

creased beyond that which we would expect in the wild, is surely significant.

Environmental senescence arises from the many injuries and stresses an organism encounters throughout life; but how does *innate* senescence arise? In the simplest case the life table of a stable population subject only to constant random mortality shows that each succeeding age group is smaller than its predecessor. If, instead of being potentially immortal, members of this population die through some sudden innate degeneration after reaching a certain age, the effect upon the population will depend upon the age at which this occurs; if it happens far enough along the survival curve there will be so few animals left alive that its occurrence will probably pass unnoticed (rather like senility in wild animals). So

that the very old are but little affected by the force of natural selection. Hence, deleterious mutations may not only find a footing here, but may also accumulate. Furthermore, natural selection must tend to push heritable degeneration further and further towards the end of the reproductive period. Here then, is one way of accounting for some aspects of innate senescence. But as few animals in the wild ever survive the risks of living long enough to reach an advanced chronological age (as we can see when we compare life tables for wild and captive animals of the same species) it is understandable why senility is so rare a natural occurrence.

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The Settlement and Metamorphosis of Marine Animals

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Thorson (1) in discussing the choice of substratum by marine larvae, points out that further detailed knowledge of life cycles indicates that larvae possess more adaptability than has been hitherto assumed.

For instance, when plankton is collected by two-net, it is not unusual to take larvae of ophiuroids or echinoids, which are in process of metamorphosis, but in Lyttelton Harbour, completely metamorphosed ophiuroids or nearly completed metamorphosed spatangoids are taken near the bottom. Specimens taken nearer the surface are less changed or not at all.

That some larvae of benthic animals will readily metamorphose is shown by fully mature larvae of *Phoronis* metamorphosing in sea-water in a glass dish by no obvious stimulus. It may be that the actinotrocha does metamorphose in open water and that the adhesive surface exposed collects detritus sufficient to weight the animal and drag it down.

According to these observations, it is legitimate to regard some settlements and metamorphoses as not being conditioned by the nature of the substrate, but at the same time recent work shows that often they are not

simple, straightforward processes taking place without reference to the substrate.

Cole et al. (2) in studying settlement of oyster larvae have shown that although freedom from silt is essential, abundant settlement occurs on cultch (shells or tiles) fouled with other attached organisms, particularly recently attached oyster spat. Much less settlement takes place on clean shells. Whether settlement is encouraged by secretion into the water of some attractive substance by spat or by fully settled young has not been determined.

Observations made by Moore (3), Pye-finch (4), Knight-Jones (5) and others, show that cyprids (one of the larval phases of barnacles) move over a surface, apparently testing it. They settle readily in cracks and scratches and in angles. Settlement was found normally to be followed by metamorphosis into the young adult.

The larvae of *Elminius modestus* settled as though gregarious (*vide* oyster spat), aggregating near previously settled forms and it is suggested that an olfactory sense may play a part in bringing them together.

Miller et al. (6) showed that the settlement of the polyzoan larvae of *Bugula* (one

of the organisms which foul ships' bottoms) is facilitated by the presence of a slime film on non-toxic substrates. However, although they prefer slime-coated to slime-free non-toxic surfaces they will, if a slime film is not available, attach themselves equally abundantly on clean, non-toxic paints.

Wilson (7) found in regard to the metamorphosis of the larvae of the polychaete, *Ophelia*, that substrates may be attractive, neutral, or repellent, with gradings within these categories. Recently it has been found that the presence of micro-organisms is a primary factor in inducing the larvae of *Ophelia* to settle and metamorphose. These micro-organisms, perhaps mainly bacteria, which are the food of the larvae, must be neither too few nor too many. Wilson says, "it is possible that not only the relative abundance of micro-organisms present influences the larvae testing the sand grains, but that different kinds are more attractive than others."

Wilson, studying wider aspects of the conditions affecting metamorphosis and settlement inquired into the nature of the change of seawater in the west and to the west of the English Channel, using the early development of *Echinus esculentus* as test material. He says that, other things apart, the water off Plymouth leads to a much poorer metamorphic response than occurred in the late 1920's and 1930's. He says that this is the first time that there has been recognised the fact that a bottom fauna may be profoundly affected by the character of the supernatant water in which the larvae would pass their planktonic lives. A slight change in the nature of the water could cause a bottom fauna, or some part of it, to be wiped out.

My own observations on *Terebratella inconspicua* and on *Tegulorhynchia nigricans* showed that their larvae would settle on naturally slimy surfaces of rocks in appropriate places in the Inner Harbour at Lyttelton and in the laboratory. Both species are commonly found attached to *Tegulorhynchia* and only very rarely is *Terebratella* found attached to *Terebratella*. I have no knowledge of the attachment of *Tegulorhynchia* to *Terebratella*. Very commonly, the shells of *Terebratella* are clean, whereas the shells of *Tegulorhynchia* carry sponges, polyzoans, hydroids, harpacticoids, polychaetes,

both errant and sedentary, as well as the brachiopods before-mentioned.

At the end of the breeding seasons, which overlap, of the two species, eight times as many young *Terebratellas* were found as *Tegulorhynchias*. *Terebratella* larvae range relatively far and wide in contrast to those of *Tegulorhynchia*. *Tegulorhynchia* is well down underneath stones, while *Terebratella* most commonly grows as a border to these colonies.

It has been noticed that the larvae did not normally metamorphose completely when settled on a clean surface or one exposed to seawater for only three or four days. Settlement on clean glass leads to abnormality and death. The mantle rudiment undergoes partial reversal and the setae of *Tegulorhynchia* project horizontally, those of *Terebratella* being too small to be seen. Detailed examination shows that the gut is shortened, but does not move through a right angle, thus remaining longitudinal instead of lying transversely, the development of the musculature is affected in some way not yet clear and no matter how contraction takes place, the mantle is unable to enclose the anterior lobe and to form the two valves.

While *Ophelia* larvae would not settle on unsuitable substrates, nor would the barnacle cyprids, nor the polyzoan larvae, the brachiopod larvae will settle usually and in great numbers on a clean glass surface, but the change is partial or not at all.

These facts, concerning worms, barnacles, polyzoans, sea-urchins, brachiopods, bring us closer to the environment than ever. We are required continually to examine more minutely the nature of the life history, in order to appreciate the relations between animal and environment, and to account for presences and absences.

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