J. mar. biol. Ass. U.K. (1962) 42, 641–654
Printed in Great Britain

THE MORPHOLOGY AND LARVAL BEHAVIOUR OF A NEW SPECIES OF *SPIRORBIS* (SERPULIDAE)

By J. M. Gee and E. W. Knight-Jones
Department of Zoology, University College of Swansea

(Text-figs. 1–4)

A study of the taxonomy (de Silva & Knight-Jones, 1962) and larval behaviour (de Silva, 1962*a*) of Spirorbinae occurring near Swansea showed the specific distinctness of three forms previously confused: (i) *Spirorbis borealis* Daudin, characteristically settling on *Fucus serratus*; (ii) *S. corallinae* de Silva & Knight-Jones, settling on *Corallina officinalis*; and (iii) *S. tridentatus* Levinsen, settling on rocks and stones in dimly lit places. At Plymouth and Dale Fort there is a fourth abundant species which must previously have been confused with *S. borealis* and is described here for the first time.

This species too is characterized particularly by the substratum on which it is found. It occurs on fairly well illuminated rocks, stones and shells, usually on an encrusting coralline alga which is abundant in the lower half of the tidal zone on most rocky shores in south-west Britain. This alga, which is dull purple and has a rather wrinkled surface, may be identified tentatively from the handbook of Newton (1931) as *Lithophyllum incrustans* Phil., though it does not form the high ridges characteristic of this species in the Mediterranean (Lewalle, 1961). Bénard (1960) described the fauna found with this alga but did not identify the *Spirorbis* associated with it. *Lithophyllum* often grows over the *Spirorbis*, but healthy worms are rarely smothered, for if this tends to occur they orientate away from the substratum, so that the growth of the tube keeps pace with the increasing thickness of the *Lithophyllum*. They thus tend to lose the close coiling in one plane which is generally characteristic of *Spirorbis*.

Various peculiarities of the morphology and distribution support the view that this is a distinct species, but it is the peculiarities of the larval behaviour which are especially distinctive. In most of the experiments on larval behaviour, the larvae were offered a choice between two substrata of similar size placed in a crystallizing-dish containing about 250 ml. of sea water. Since the larvae are photosensitive the dishes were placed inside a narrow white box, with its long axis directed towards the light source and the experimental substrata on opposite sides (Knight-Jones, 1951). In an experiment involving choice between several substrata, these were placed round the periphery of a large dish, which was then rotated on a turn-table at a slow, constant speed, to ensure that all were similarly illuminated (Crisp & Ryland, 1960). Details of other experiments are given later.

Spirorbis (Laeospira) rupestris nov.sp.

Tube sinistrally coiled, white, opaque, calcareous and often heavily encrusted with *Lithophyllum*. Not ridged longitudinally but with well marked transverse growth lines. Coiling sometimes irregular. Usually 2–3 whorls, the inner occasionally obscured by the outer (Fig. 1G). Mouth of tube smooth, rounded and sometimes turned away from the substratum. Maximum diameter across outer whorl 4·5 mm.

Tentacles usually nine. Terminal filament 3–5 times as long as distal pinnules in live specimens. Operculum slightly funnel-shaped terminally. Opercular plate bears calcified, short proximal process or 'talon', slightly indented in centre of proximal margin (Fig. 1C).

Thorax of three setigerous segments. Distal part of collar setae about 0·12 mm long, consisting of a proximal fin and a distal blade, separated by a well marked gap.

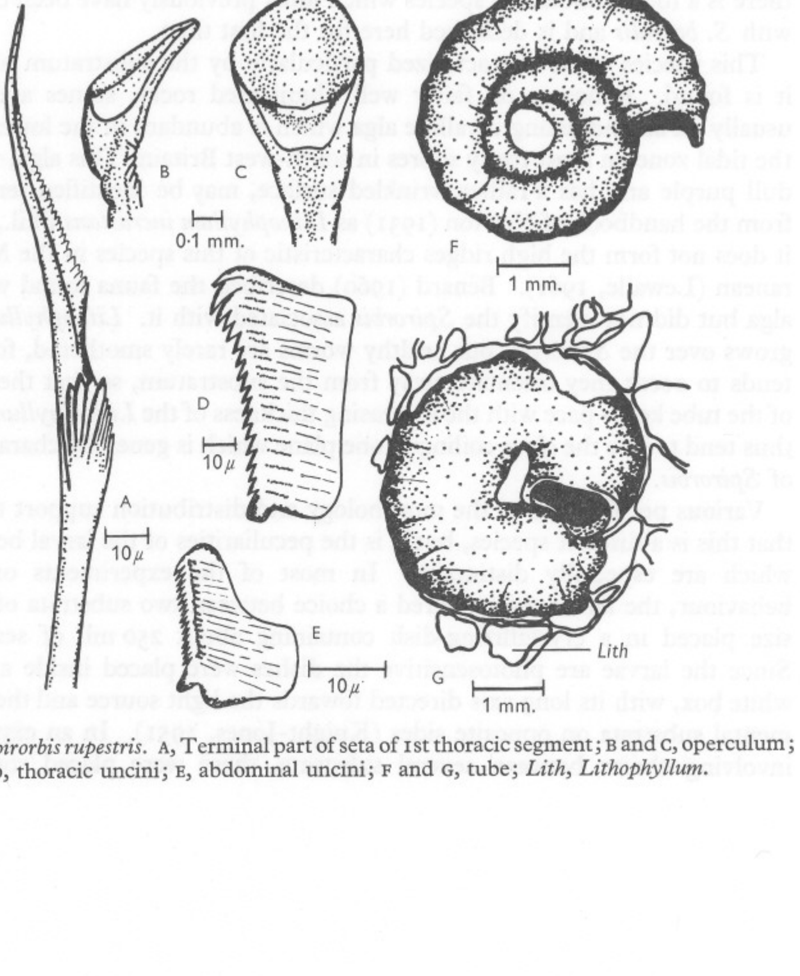

Fig. 1. *Spirorbis rupestris*. A, Terminal part of seta of 1st thoracic segment; B and C, operculum; D, thoracic uncini; E, abdominal uncini; F and G, tube; *Lith*, *Lithophyllum*.

Teeth of proximal fin large near gap between fin and blade, decreasing in size proximally. Blade with serrations on free edge (Fig. 1A). Setae of second segment long and fine with a finely serrated blade. On third thoracic segment, in addition to setae of the preceding type, there are about six sickle-shaped setae, plicate at the concave edge. Thoracic uncini about 0·07 mm long and almost rectangular (Fig. 1D), with slightly concave edge bearing seventeen teeth, decreasing in size towards a terminal rounded peg-like tooth, which is larger than the others and slightly bifid in end view.

Abdomen of about 24–28 segments of which the first two are female. Abdominal setae geniculate with serrations on distal edge. Uncini about 0·02 mm long with straight, finely serrated edge bearing a large terminal tooth (Fig. 1E). Total body length, excluding tentacles, about 4 mm. Body colour usually bright red and orange, especially in the abdominal region. The colour names given in Table 1 were obtained by comparison with the standard colour charts of Ridgeway (1912), and ISCC-NBS (Kelly & Judd, 1955).

TABLE 1. COLOURS OF *SPIRORBIS RUPESTRIS*

	Colour	Ridgeway	Munsell	ISCC-NBS
Tentacles	Colourless, tinged Cosse green by blood	29 GG–Yi	5 GY 5·8/9·0	sYG 117
Collar	Colourless	—	—	—
Thoracic membrane	Tinged Grenadine red	7 R–O	8·5 R 5·4/13·0	vrO 34
Thorax	Tinged Grenadine red	7 R–O	8·5 R 5·4/13·0	vrO 34
Stomach	Yellow ochre often with darker markings	17′ O–7	10 YR 5·8/7·0	dOY–72
Abdomen	Cadmium orange with darker segmental markings	130 Y–O	5 YR 6·0/14·0	v 048, S 050

Reproduction. Ripe ova 0·11–0·18 mm. in diameter and orange brown. Embryos incubated in tube, 10–35 at a time. Larvae 0·4 mm. long, bright orange red with one median tuft of apical cilia. Two pairs of eyes, anterior pair small and red, posterior pair large with black pigment cups and red centre. One yellow, median, dorsal, thoracico-abdominal primary shell gland with well marked duct posteriorly. Two pairs of abdominal uncini (Fig. 2).

Habitat. On fairly well-illuminated stones and rocks in lower half of tidal zone, particularly on sheltered shores, or where the sea water is free from silt. Usually associated with *Lithophyllum*.

LARVAL BEHAVIOUR

Swimming, crawling and attachment

There are several accounts of larval behaviour in *Spirorbis borealis* (Garbarini, 1936; Knight- Jones, 1951, 1953; Gross & Knight-Jones, 1957; Wisely, 1960; de Silva, 1962*a*). On hatching, the larvae generally swim directly towards the light, with the body rotating. They may remain on the lighted side of a dish for several minutes, swimming backwards and forwards, but soon become negative to light and thus readily find dark surfaces, such as *Fucus* fronds. On such a surface a larva stops rotating and crawls with the ventral cilia, probably laying a mucous trail. The prototrochal cilia seem to be active, as in swimming, but crawling differs from swimming in its reduced speed, absence of rotation and adherence to a surface. A crawling larva usually swims off again and becomes positive to light for short periods. Thus alternately swimming and crawling, it visits a number of surfaces before it finds the one on which it settles.

Larvae of *Spirorbis rupestris* behave rather differently. To compare the two species chains of embryos were obtained by breaking open the parent tubes, extracting the embryo chains and leaving them in dishes of clean sea-water. Liberation of larvae then occurs readily or can be speeded up by gently prodding the embryo chain with a fine needle or camel hair brush. De Silva (1958) has shown that the behaviour of larvae of *S. borealis* artificially liberated in this way is similar to that of naturally liberated larvae.

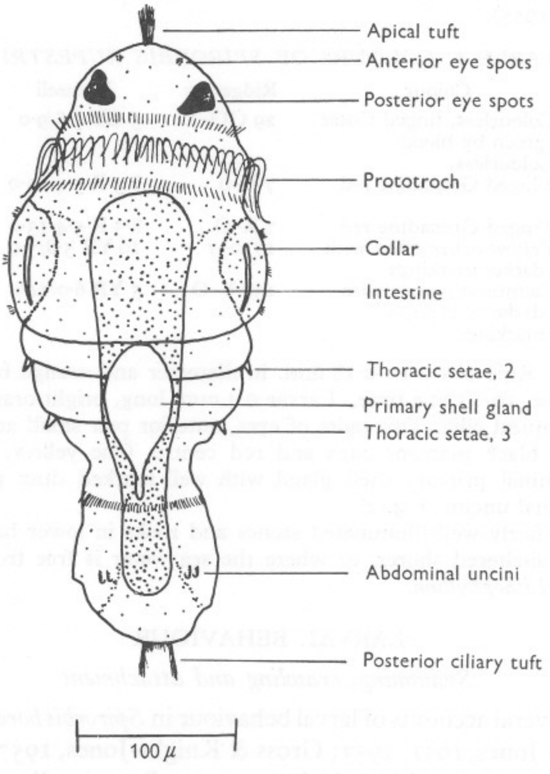

Fig. 2. Larva of *Spirorbis rupestris*.

On hatching, most larvae of *S. borealis* swam towards the light and the remainder swam away from it, but larvae of *S. rupestris* seemed reluctant to swim. They crawled about at random close to the point of hatching. The prototrochal cilia appeared to be beating normally but the larvae were crawling and not swimming. A stream of water from a pipette sometimes failed to move the larvae from the substratum, to which they appeared to be attached by a mucous strand from the abdominal region (not from the primary shell gland). If settlement did not occur during this crawling phase the larvae became pelagic but only after successfully freeing themselves from the mucous trail. They did this by swimming vigorously round in tight circles, usually in planes at steep angles to the substratum. When free they swam directly to the darker side of the dish and took up a truly pelagic existence which sometimes lasted for more than six hours.

If a favourable substratum is present, however, larvae of *S. rupestris* rarely swim at all. To illustrate this striking difference from *S. borealis* a hatching egg-string of each species was placed separately in the centre of a Perspex box, surrounded on three sides by black paper and lit from the remaining side. In some experiments the egg-string was placed directly on the Perspex, in others on a piece of the substratum known to be favourable for the attachment of the species concerned, i.e. *Lithophyllum* or *Fucus serratus*. The results of a series of such experiments are shown in Table 2.

TABLE 2. IMMEDIATE POST-HATCHING BEHAVIOUR OF *SPIRORBIS RUPESTRIS* AND *S. BOREALIS* LARVAE

(Larvae presented with (S.U.) a substratum of smooth Perspex unfavourable for settlement or (S.F.) a substratum favourable for settlement of the species (*Lithophyllum* or *Fucus* respectively). The figures show the percentages which swam positive or negative to light or remained crawling and/or settling.)

		Movement in first 10 sec			Movement in next 30 sec			Later movement after remaining for 40 sec		
		%+	%−	% rem.	%+	%−	% rem.	%+	%−	% rem. settled
S. rupestris	S.U.	0	3	97	0	4	93	18	75	0
	S.F.	0	0	100	0	0	100	0	9	91
S. borealis	S.U.	56	13	31	14	6	11	10	1	0
	S.F.	10	0	90	60	2	28	25	2	1

As Table 2 shows, very few of the larvae of *S. rupestris* became pelagic within the first 40 sec after hatching, but if the substratum was unfavourable, of Perspex, they all eventually become pelagic, the great majority being negative to light from the beginning of their pelagic stage. When the larvae hatched in contact with *Lithophyllum* there was usually no pelagic phase at all in this species. In contrast to this practically all *S. borealis* larvae embarked upon a pelagic stage, even when they hatched in contact with a favourable substratum, and the majority were initially positive to light.

This behaviour will presumably lead to the majority of *S. rupestris* becoming attached to the same piece of rock as their parents, whereas a much smaller proportion of *S. borealis* will become attached to the parental *Fucus* frond. To illustrate this difference egg-strings of each species were placed on pieces of the appropriate substratum which already bore settled individuals. These pieces lay centrally in clean glass dishes which had just been filled with sea water and were illuminated from one side. A similar piece of substratum was placed on the light side and on the dark side of each dish, but these were without egg-strings. After the larvae had hatched and settled the numbers attached to the central substratum and to each of the other substrata were recorded (Tables 3 and 4).

TABLE 3. SETTLEMENT OF *S. RUPESTRIS*

(Numbers settling on the upper/lower surfaces of pieces of limestone which bore previously settled individuals and were placed respectively in the centre and on the light and dark sides of experimental vessels. In each experiment the larvae were derived from egg strings placed on the central piece of limestone.)

No. of experiment	Centre	Light side	Dark side	% migrating from centre
1	27/0	1/0	6/0	21
2	30/0	1/1	12/2	34
3	1/10	0/0	0/1	8*
4	14/2	0/0	3/15	54
5	20/3	0/0	0/3	12*
6	10/5	2/0	1/14	51
7	12/1	1/0	5/6	48
8	10/9	0/0	0/2	10*
9	10/0	1/0	2/4	42
Totals	164	7	76	Mean 34

* *Lithophyllum* present on central substratum.

TABLE 4. SETTLEMENT OF *SPIRORBIS BOREALIS*

(Numbers settling on pieces of *Fucus serratus* which bore previously settled individuals. Other conditions as in Table 3.)

No. of experiment	Centre	Light side	Dark side	% migrating from centre
1	12/3	18/5	10/36	83
2	16/15	1/1	12/35	60
3	2/1	31/29	27/5	97
4	5/14	10/32	20/23	81
5	2/6	8/4	8/8	80
6	2/4	10/6	3/9	84
Totals	82	155	207	Mean 82

As Table 3 shows, 66% of the larvae of *S. rupestris* settled on the central substratum where they were first liberated and very few settled on the lighted side of the dish. The substrata used for this species were pieces of limestone rock which had been previously presented to settling larvae. In three of the experiments the central piece bore a small patch of *Lithophyllum*, and in these 90% of the larvae settled without swimming away. Later experiments confirmed that *Lithophyllum* plays a part in inducing settlement (p. 648).

In the experiments with *S. borealis* (Table 4), in which the substrata used were pieces of *Fucus serratus* bearing previously settled *Spirorbis*, only 18% of the larvae settled on the central substratum and considerable numbers settled on the lighted side of the dish.

If larvae of *S. rupestris* become pelagic in a dish they swim about for many minutes on the side remote from the light, but if they fail to find a suitable substratum there they explore the whole dish, occasionally coming to the lighted side and crawling for short periods on any substrata which they encounter.

When larvae intend to settle on a surface they crawl more slowly upon it and frequently change direction by flexing the abdomen. They thus explore thoroughly the area within which they will settle. Eventually, after turning repeatedly in one place, locomotion ceases and the primary shell gland, situated in the dorsal mid-line between thorax and abdomen, discharges a a milky mucous fluid. This flows round the body and forms the initial tube whilst the metamorphosing larva rolls repeatedly about its longitudinal axis, first in one direction and then in the other. Finally it rolls over on to its back, its tentacles extend, its head shrinks and its thoracic membrane folds back round the mouth of the mucous tube. Under this membrane the calcigerous glands typical of serpulids (Hedley, 1956) take up the task of tube formation. Metamorphosis and the preceding pattern of settlement behaviour therefore agree in detail with those described (Knight-Jones, 1951) for *S. borealis*.

Choice of substrata

On some shores where both *Lithophyllum* and *Fucus serratus* are abundant, *S. rupestris* is abundant and *S. borealis* scarce or absent. On such a shore (e.g. Combe Martin, North Devon) the *Fucus* is bare of *Spirorbis*. In other places (e.g. Worm's Head, Glamorgan) this condition is reversed; *S. borealis* is fairly common on *Fucus*, *S. rupestris* is absent and *Lithophyllum* is without *Spirorbis*. Such observations indicate that the larvae of each species do not settle on the alga which forms the characteristic substratum of the other.

In a series of ten replicate laboratory experiments larvae of *S. borealis* were offered a choice between pieces of rock bearing *Lithophyllum* and pieces of *Fucus serratus* of similar size. About twenty larvae were used in each experiment. The results (Table 5*a*) showed that *Lithophyllum* is indeed very unfavourable for the settlement of this species. The majority of the larvae settled on *Fucus*.

In two similar series, each of eight experiments, larvae of *S. rupestris* were allowed to choose between *Lithophyllum* and *Fucus*, and between *Lithophyllum* and *Corallina officinalis* (Table 5*b* and *c* respectively). Varying numbers of larvae were used and these settled very readily on *Lithophyllum* but scarcely at all on the other algae.

Most larvae of *S. rupestris*, however, settled not on the *Lithophyllum* itself, but on the piece of rock which the *Lithophyllum* was encrusting. This was old red sandstone, freshly chipped from bedrock in the lower half of the tidal zone and very rough in texture. In a further series of eight experiments larvae were given a choice between four substrata: (1) a sandstone pebble smoothed by abrasion and freshly collected from a pool at a low level in the tidal zone, (2) a rough piece of sandstone, freshly chipped from the middle of a piece of bedrock, (3) a piece of *Fucus serratus*, and (4) a piece of thick encrustation of *Liphophyllum* completely separated from the rock which had borne it. The rough unpigmented side of the *Lithophyllum*, which had been broken away from the substratum, was placed facing downwards.

TABLE 5. SETTLEMENT OF *SPIRORBIS* LARVAE

(*a*) *S. borealis* choosing between *Fucus serratus* and *Lithophyllum*

Settled on *Fucus*	13, 19, 5, 12, 8, 19, 15, 17, 1, 1	Total 110
Settled on *Lithophyllum*	3, 0, 0, 0, 0, 1, 0, 0, 1, 2	Total 7
Settled on rock	0, 0, 0, 0, 0, 0, 5, 0, 1, 0	Total 6

(*b*) *S. rupestris* choosing between *F. serratus* and *Lithophyllum*

Settled on *Fucus*	0, 0, 0, 0, 0, 0, 0, 0,	Total 0
Settled on *Lithophyllum*	7, 1, 5, 3, 2, 2, 25, 2(+9)*	Total 56
Settled on rock	31, 30, 23, 11, 5, 5, 30, 38	Total 173

(*c*) *S. rupestris* choosing between *Corallina officinalis* and *Lithophyllum*

Settled on *Corallina*	0, 0, 0, 0, 0, 0, 6	Total 6
Settled on *Lithophyllum*	7, 12, 4, 5, 3, 11, 10, 9	Total 61
Settled on rock	15, 12, 7, 8, 7, 15, 20, 12	Total 96

* Here part of the reverse side of the *Lithophyllum* encrustation was exposed and nine larvae settled on this rough surface.

In these experiments (Table 6) no larvae settled on the *Fucus* and few on the smooth sandstone. Considerable numbers settled on the rough sandstone but twice as many settled on the *Lithophyllum*, the numbers on the two sides being similar.

It would appear that a rock surface is particularly favourable for settlement if it is immediately adjacent to *Lithophyllum*. Further evidence that this is so was derived from a series of ten experiments in which larvae were allowed to choose between two pieces of rock which were similar except that one was partially encrusted by *Lithophyllum*. About three times as many settled on the encrusted rock as on the other (Table 7), but as previously (Table 5 *b* and *c*) the majority settled, not on the *Lithophyllum* itself, but on the adjacent rock surface.

The following experiment confirmed that *Lithophyllum* has a very important effect in stimulating settlement and metamorphosis. Pieces of rock, similar but with and without *Lithophyllum*, were placed in the centres of separate dishes, which were housed in a black box illuminated from above. Equal numbers of larvae were introduced into each dish and the numbers settling and metamorphosing on each substratum were counted at intervals of 15 min for $2\frac{1}{4}$ h (Fig. 3). A total of sixty-six larvae was used in each dish. When there was *Lithophyllum* in the dish the larvae settled very readily, whereas without it only about 15% settled. The heavier settlement previously on stones lacking *Lithophyllum* may perhaps have been due to the fact that there was *Litho-*

phyllum elsewhere in the dishes in those experiments. Crisp & Williams (1960) have shown that *Fucus* extracts promote settlement of bryozoan larvae.

TABLE 6. SETTLEMENT OF *S. RUPESTRIS*

(Eight experiments involving a choice between *Fucus serratus*, *Lithophyllum*, smooth pebbles and freshly cut rock chippings.)

No. of experiment	*Fucus serratus*	*Lithophyllum* top/bottom	Smooth pebble	Rock chipping
1	0	14/11	0	7
2	0	10/15	2	8
3	0	5/4	0	1
4	0	6/5	8	2
5	0	15/16	3	9
6	0	7/38	0	22
7	0	33/26	5	47
8	0	39/32	1	26
Totals	0	129/147	19	122

TABLE 7. SETTLEMENT OF *SPIRORBIS RUPESTRIS*

(Ten experiments involving a choice between a stone bearing *Lithophyllum* and a stone without *Lithophyllum*.)

Stone with *Lithophyllum*	6, 7, 6, 16, 7, 8, 15, 7, 8, 10	Total 90
Stone without *Lithophyllum*	0, 2, 2, 4, 6, 4, 4, 2, 3, 5	Total 32

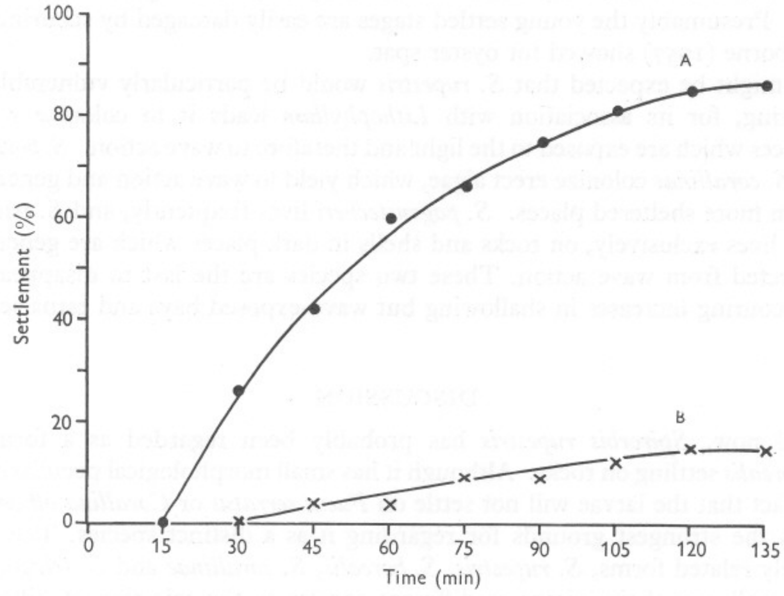

Fig. 3. Rates of settlement of *Spirorbis rupestris* larvae A, on rock with *Lithophyllum* attached; B, on bare rock.

DISTRIBUTION OF SPIRORBINAE ROUND SOUTH-WEST ENGLAND AND WALES

A search was made for the five common littoral species of Spirorbinae (de Silva & Knight-Jones, 1962) at each of the forty-four localities marked in Fig. 4, particularly in the rather sheltered rocky places which are most favourable for these forms (Moyse & Nelson-Smith, 1962). All five species are generally abundant in the lower half of the tidal zone on western and southern shores where the ten-fathom line lies close to the coast. In such places they can be found in large numbers by searching for only a few minutes. In shallower water, where the rocks tend to be scoured by wave-borne particles, all five species become progressively scarcer. None was recorded as absent until at least half an hour had been spent looking for it in that locality.

As Fig. 4 indicates, *S. rupestris* is found on open shores only where the ten-fathom line lies close to the coast. If conditions are sufficiently sheltered, however, it can live in very turbid water. It extends about 15 miles up Milford Haven, for instance, attached to rocks beneath *Ascophyllum*. Apparently it is the combination of turbidity with wave action which is fatal to it. This would account for its absence from the northern shores of the Bristol Channel, where the water is remarkably turbid throughout most of the year. Presumably the young settled stages are easily damaged by scouring, as Shelborne (1957) showed for oyster spat.

It might be expected that *S. rupestris* would be particularly vulnerable to scouring, for its association with *Lithophyllum* leads it to colonize rocky surfaces which are exposed to the light and therefore to wave action. *S. borealis* and *S. corallinae* colonize erect algae, which yield to wave action and generally live in more sheltered places. *S. pagenstecheri* lives frequently, and *S. tridentatus* lives exclusively, on rocks and shells in dark places which are generally protected from wave action. These two species are the last to disappear as the scouring increases in shallowing but wave-exposed bays and estuaries.

DISCUSSION

Until now, *Spirorbis rupestris* has probably been regarded as a form of *S. borealis* settling on rocks. Although it has small morphological peculiarities, the fact that the larvae will not settle on *Fucus serratus* or *Corallina officinalis* gives the strongest grounds for regarding it as a distinct species. The four closely related forms, *S. rupestris*, *S. borealis*, *S. corallinae* and *S. tridentatus* may well owe their origins as different species to the selection of different substrata, with consequent isolation (de Silva, 1962*a*). Certainly they illustrate well enough the general principle that closely related species are allopatric, for though they may occur in the same rock pool they live in different parts of the pool. Within such a pool, moreover, each species retains its distinctive character. There is little or no evidence of hybridization, a remarkable point considering that fertilization probably involves sperm transference by water currents.

The more distantly related species, *S. pagenstecheri* is physiologically tougher (de Silva, 1962*b*) and catholic in its choice of substrata, living sympatrically with each of the other four species.

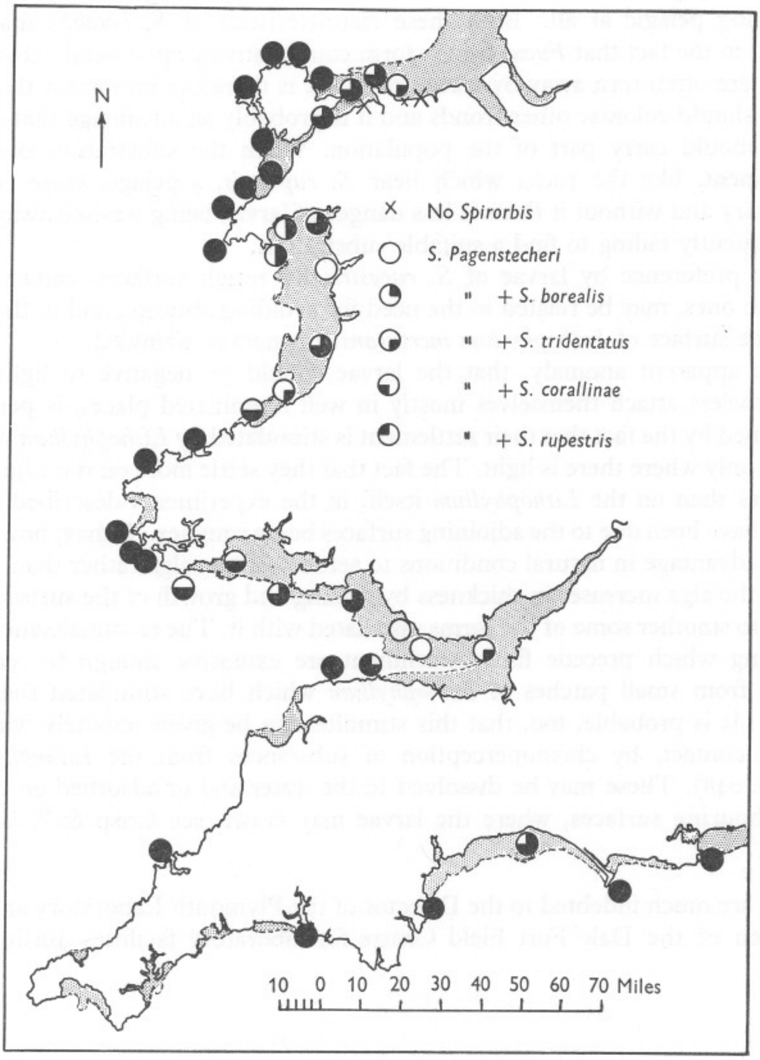

Fig. 4. The distribution of Spirorbinae round south-west England and Wales. Shaded areas are within the 10-fathom line.

Of these four close relatives, *S. borealis* does not seem to have specialized in substratum selection to the same degree as the others, for whilst preferring *F. serratus* it will settle quite readily on a number of other algae and on filmed rock surfaces. *S. borealis* is also more variable than *S. rupestris* in its larval behaviour immediately after liberation. Although the larvae are usually pelagic and initially positive to light, some egg-strings produced larvae which were negative and a few, hatching in contact with *Fucus* already colonized by *S. borealis*, produced larvae which settled after crawling briefly, without becoming pelagic at all. Both these characteristics of *S. borealis* may be related to the fact that *Fucus* fronds form comparatively ephemeral substrata, which are often torn away by wave action. It is therefore important that the larvae should colonize other fronds and it is probably an advantage that other algae should carry part of the population. When the substratum is more permanent, like the rocks which bear *S. rupestris*, a pelagic stage is less necessary and without it there is less danger of larvae being washed away and subsequently failing to find a suitable substratum.

The preference by larvae of *S. rupestris* for rough surfaces, rather than smooth ones, may be related to the need for avoiding abrasion and to the fact that the surface of *Lithophyllum incrustans* is generally wrinkled.

The apparent anomaly, that the larvae should be negative to light but nevertheless attach themselves mostly in well illuminated places, is perhaps explained by the fact that their settlement is stimulated by *Lithophyllum* which grows only where there is light. The fact that they settle more on the adjoining surfaces than on the *Lithophyllum* itself, in the experiments described here, could have been due to the adjoining surfaces being rougher. It may, however, be an advantage in natural conditions to settle near the alga rather than upon it, for the alga increases in thickness by folding and growth of the surface and tends to smother some of the forms associated with it. The reconnaissances by crawling which precede final attachment are extensive enough to remove larvae from small patches of *Lithophyllum* which have stimulated them to settle. It is probable, too, that this stimulus can be given remotely without actual contact, by chemoperception of substances from the *Lithophyllum* (see p. 648). These may be dissolved in the water and/or adsorbed on to the neighbouring surfaces, where the larvae may crawl (see Crisp & Williams, 1960).

We are much indebted to the Director of the Plymouth Laboratory and the Warden of the Dale Fort Field Centre for laboratory facilities during this work.

SUMMARY

Spirorbis rupestris sp.nov. has a sinistrally coiled, unridged tube and is distinguished from *S. borealis* Daudin only by colour, small morphological details and striking differences in larval behaviour. Though the larvae are capable of swimming, they do not usually do so, but crawl about and soon attach themselves to rock surfaces near the tubes of their parents, particularly when stimulated by the presence of the coralline alga *Lithophyllum incrustans*. They will not settle on *Fucus serratus*.

S. rupestris is found typically on rock surfaces in well-illuminated places throughout the lower half of the shore, generally associated with *Lithophyllum*. It is abundant on the shores of south-west Britain, except where there is scouring by wave-borne particles.

REFERENCES

BÉNARD, F., 1960. La faunule associée au *Lithophyllum incrustans* Phil. des cuvettes de la région de Roscoff. *Cahiers de Biologie marine*, T. 1, pp. 89–102.

CRISP, D. J. & RYLAND, J. S., 1960. Influence of filming and of surface texture on the settlement of marine organisms. *Nature, Lond.*, Vol. 185, p. 119.

CRISP, D. J. & WILLIAMS, G. B., 1960. Effects of extracts from fucoids in promoting settlement of epiphytic Polyzoa. *Nature, Lond.*, Vol. 188, pp. 1206–7.

DE SILVA, P. H. D. H., 1958. Use of artificially liberated larvae in experiments on settling behaviour of *Spirorbis*. *Nature, Lond.*, Vol. 182, pp. 1751–2.

—— 1962*a*. Experiments on choice of substrata by *Spirorbis* larvae (Serpulidae). *J. exp. Biol.*, Vol. 39, pp. 483–490.

—— 1962*b*. Studies on the biology of Spirorbinae (Polychaeta). (In the Press.)

DE SILVA, P. H. D. H. & KNIGHT-JONES, E. W., 1962. *Spirorbis corallinae* sp.nov. and some other Spirorbinae (Serpulidae) common on British shores. *J. mar. biol. Ass. U.K.*, Vol. 42, pp. 601–8.

GARBARINI, P., 1936. Le choix du support pour les larvae de *Spirorbis borealis* Daudin. *C.R. Soc. Biol., Paris*, T. 122, pp. 158–60.

GROSS, J. &. KNIGHT-JONES, E. W., 1957. The settlement of *Spirorbis borealis* on algae. *Rep. Challenger Soc.*, Vol. 3, No. 9, p. 18.

HEDLEY, R. H., 1956. Studies in serpulid tube formation. II. The calcium-secreting glands in the peristomium of *Spirorbis*, *Hydroides* and *Serpula*. *Quart. J. micr. Sci.*, Vol. 97, pp. 421–7.

KELLY, K. L. & JUDD, D. B., 1955. *The ISCC-NBS method of designating colours and a dictionary of colour names*. Washington D.C.: National Bureau of Standards, Circular 553.

KNIGHT-JONES, E. W., 1951. Gregariousness and some other aspects of the setting behaviour of *Spirorbis*. *J. mar. biol. Ass. U.K.*, Vol. 30, pp. 201–22.

—— 1953. Decreased discrimination during setting after prolonged planktonic life of larvae of *Spirorbis borealis* (Serpulidae). *J. mar. biol. Ass. U.K.*, Vol. 32, pp. 337–45.

LEWALLE, J., 1961. Détermination macroscopique des algues rouges calcaires (Corallinaceae et Squamariaceae partim) du golfe de Naples. *Pubbl. Staz. zool. Napoli*, Vol. 32, pp. 241–71.

MOYSE, J. & NELSON-SMITH, A., 1962. Zonation of animals and plants on rocky shores around Dale, Pembrokeshire. *Field Studies* (in the Press).

NEWTON, L., 1931. *A Handbook of the British Seaweeds.* London: British Mus. (Nat. Hist.)

RIDGEWAY, R., 1912. *Colour Standards and Colour Nomenclature.* Washington D.C.

SHELBOURNE, J. E., 1957. The 1951 oyster stock in the Rivers Crouch and Roach, Essex. *Fish. Invest. Lond.*, Ser. 2, Vol. 21, pt. 2, 27 pp.

WISELEY, B., 1960. Observations on the settling behaviour of larvae of the tubeworm *Spirorbis borealis*, Daudin (Polychaeta). *Aust. J. mar. freshw. Res.*, Vol. 11, pp. 55–72.