27. x.	31	100	—
	3–5. xi.	85	56	—
	9. xi.	58	31	—
	20. xi.	20	0	—
1950	12. x.	40	100	—
	18. x.	36	94	—
	23–26. x.	52	41	+ (peak)
	4. xi.	64	5	—
	9. xi.	9	0	—
1951	20. ix.	44	100	—
	1. x.	25	100	—
	14–16. x.	25	100	—
	18. x.	21	100	—
	29–31. x.	89	82	+
	1, 2. xi.	91	73	+ (peak)
	7. xi.	34	41	+
	13–14. xi.	109	4	+
1952	19, 20. ix.	223	68	—
	23–25. ix.	328	65	—
	1–3. x.	441	64	—
	7–9. x.	320	63	—
	12–14. x.	207	78	—
	16. x.	201	52	+ (peak)
	17. x.	311	48	+ (peak)
	18. x.	164	42	+ (peak)
	19. x.	75	36	+ (peak)
	20. x.	141	25	+
	21. x.	106	18	+

Dublin (*Booterstown*)

Spawning in this littoral population was never observed on the shore, but the beginning of the breeding season in 1955 and 1957 can be determined within narrow limits from collection records. Taking 1957 first, the first significant drop in the percentage of worms containing genital products occurred between 6 and 12 November (Table 4). Thus, unlike the above observations at St Andrews, spawning commenced during full moon springs (Fig. 2A). However, the beginning of spawning was again marked by a fall in minimum temperatures.

The position was more complicated in 1955. In regular collections during the summer (of approximately 60 worms/collection) the percentage of the total worm population containing genital products varied between 93% and 98%. Between 27 October and 4 November this percentage dropped to 83%.

TABLE 4. RECORDS OF COLLECTIONS FROM A SINGLE POPULATION AT BOOTERSTOWN, DUBLIN

	Date	Total worms examined	Percentage containing genital products
1957	30. ix.	41	73
	15. x.	38	95
	22. x.	49	85
	29. x.	43	91
	6. xi.	40	82
	12. xi.	50	60
	18. xi.	38	48
1955	6. x.	32	97
	14. x.	57	95
	20. x.	59	93
	24. x.	50	98
	27. x.	70	94
	4. xi.	44	83
	9, 10, 11. xi.	125	82
	16. xi.	60	52
	18. xi.	72	38
1954	6, 8. x.	45	87
	18. x.	31	90
	31. x.	72	85
	4. xi.	36	83
	15. xi.	45	69

In view of the lack of variation in sampling during the season, this drop in the percentage of worms containing genital products was interpreted as indicating the beginning of spawning. There was, however, no further increase in the number of spent worms up to 11 November (Table 4). The main spawning appears to have commenced between 11 and 16 November, during which time the percentage of worms containing genital products fell rapidly to 52%. Both the slight earlier spawning and the main spawning appear to have commenced during spring tides (Fig. 2B). Minimum air temperatures fell abruptly to 32° F on 16–18 October and there ensued a period of cold weather with the lowest temperature (31° F) occurring on 29 October. This coincided with the first slight drop in the percentage of worms containing genital products. Thereafter, air temperatures rose rapidly; the lowest recorded (at low tide) during the next 10 days was 51° F. This was followed by a second period of falling temperatures which coincided with the beginning of the main breeding season (Fig. 2B).

Only a limited amount of data is available for the 1954 season (Table 4). The first major drop in the percentage of worms containing genital products occurred between 4 and 15 November, but this drop is of doubtful significance as no further collections were made. This period was preceded by a sharp fall in minimum air temperatures, but in this case only to 37° C. There was no record of spawning at Booterstown in 1953 (see below).

Dublin (*Seapoint*)

The breeding season of the laminarian population at Seapoint was never fixed with accuracy, but the following observations were made during 1953, 1954 and 1957. In 1953, 75% of the Seapoint population were spent on 4 November, although there was no indication of the Booterstown population even beginning to breed as late as 12 November, when collecting was discontinued. On 9 November 1954, 89% of the Seapoint worms were spent when breeding was just beginning at Booterstown. Finally, in 1957 there was evidence to show that breeding was under way around 9 October at Seapoint, and in this case the season did not commence at Booterstown until 6/12 November. Although in each year, spawning at Seapoint was preceded by gradually falling temperatures (as at St Andrews in 1950) the minimum recorded prior to spawning (37°–40° F) was not so low as that usually associated with spawning in littoral populations.

DISCUSSION

The evidence of Newell (1948) and Duncan (1953) that in most areas around the British Isles autumn-spawning *Arenicola* begin to breed during spring tides, while the peak of spawning occurs during neaps, cannot be disputed. Although spawning was not observed on the shore at Dublin, and in consequence little can be said about the occurrence of the peak, evidence that spawning commences during spring tides tends to support their observations. On the other hand, there is no doubt that in some areas, e.g. St Andrews, the opposite occurs. Spawning begins during neaps, and its peak occurs during springs. If Pirlot's (1933) 'spawning crisis' is equivalent to the peak of spawning his evidence supports this statement. This variation suggests that tidal or lunar conditions cannot alone control the onset of spawning in *Arenicola*. Similarly, rough and calm weather vary in relation to the breeding season. Observations made at St Andrews again agree with Pirlot in this respect.

The present paper was stimulated by the subjective observation, over many years, that spawning at St Andrews is first seen on frosty mornings. Examination of the meteorological records presented in this paper, shows that there is an apparent correlation between the first fall in air temperatures to the autumnal minimum and the onset of spawning, at least in littoral populations.

Whether this correlation has any significance depends in part on the extent to which *Arenicola* may be exposed to a sudden fall in air temperatures during the intertidal period. Southward (1958) has shown that, in winter, during daylight, air temperatures close to rocks on the shore and the body temperatures of animals are generally higher than screen air temperatures read even at a nearby site. However, on an isolated occasion when there appears to have been a sudden cold spell (18 November 1953, Table 4, p. 59) Southward shows that at 10 a.m., after 7 h exposure, screen air temperatures, shore temperatures and the average body temperatures of barnacles and top shells lay within the range 6·8° C to 7·9° C. Previously, Bruce (1928) had stated that at 9 a.m. G.M.T. air temperatures and the surface temperatures of beach sands are approximately isothermal. With a low tide at night or in the early morning, there may, therefore, be little mitigation of a sudden and severe fall in air temperature on the sand. Further, during cold weather in the autumn, the sand surface must be subjected to repeated changes in temperature between tidal and intertidal periods as even inshore waters are still relatively warm (Bruce, 1928; Southward, 1958). It might still be argued that by their burrowing habit lugworms escape these changes of surface temperature. Bruce (1928) has shown that at 20 cm the temperature of the sand is similar to that of inshore water. However, Wells (1945, 1949) has suggested that during the intertidal phase the lugworm makes periodic excursions towards the surface in the course of 'aerial respiration' or to test the temperature and salinity of the surface water. There seems little doubt that in this way the lugworm is exposed to surface conditions.

It is suggested, therefore, that the spawning of autumn-breeding *Arenicola* is stimulated, at least indirectly, by the first fall in air temperature to the seasonal minimum. The effect of this fall in temperature is emphasized by the marked difference between sea and air temperatures at that time. In view of the occurrence of a spring breeding season, reported in this paper, it may later be proved that it is merely a distinct change in temperature which is required to initiate spawning once the worms have matured. This problem is now being investigated experimentally.

Contributory evidence for the above hypothesis may be found in the fact that as the eggs develop in the coelom, they rapidly assume the size of mature eggs but are retained in the body cavity for some weeks before spawning actually takes place. A similar observation has been made by Newell (personal communication). This seems to support the idea that spawning is induced by a sudden stimulus such as temperature change rather than by rhythmic tidal influences.

The relatively early spawning of laminarian forms in response to less marked falls in temperature could be explained by the fact that these worms, covered for prolonged periods during neaps, are conditioned to relatively constant temperatures. Thus when exposed during spring tides they may respond to a fall in temperature much less violent than that required to initiate spawning in their littoral neighbours. In this case, there would be an additional element of tidal control.

Although spawning will continue in the face of rising temperatures (Figs. 1 and 2), there may be a fixed temperature above which spawning will not take place. Thus in 1955 (Fig. 2B) slight spawning appears to have coincided with a fall in temperature and then ceased for a period of 7 days, during which the weather was unusually warm (minimum air temperature 51° F). Subsequently, there was a second fall in temperature and the main breeding season commenced. It has also been found that experiments on the artificial stimulation of spawning in *Arenicola* fail at about 57° F (14° C) but the results improve below 53° F (12° C) (unpublished work).

The above hypothesis for the environmental control of spawning in *Arenicola* might explain some of the observations in Duncan's (1953) paper. The earlier spawning among populations on the east coast of Britain than on the west coast may be due to the earlier occurrence of low temperatures on the east coast. The onset of spawning in any one area at about the same time each year may be due to the fact that the first major drop in temperature during the autumn in any given place tends to occur during the same fortnight to three weeks every year (Figs. 1 and 2).

SUMMARY

A spring spawning occurs among *Arenicola marina* on Fairlie Sands, Millport. Although laminarian in situation the vast majority of these worms belong to the 'littoral variety'. This unusual breeding season is, therefore, unrelated to varietal differences. A hypothesis is given for the possibility and at the same time the rarity of spring-spawning populations in Britain. At St Andrews the breeding season occurs during the second fortnight of October, but is unusual in that it begins during neap tides with the peak during the following springs. Breeding in the littoral population at Booterstown (Dublin) is more conventional in that it begins during spring tides; in this case during the first fortnight in November. It is shown that over several years the breeding season of littoral populations at St Andrews and Dublin is preceded by, or coincides with, the first sharp fall in air temperatures to approximately the autumnal minimum. It is suggested that this fall in temperature provides the spawning stimulus for autumn-breeding lugworms. In view of the spring breeding season reported here, it is possibly only a distinct change of temperature which is required to initiate spawning. The earlier spawning of laminarian forms in response to a lesser temperature stimulus, may be due to an element of tidal control.

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