The Association Between Polyzoa and Algal Substrata
Author(s): J. S. Ryland
Source: *Journal of Animal Ecology*, Vol. 31, No. 2 (Jun., 1962), pp. 331-338
Published by: British Ecological Society
Stable URL: https://www.jstor.org/stable/2145

THE ASSOCIATION BETWEEN POLYZOA AND ALGAL SUBSTRATA

By J. S. RYLAND*

Marine Biology Station, Menai Bridge

The relationship between benthic animals and the substratum in or on which they occur is one of fundamental importance. There is increasing evidence that the settlement of marine invertebrate larvae is far from haphazard, and that larvae search for and metamorphose after finding a suitable substratum (Jägersten 1940, Wilson 1952, Silén 1954, Crisp & Ryland 1960, Scheltema 1961). It is no doubt this selectivity that explains the obvious associations found between certain species of sessile organism and particular substrata. A number of these occur in the Polyzoa.

Associations between Polyzoa and algal substrata have been noted in a number of earlier papers dealing with the French coast (Joliet 1877, Prenant & Teissier 1924, Prenant 1927, 1932) and the Baltic (Bock 1950, 1954), while a detailed study was made by Rogick & Croasdale (1949) in the region of Woods Hole. More recently the selection of algal substrata by polyzoan larvae has been experimentally investigated (Ryland 1959 a, b, Crisp & Williams 1960). Some information concerning associations around the coasts of the British Isles was given by Hincks (1880) and in the *Plymouth Marine Fauna* (Marine Biological Association 1957), but there has been no detailed study of this subject.

The observations presented here, made during the years 1956-59, refer almost exclusively to the coast of Wales. The majority came from the Menai Straits and the shores of Anglesey and the Lleyn; others were made in the Milford Haven area. A general account of the rocky shores of Anglesey was given by Lewis (1953).

METHOD

Whenever collections of Polyzoa were made the associated substrata were recorded. Visits were made to a number of shores of different types and having various degrees of shelter, specimens being collected to give, simultaneously, information on distribution, ecology and breeding season. Such a survey covered a wider range of species than a strictly quantitative survey in a restricted area would have done, though neither frequency nor biomass could be assessed accurately. Every association recorded on any expedition was entered once in a table, irrespective of frequency of occurrence. The resulting picture is certainly quite accurate, for visits to shores poor in Polyzoa, where only the most characteristic associations could be found, balance those to sheltered shores which supplied diversity. The results obtained by this method are in accord with those obtained by Colman (1940) in a quantitative survey, though he found only the commonest species.

Nomenclature of the Polyzoa in general follows the *Plymouth Marine Fauna* (Marine Biological Association 1957), the authorities being given in Table 1. Nomenclature of algae follows Parke (1953) and the authorities are indicated in Table 2.

* Present address: Fisheries Laboratory, Lowestoft.

Table 1. *The occurrence of Polyzoa on various types of substratum*

	Substrata							
	Stones and boulders	Shells	Wooden structures	Ascidian tests	Hydroids	Polyzoans	Algae	Total number of observations
CYCLOSTOMATA								
Crisidia cornuta (L.)	9				5	3	12	29
Crisia eburnea (L.)	2			1	6	2	23	34
C. aculeata Hassall	11	1			1		7	20
C. denticulata (Lamarck)	6			1	1	1	8	17
Tubulipora phalangea Couch	3					1	4	8
Diastopora patina (Lamarck)	6	3			1	1		11
Lichenopora hispida (Fleming)	6	2						8
CHEILOSTOMATA-ANASCA								
Aetea anguina (L.)	4				2	6	4	16
Scruparia chelata (L.)	1				2	3	3	9
S. ambigua (d'Orbigny)	1	1			2	12	10	26
Membranipora membranacea (L.)							32	32
Electra pilosa (L.)	17	3			6	4	108	138
E. crustulenta (Pallas)	1	1					3	5
Conopeum reticulum (L.)	15	4						19
Cauloramphus spinifera (Johnston)	4							4
Callopora lineata (L.)	17						21	38
C. dumerilii (Audouin)	2	2				1		5
Scrupocellaria scruposa (L.)	11	4			2		6	23
S. reptans (L.)	6			1		1	14	22
Bicellariella ciliata (L.)	4				3	1		8
Bugula plumosa (Pallas)	1		1		1	1		4
B. flabellata (Thompson)	7	3	1		1	12	2	26
B. fulva Ryland	1		1			1	1	4
B. turbinata Alder	4							4
Cribrilina punctata (Hassall)	7	5						12
CHEILOSTOMATA-ASCOPHORA								
Celleporella hyalina (L.)	6	2			1	1	44	54
Escharella immersa (Fleming)	11	3						14
Schizoporella unicornis (Johnston)	9					1	3	13
Schizomavella auriculata (Hassall)	2	2						4
S. linearis (Hassall)	11	1				2	3	17
Escharina spinifera (Johnston)	5						13	18
Cryptosula pallasiana (Moll)	22	4	3				4	33
Microporella ciliata (Pallas)	3	1					8	12
Fenestrulina malusii (Audouin)	1	1		1		1		4
Escharoides coccineus (Abildgaard)	14	2				1	28	45
Umbonula littoralis Hastings	2						4	6
Cellepora avicularis Hincks	1				4	2		7
C. pumicosa L.	8	3				1	1	13
Celleporina hassallii Johnston	1	1				1	8	11
CTENOSTOMATA-CARNOSA								
Alcyonidium gelatinosum (L.)	7						1	8
A. polyoum (Hassall)	8						26	34
A. hirsutum (Fleming)	2					1	54	57
Flustrellidra hispida (Fabricius)	2						52	54
CTENOSTOMATA-STOLONIFERA								
Bowerbankia imbricata (Adams)	1		1				12	14
B. gracilis Leidy (= *caudata* (Hincks))	4	1	1			2	1	9
Amathia lendigera (L.)	1					1	8	10
Valkeria uva (L.)					1	5	22	28

OBSERVATIONS AND DISCUSSION

Table 1 presents a generalized picture of the way in which Polyzoa are associated with substrata. On sheltered shores and below tide-marks Polyzoa incrust quite small stones, but in Table 1 this heading also includes the underside of boulders and the surface of rock overhangs. It can be seen that while some of the species found on stones and rock were also found commonly on shells, e.g. *Diastopora patina* and *Schizomavella auriculata*, others, e.g. *Callopora lineata*, were not. Records on shells can usually only be obtained by dredging, but shells appear to present a favourable substratum for many species of Polyzoa. Further, shells of *Chlamys opercularis* (L.) and *Pecten maximus* (L.) more frequently carry colonies than do those of *Cyprina islandica* (L.) and *Modiolus modiolus* (L.). This subject requires further investigation.

Species most characteristic of stones often do not colonize algae. For those that occur on both, e.g. *Callopora lineata* and *Escharoides coccineus*, the algal records refer mainly to *Laminaria* holdfasts. Perhaps the most important comment concerns *Cryptosula pallasiana*. In the Menai Straits, and elsewhere around British coasts, this is the commonest species on stones and is rarely found on algae. Yet in the fjords of the Bergen area of Norway this species incrusts the littoral Fucaceae and is not found on stones, though it occurs on *Mytilus edulis* L. shells. Evidently substratum preferences may not be constant throughout the entire range of a species.

Table 2 shows in more detail the associations between polyzoans and particular species of alga, and the data for the commonest species of Polyzoa, derived from Tables 1 and 2, have been presented graphically in Fig. 1. From this it can be seen that while *Electra pilosa* and *Celleporella hyalina* show no preferences for particular substrata, some species show clearly marked preferences. Some of these are considered in more detail below, and figures of them for purposes of identification have been given elsewhere (Ryland 1962).

The only species really characteristic of *Ascophyllum nodosum* was *Bowerbankia imbricata*, which agrees with the observations of Prenant & Teissier (1924) for Roscoff. This alga does not carry a rich fauna of epiphytes, perhaps on account of its relatively high position on the shore, so it is interesting to find that the hydroid *Clava squamata* (O. F. Müller) displays the same preference, while *Dynamena pumila* (L.) and *Laomedea flexuosa* Hincks are characteristic (Prenant 1927, Colman 1940). The three carnosan polyzoans so characteristic of *Fucus serratus* were rarely found on *Ascophyllum*, though Colman (1940) recorded *Flustrellidra hispida* on *Ascophyllum* at Wembury and Ebling *et al.* (1960), working in Lough Ine, noted that it was ' ... found at almost all the stations where *Ascophyllum* occurred'. The preferred substratum, *Fucus serratus*, however, is absent from the greater part of the lough. In selection experiments Ryland (1959b) found that *Flustrellidra* larvae did not settle on *Ascophyllum*, though Crisp & Williams (1960) found that *Ascophyllum* extract associated with a bacterial film was attractive to them.

No particularly characteristic association between a polyzoan and *Fucus vesiculosus* has been recorded, though several have been found on it.

Flustrellidra hispida, *Alcyonidium hirsutum* and *A. polyoum* all reach their maximum abundance on *Fucus serratus* (Fig. 1). This alga was also found to be by far the most attractive to the larvae (Ryland 1959b). It is now possible to compare these experimental findings with quantitatively expressed field observations (Fig. 2). Beside the results of a series of such choice experiments, performed with larvae of *Flustrellidra hispida* and *Alcyonidium hirsutum*, are shown the percentage number of observations of each association

Table 2. *The association of Polyzoa with algae*

In the records from *Laminaria* holdfasts, *L. digitata* (Huds.) Lamx. and *L. hyperborea* (Gunn.) Fosl. have not been distinguished. The observations for *Membranipora membranacea*, marked with an asterisk, refer to *Laminaria* fronds and not to holdfasts.

	CHLOROPHYCEAE		PHAEOPHYCEAE									RHODOPHYCEAE											
POLYZOA	*Cladophora rupestris* (L.) Kütz.	*Ulva lactuca* L.	*Ascophyllum nodosum* (L.) Le Jol.	*Bifurcaria rotunda* (Huds.) Papenf.	*Dictyota dichotoma* (Huds.) Lamx.	*Fucus serratus* L.	*Fucus vesiculosus* L.	*Halidrys siliquosa* (L.) Lyngb.	*Laminaria* holdfasts	*Laminaria saccharina* (L.) Lamx.	*Saccorhiza polyschides* (Lightf.) Batt.	*Ceramium rubrum* (Huds.) Ag.	*Chondrus crispus* (L.) Stackh.	*Corallina officinalis* L.	*Dilsea carnosa* (Schmidel) Kuntze	*Furcellaria fastigiata* (L.) Lamx.	*Gigartina stellata* (Stackh.) Batt.	*Phyllophora membranifolia* (Good. & Woodw.) J. Ag.	*Phycodrys rubens* (Huds.) Batt.	*Plocamium coccineum* (Huds.) Lyngb.	*Polyides caprinus* (Gunn.) Papenf.	*Rhodymenia palmata* (L.) Grev.	Total number of observations
Crisidia cornuta									4				1	1				4	1	1			12
Crisia eburnea	3	1							2	1			1	1		1		5	1	4			20
C. aculeata									3									3		1			7
C. denticulata			1						2		1		1					2	1				8
Scruparia ambigua	2								5			1						1					9
Membranipora membranacea			3			7		1	18*	3													32
Electra pilosa	2	2			3	22	2		20	2	1	1	17	4	2	8	4	2	2	5	1	5	105
Callopora lineata									18	1	1				1								21
Scrupocellaria scruposa								1	5														6
S. reptans				1				1	8	2						1							13
Celleporella hyalina	1	2	2		1	7			18	6	1	1	2		1				1			1	44
Escharina spinifera						1			7							3			1				12
Microporella ciliata									7	1													8
Escharoides coccineus						1			15		1					1							18
Celleporina hassallii									8														8
Alcyonidium polyoum			3			15	1		3							3					2		27
A. hirsutum						23			1				12			8	5	4					53
Flustrellidra hispida			3			23	1		7	1			2			1	10						48
Bowerbankia imbricata			4			2	2	1	1							1					1		12
Amathia lendigera								6	1	1													8
Valkeria uva	4		2					5	1				1	2		1			1	1	1		19

recorded during the present investigation. The leading position of *Fucus serratus* is clearly apparent. That settlement experiments have shown a lower percentage than shore observations is evidently related to the favourability of *F. spiralis* L. to settling larvae:

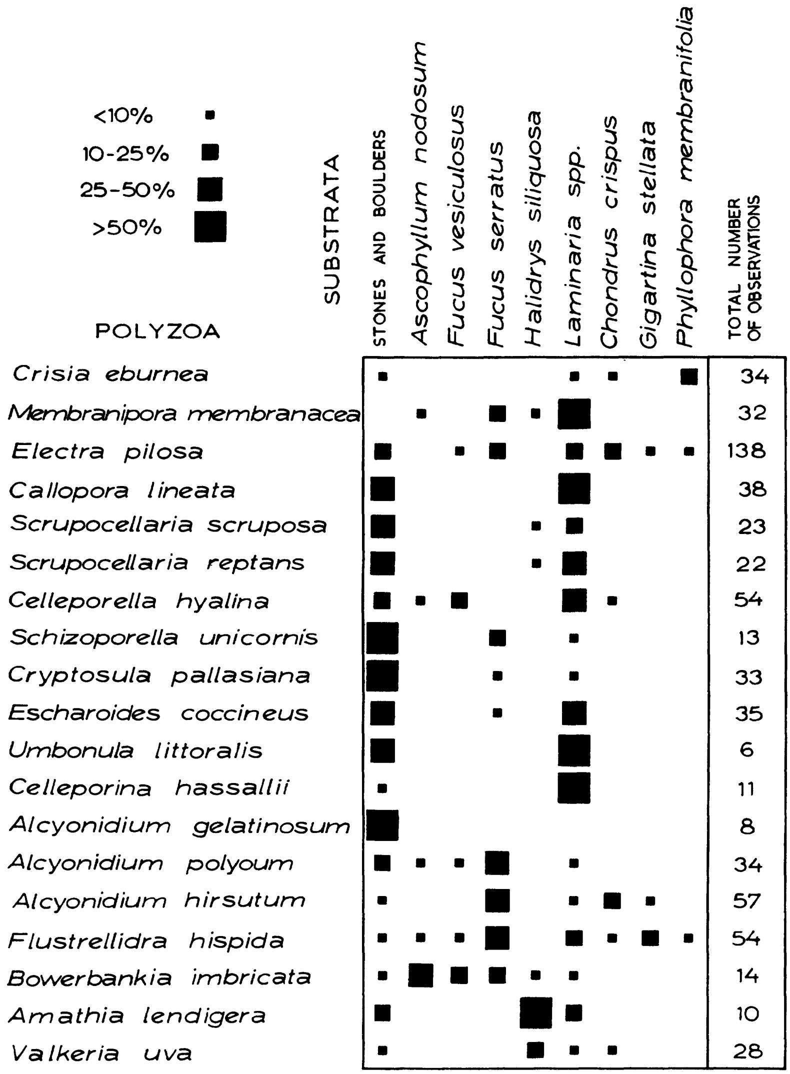

FIG. 1. The association of common polyzoans with stones and boulders and with the principal algae of the midlittoral zone and the infralittoral fringe. Observations concerning *Laminaria* refer to *L. digitata*, *L. hyperborea* and *L. saccharina*. *Membranipora membranacea* occurs mainly on the fronds of the first two species; *Electra pilosa* may also be found on fronds; *Celleporella hyalina* occurs on *Laminaria saccharina* fronds as well as on the rhizoids of the other species. The rest of the records are based on *Laminaria* holdfasts and refer principally to *L. digitata* and to some extent to *L. hyperborea*.

in nature this species presumably occurs too high on the shore to be colonized by polyzoans. Both techniques demonstrate the comparative favourability of *Gigartina stellata* and *Chondrus crispus* and, equally, the unfavourability of *Ascophyllum* and *Rhodymenia palmata*. Thus the experimental findings and the present observations are in close accord.

Like *Ascophyllum*, *Halidrys siliquosa* is an alga which seems generally unfavourable to most species of Polyzoa. Not even *Electra pilosa* has been recorded on it, and *Celleporella hyalina* clearly avoids it (Ryland 1959b). Yet in the Menai Straits *Valkeria uva*

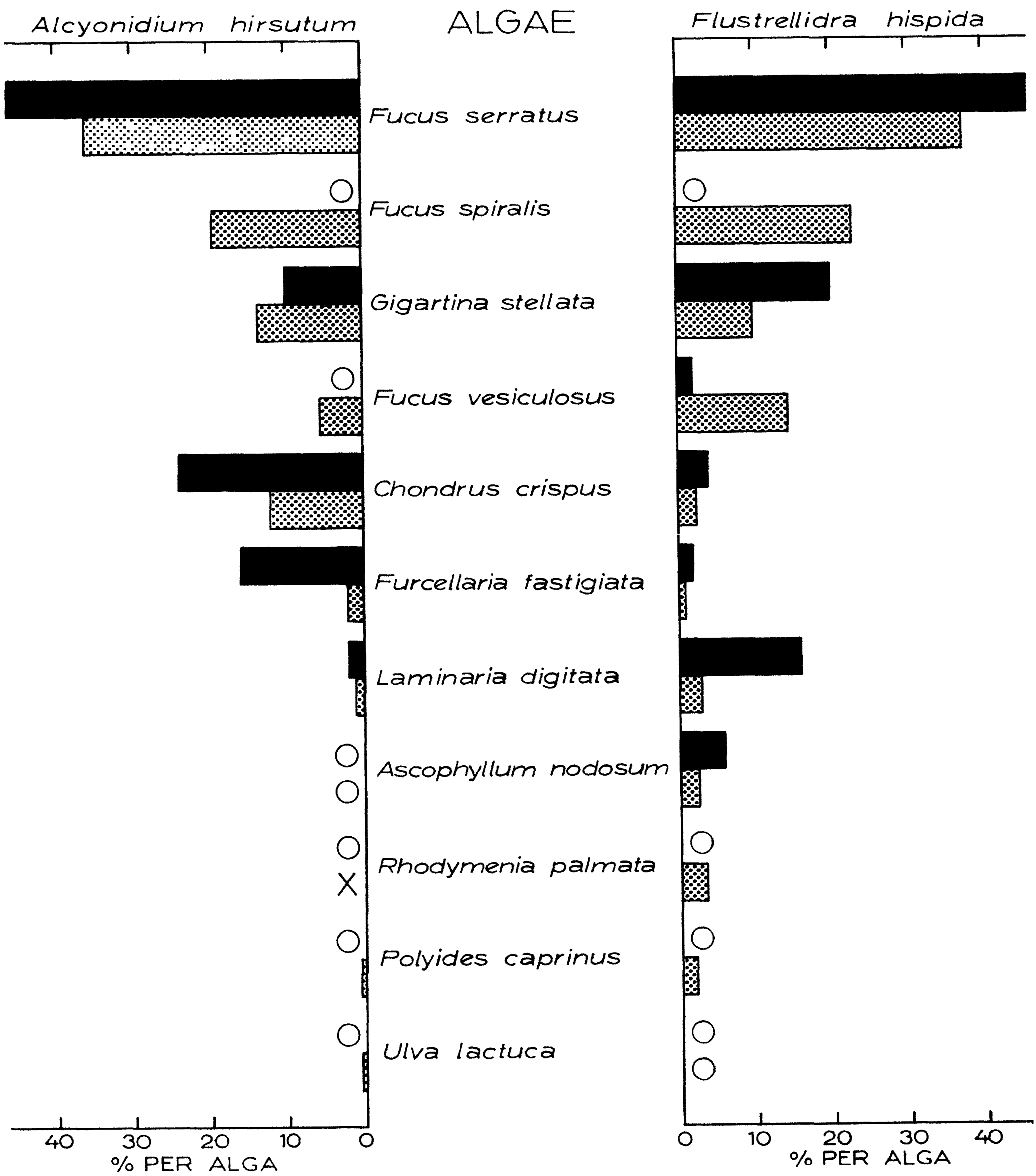

FIG. 2. The association of *Alyconidium hirsutum* and *Flustrellidra hispida* with algae. The natural occurrence of these polyzoans on algae (from Table 2) is shown in black, and the results of selection experiments (data from Ryland 1959b) in stipple. In addition to the results shown in the histogram, 8% of the records of *Alcyonidium hirsutum* were from *Phyllophora membranifolia*, which was not tested in the experiments; 7·5% of *Alcyonidium hirsutum* larvae and 0·25% of those of *Flustrellidra hispida* settled on *Pelvetia canaliculata* in the experiments, but neither species has ever been found on this alga on the shore. *Rhodymenia* was not used in the experiments with *Alcyonidium hirsutum*.

and *Amathia lendigera* occur on it in great abundance. *Mimosella gracilis* Hincks, likewise one of the Stolonifera, is also reported characteristically to be found on *Halidrys* (Hincks 1880). The hydroid *Aglaophenia pluma* (L.), which accompanies *Valkeria* and *Amathia* in the Menai Straits, was similarly recorded from Roscoff by Prenant & Teissier (1924), and Prenant (1927) distinguished a community founded on *Halidrys* and *Cystoseira* spp. characterized by *Aglaophenia pluma* and *Valkeria uva*. These authors gave lists of epiphytes found on the bases of *Cystoseira*, which included *Amathia*; but algae of this genus are not common in the North Wales area.

Chorda filum (L.) Stackh., which occurs with *Halidrys* and *Laminaria saccharina* in a sheltered part of the Menai Straits, does not carry polyzoan epiphytes.

Only the specially adapted *Membranipora membranacea*, with its flexible zoaria, is able to form extensive colonies on the fronds of *Laminaria* in any but the most sheltered waters. *L. saccharina* seems the least favoured by this species. The remarkable abundance of *Celleporella hyalina* on fronds of *Laminaria saccharina* in parts of the Menai Straits has previously been discussed (Ryland 1959b). Yet fronds of the alga were not specially attractive to the larvae of *Celleporella hyalina*, and the association was not found by Prenant & Teissier (1924) or Prenant (1927). In other areas, such as the Baltic (Bock 1950, 1954), Scottish sea-lochs and the west Norwegian fjords, *Laminaria* (? *saccharina*) can be dredged from a few metres depth covered with colonies of such species as *Callopora craticula* (Alder), *C. dumerilii*, *Scrupocellaria reptans*, *Cribrilina annulata* (Fabricius) and *Microporella ciliata*. In both cases shelter is obviously a factor of major importance.

The large holdfasts of *Laminaria digitata* and *L. hyperborea* form a very favourable habitat (Table 2), perhaps on account of the shelter they provide. Colman (1940), in a very small sample from Wembury, recorded nine species of Polyzoa, *Celleporella hyalina* and *Celleporina hassallii* being found most often. In the present studies thirty-two species have been found in this habitat, the most typical being shown in Fig. 1.

Since a number of marked preferences for substratum have been demonstrated, the conclusion of Sloane *et al.* (1961), working in the Lough Ine rapids, that 'A clear preference for particular algae as a substrate is not shown by any species', at first sight seems surprising. But the significant fact associated with the preferences shown in Fig. 1 is that all the species concerned are characteristic of the lower part of the intertidal zone, whereas Sloane and his collaborators were collecting their material from beyond the low-water level of spring tides. Thus the interesting point emerges that species living on the shore may show striking preferences of substratum, whereas those living in the infralittoral do not. It seems justifiable to conclude that selection of substratum by settling larvae plays an important role in maintaining species at a suitable tidal level. Moreover, such preferences are not confined to Polyzoa, but seem to apply to serpulids (Knight-Jones & de Silva 1959) and to certain hydroids.

Nevertheless, instances of preferences existing in infralittoral Polyzoa have been recorded, such as the Mediterranean species *Electra posidoniae* Gautier, which occurs on the fronds of *Posidonia oceanica* Delile and related plants (Gautier 1954).

ACKNOWLEDGMENTS

I should like to thank Drs A. P. Austin and W. E. Jones for assistance with the identification of algae, and Dr D. J. Crisp for reading and commenting on the manuscript. This work was carried out during tenure of a Development Commission grant.

SUMMARY

1. Observations have been presented on the associations between forty-seven species of Polyzoa and the substrata on which they occur, with particular reference to algae.

2. The data show that many of the intertidal species exhibit definite preferences, and these have been compared with results from selection experiments using polyzoan larvae. There is close agreement.

3. Since infralittoral species do not appear to exhibit such marked preferences, it is suggested that substratum selection by settling larvae may have an important role in helping to determine the distribution in relation to tidal level of Polyzoa on the shore.

REFERENCES

Bock, K. J. (1950). Über die Bryozoen und Kamptozoen der Kieler Bucht. *Kieler Meeresforsch.* **7,** 161-6.

Bock, K. J. (1954). Einige Zahlen zur Bewuchsdichte von Epizoen auf Laminarien aus der östlichen Kieler Bucht. *Veröff. Inst. Meeresf. Bremerhaven,* **3,** 42-5.

Colman, J. (1940). On the fauna inhabiting intertidal seaweeds. *J. Mar. Biol. Ass. U.K.* **24,** 129-83.

Crisp, D. J. & Ryland, J. S. (1960). Influence of filming and of surface texture on the settlement of marine organisms. *Nature, Lond.* **185,** 119.

Crisp, D. J. & Williams, G. B. (1960). Effect of extracts from fucoids in promoting settlement of epiphytic Polyzoa. *Nature, Lond.* **188,** 1206-7.

Ebling, F. J., Sleigh, M. A., Sloane, J. F. & Kitching, J. A. (1960). The ecology of Lough Ine. VII. Distribution of some common plants and animals in the littoral and shallow sub-littoral regions. *J. Ecol.* **48,** 29-53.

Gautier, Y. V. (1954). Sur *l'Electra pilosa* des feuilles de Posidonies. *Vie et Milieu,* **5,** 65-70.

Hincks, T. (1880). *A History of the British Marine Polyzoa.* London.

Jägersten, G. (1940). Die Abhängigkeit der Metamorphose vom Substrat des Biotops bei *Protodrilus. Ark. Zool.* **32A** (17), 1-12.

Joliet, L. (1877). Contributions à l'histoire naturelle des bryozoaires des côtes de France. *Arch. Zool. Exp. Gén.* **6,** 193-304.

Knight-Jones, E. W. & de Silva, P. H. D. H. (1959). The setting behaviour and ecology of Spirorbinae (Serpulidae). *Proc. XVth Int. Congr. Zool.* 241–3.

Lewis, J. R. (1953). The ecology of rocky shores around Anglesey. *Proc. Zool. Soc. Lond.* **123,** 481-549.

Marine Biological Association (1957). *Plymouth Marine Fauna* (3rd ed.). Plymouth.

Parke, M. (1953). A preliminary check-list of British marine algae. *J. Mar. Biol. Ass. U.K.* **32,** 497-520.

Prenant, M. (1927). Notes éthologiques sur la faune marine sessile des environs de Roscoff, II. *Trav. Sta. Biol. Roscoff,* **6,** 5-58.

Prenant, M. (1932). Études de bionomie intercotidiale. La baie et la pointe de Quiberon. *Trav. Sta. Biol. Roscoff,* **10,** 37-103.

Prenant, M. & Teissier, G. (1924). Notes éthologiques sur la faune marine sessile des environs de Roscoff: Cirripèdes, Bryozoaires, Hydraires. *Trav. Sta. Biol. Roscoff,* **2,** 3-49.

Rogick, M. D. & Croasdale, H. (1949). Studies on marine Bryozoa. III. Woods Hole region Bryozoa associated with algae. *Biol. Bull., Wood's Hole,* **96,** 32-69.

Ryland, J. S. (1959a). The settlement of Polyzoa larvae on algae. *Proc. XVth Int. Congr. Zool.* 236-9.

Ryland, J. S. (1959b). Experiments on the selection of algal substrates by polyzoan larvae. *J. Exp. Biol.* **36,** 613-31.

Ryland, J. S. (1962). Biology and identification of intertidal Polyzoa. *Field Studies,* **1** (4).

Scheltema, R. (1961). Metamorphosis of the veliger larvae of *Nassarius obsoletus* (Gastropoda) in response to bottom sediment. *Biol. Bull., Wood's Hole,* **120,** 92-109.

Silén, L. (1954). Developmental biology of Phoronidae in the Gullmar Fiord area (west coast of Sweden). *Acta Zool. Stockh.* **35,** 215-57.

Sloane, J. F., Bassindale, R., Davenport, E. W., Ebling, F. J. & Kitching, J. A. (1961). The ecology of Lough Ine. IX. The fauna and flora associated with undergrowth-forming algae in the rapids area. *J. Ecol.* **49,** 353-68.

Wilson, D. P. (1952). The influence of the nature of the substratum on the metamorphosis of the larvae of marine animals, especially the larva of *Ophelia bicornis* Savigny. *Ann. Inst. Océanogr. Monaco,* **27,** 49-156.