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MODERN ASPECTS OF MARINE LEVEL-BOTTOM ANIMAL COMMUNITIES

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Modern biologists are entangled in such numerous problems that their total staff is far too small to tackle but a fraction of them. It seems reasonable, therefore, that we should concentrate on the solution of those problems which may help most to widen our general view. This is the reason why I propose to call your attention to the advantage of studying marine level-bottom communities in the sense described by C. G. Joh. Petersen (1911, 1913, 1918). It is a field which now seems to be ripe for world-wide teamwork and which at the same time has economic implications, since it concerns the feeding grounds of most of our bottom-dwelling food fish, especially of the cod- and flounder-groups.

The level-bottom areas of the sea are among the most uniform flats on our globe, and from these areas extensive series of quantitative level-bottom samples, procured by aid of the Petersen grab and similar instruments, have been brought together during the last 35 years: from the high arctic areas to the tropics and from the shore to more than 10,000 m depth (Spärck, 1935, 1936a, 1937; Jones, 1950; Thorson, 1952). Roughly, this comprehensive material has demonstrated a most remarkable fact, that the same types of level-bottom substrata at similar depths are quantitatively dominated by invertebrates belonging to the same genera but to different species.

Different communities, always including species of the lamellibranch genera *Macoma*, *Cardium* and *Mya* as dominants and always associated with mixed bottoms just below the tidal zone, are known from high-arctic as well as boreal-atlantic seas, from the Pacific coast of the United States, from Japan, from East Africa, and so on, thus making a chain of "parallel" *Macoma* communities that replace each other in accordance with latitude and temperature. Chains of parallel *Venus* communities, always associated with sandy bottoms in shallow water and dominated by the lamellibranch genera *Venus* and *Spisula* or *Mactra*, are known from East Greenland, the North Sea, the Mediterranean, and the Persian Gulf. Chains of parallel communities of
brittle stars, associated with muddy bottoms in somewhat deeper water and dominated by replacing species of the genera *Amphiura*, *Amphiodia*, and *Amphioplus*, are known from the North Atlantic, the Black Sea, the Persian Gulf, Japan, New Zealand, the coast of Chile, and the Vancouver region.

Having here given examples from sandy, mixed, and muddy bottoms, we find that each series of parallel communities shows uniform features qualitatively as well as quantitatively everywhere.

Of approximately one million species of recent animals reported thus far (Pratt, 1935; Muller and Campbell, 1954; Hyman, 1955), only about 16% are marine. However, more than 80% of the animals inhabiting the sea bottom, which is only a fraction of the total marine fauna, are associated with rocks, stones, vegetation, coral reefs, etc. This means that level-bottom areas, though covering more than half of the surface of our globe, are inhabited by only 2–3% of all recent species of animals; this fact further demonstrates the simplicity of these areas as an ideal field for ecological work. Among these 2–3% only a small fraction, comprising astonishingly few genera and species, will prove to be quantitatively dominant on the level bottom, and these few genera one day will be the geological guide fossils for our period as were the ammonites, belemnites, and trilobites in prehistoric seas.

This uniformity and paucity in number among level-bottom species, as compared with the fauna of marine rocks, reefs, and vegetation, is not at all surprising. While the reefs, especially those of tropical littoral zones, offer a lot of varying microlandscapes to their inhabitants, a fact which in the long run must be ideal for speciation, just the opposite is the case on the level sea bottom. A sandy bottom has roughly the same appearance and structure whether in cold or in warm seas. It consists of the same type of substratum, thus being a habitat for morphologically the same types of invertebrates whenever it occurs. This, of course, is also the case for mixed and for muddy bottoms. Quantitative samples give further proof of this; a square meter of level bottom at the same depths and of the same substratum will comprise roughly the same number of invertebrate species whether in the arctic or in the tropics.

The only fundamental difference between an arctic and a tropical level bottom of the same type is the temperature of the sea in which it occurs. Therefore, it seems most urgent to clear up finally the old question as to whether or not marine invertebrates are adapted to the temperatures at which they normally occur. Comparisons of the metabolic rate of marine lamellibranchs within the same or closely related genera seem to show that a total adaptation or a close
approach to such an adaptation actually takes place (Spärck, 1936b; Thorson, 1936). A series of experiments by Fox (1937, 1939a, 1939b) and by Wingfield (1939), which apparently contradicted such temperature adaptations, have recently been corrected by Thorson (1952) and Berg (1953) who show convincingly that an adaptation actually takes place if body weight and age are taken into account. A recent paper by Scholander, et al. (1953), based upon several groups of marine poikilotherms, supports the same view: that a total or nearly total adaptation to temperature has taken place.¹

Since this rule of adaptation seems to hold good for the different species of the same genus which replace each other in accordance with latitude and temperature, it will also hold good within a series of parallel level-bottom communities, because here again we have different species of the same genera replacing each other as the dominant animals. Furthermore, this means that, within a chain of parallel level-bottom communities, an arctic community will have roughly the same metabolic rate and rate of growth at 0° C as its boreal parallel at about 8° C, its mediterranean parallel at about 12° C, and its tropical parallels at still higher temperatures. In other words, the mutual competition among species, for instance within an arctic Macoma community, will be totally or nearly identical to the competition within the parallel Macoma communities from boreal, mediterranean, or tropical seas, and so on. The animals within the whole series of parallel level-bottom communities thus have to face the same problems in their struggle for life, whether the community inhabits high latitude seas or lives near the equator.

The practical value of this discovery to ecological workers is evident. A team of scientists studying parallel communities in different seas and latitudes, such as those of Macoma, Amphiura, or even Venus, might work in close collaboration, knowing that any observation on predation, mode of feeding, competition, or growth done on any coast will be a direct help in explaining similar phenomena in all parallel communities in other seas as well. However, the basis for such teamwork must be a thorough quantitative mapping of the level-bottom communities, especially along such coastal stretches where permanent biological stations are situated.

Having developed the concept of parallel level-bottom communities, it seems reasonable to inquire what this concept actually represents. Most modern ecologists agree in regarding the level-bottom communities as good statistical units. The question is: are they ecological units also and, if so, on what ecological relations do they depend? Are we concerned with a relation between the animals and the sub-

¹See also Bullock, 1955.
stratum they inhabit or with a mutual relation between the animals within the community or with a combination of both?

In other words: How is a level-bottom community established?

The larval ecology may help to give us the answer. In arctic-antarctic coastal areas and in the deep sea, the level-bottom communities are composed of species with large yolky eggs and with a nonpelagic development. But in shallow water, which is where most of our bottom-dwelling food fish are concentrated, development by pelagic larvae prevails already in cold-temperate seas and is totally dominant in tropical areas (Thorson, 1950, 1952).

The pelagic larval life of most level-bottom species is hazardous. Fluctuations in temperature, food supply, and in the stock of enemies will decide which set of species is going to perish and which is going to survive until metamorphosis each season. The stock of surviving species varies much from year to year. Large numbers of a species in the plankton may reach the stage of metamorphosis one year but be totally lacking the next. And it is from these fluctuating sets of larval species that the level-bottom communities have to be recruited.

Vertical pump collections have shown that most species of planktonic larvae are restricted to rather thin horizontal strata of water, the vertical range of which is often only a few meters (Thorson, 1946). These larvae, being extremely sensitive to light, salinity, and temperature, stick to the stratum which most closely fulfills their varying needs. Larvae which, when ready to metamorphose, are photopositive and at the same time resistant to low salinity and varying temperature will crowd in the surface layers and will accordingly never get in contact with muddy bottoms in deep water. Contrary to this, larvae which are photonegative, preferring at the same time high salinity and a stable temperature, will crowd in the deeper layers and will never get in contact with a sandy bottom in quite shallow water. Thus, out of the number of larval species which survive until metamorphosis and which qualitatively and quantitatively may vary enormously from year to year, only a selected and often reduced set of species will get in contact with each type of bottom, and each level-bottom area must be recruited from this narrow set of "existing probabilities."

Wilson (1937, 1948a, 1948b, 1952), in a series of remarkable experiments, has shown that the larvae of several polychaetes, when ready to metamorphose, will critically examine the bottom substratum

2 Banse (1955) confirms the narrow horizontal stratification of planktonic larvae, which he, however, is inclined to explain more by the biological than by the physical qualities of the water masses.
to which they are exposed. If they find it attractive, they settle. If they find it less attractive or directly repellent, they will continue their pelagic life for days or even weeks. During such a prolonged larval life these larvae test the substratum at intervals as they are transported by the current directly over the bottom. Since such a transport at only half a knot, for instance, may carry the larvae about 170 km per week, their chance to find a favorable substratum seems fairly good.

Laboratory experiments confirming this have been made also on some archiannelids, some echinoderms, and on some other polychaetes. The question, whether similar reactions occur also within other groups of marine invertebrates and under natural conditions, has been answered positively by Erik Smidt (1951). In the Danish Waddensea the flood comes in from the North Sea at regular intervals, bringing with it a lot of “foreign” larvae ready to settle. During a thorough study of the microfauna of the Waddensea bottom throughout the year, Smidt did not find a single young bottom stage of any of the high-tide larvae mentioned above. In the microsamples examined, only such bottom invertebrates which also inhabit the Waddensea as adults were present as newly-settled young.

The so-called “gregariousness phenomenon” is known for such sessile hermaphroditic species as oysters, balanids, and Spirorbis, in which larvae are attracted by secretions or excretions of adults of their own species. This phenomenon will hardly occur among level-bottom invertebrates, since young of lamellibranchs, for instance, settling on a level bottom area among dense populations of adults of their own species, are directly known to lose out because they are unable to compete successfully with the adults.3

Thus, to all larvae of level-bottom invertebrates hitherto examined in the laboratory or in nature the bottom substratum seems to be the main factor that is responsible for their settling and, accordingly, for the qualitative composition of each level-bottom community.4

But is this rule valid for all types of settling larvae? What about the larvae of predators? Are they attracted by the substratum only or, perhaps preferably, by the presence of such prey animals as those on which their future life will be totally dependent? During their pelagic larval life, predators such as starfish, brittle stars, Polynices,

3 See Knight-Jones (1951a, 1951b) and Knight-Jones and Stevenson (1950) on the gregariousness phenomenon. See also Thorson (1952: 291–292) for discussion of this subject.

4 Exceptions to this rule may occur among those species of lamellibranchs which attach themselves by a byssus during their early life on the bottom and which bury in the substratum when they grow up.
etc. are dependent on and controlled by the same type of food as are the larvae of their prey, namely phytoplankton. This fact supports the view that even metamorphosing larvae of such predators have hardly any urgent need of animal food, since they may prolong their pelagic life after having tested a repellent bottom and since, during this prolongation, they will continue to feed on a vegetable diet. Furthermore, the ability of even adult *Asterias* to trace their prey by sensory activity is poor (Galtsoff and Loosanoff, 1939). It is known that some starfish do not hunt prey until at least three days after settling (Coe, 1912), while other starfish and some *Polynices* are known to settle earlier or at the same time as their prey (Mead, 1899; Orton and Fraser, 1930; Davis, 1925). These facts and several others seem to support the view that the settling of level-bottom predators is induced by a stimulus from the substratum and not by the prey which live on it and which will be hunted later on by the predators.

This discovery, that the bottom substratum seems to be the "master factor" which is responsible for the settling of nearly all pelagic larvae of level-bottom invertebrates and which accordingly is responsible for the qualitative composition of the level-bottom communities, is more valuable to marine ecologists than is immediately apparent. It must be remembered that in the open sea the uppermost layer of the level-bottom substratum tells us the story of recent sedimentation. This means roughly that a muddy bottom will normally be an indicator of calm water at somewhat greater depth, with a rather stable temperature and salinity; on the other hand, a bottom covered with coarse sand will normally result from turbulent water, found at rather shallow depths, with larger fluctuations in temperature and salinity. In this way the substratum will be responsible for the composition of the fauna and at the same time will act as a common denominator that tells us a good deal about the ecological conditions.

The fact that pelagic larvae of most predators are controlled by the same vegetable diet (phytoplankton) as are the larvae of their prey will also influence remarkably the balance between the number of predators and prey on the bottom; i.e., the balance between supply and demand. However, several predators have a longer life cycle than most of their prey; thus they are present in large numbers as adults when a new generation of prey settles down. In such cases it might be expected that dense populations of predators would totally "wipe out" all species of prey animals in a level-bottom community.

This might be expected especially in the case of the densely crowding and voracious brittle stars. For instance, the arms of *Ophiura* and
Amphiura on several mixed and muddy bottoms in all latitudes of our globe make so dense a network that every square centimeter of bottom is searched for prey every 24 hours. It seems surprising, therefore, that newly-settled prey animals, for instance the lamellibranchs, are able to survive this heavy predation during their first two months on the bottom when they are still tiny enough to be ingested by the brittle stars.

I hope that what I am going to say now will demonstrate the understanding of the balance within level-bottom communities which might be gained by 1) comparing a series of parallel communities, 2) focussing upon the biology of one of their dominant genera, and 3) studying carefully the biology of a species of this genus within one of the communities in order finally to generalize the results obtained for all of the parallels.

Let us focus upon the densely crowding Amphiura species which are known to dominate the Amphiura communities from the North Atlantic, the Black Sea, the Persian Gulf, Japan, New Zealand, etc., and let us see how they behave in the Danish Sound. Just at the time when larvae of prey animals settle in large quantities from the plankton, apparently running the danger of being quickly and totally eaten by the crowding brittle stars, these amphiurans enter a "passive period" of about two months during which they do not eat at all. During the first month they are loading up for spawning. Their swelling gonads completely fill out the disk, the stomach is reduced and its wall is even in histolysis. After spawning these stomach walls have to be built up again before the amphiurans can start their feeding activity; this process of building up will take about another month. When the brittle stars have finally regained their appetite, most of the young prey animals which settled during the last two months have grown to such a size that they are too large to be ingested by the brittle stars. It may hardly be questioned that these passive periods among the amphiurans and the stimulating influence of the substratum on settling larvae are the two fundamental factors governing the species composition of all Amphiura communities.

Several other predators among marine invertebrates have similar passive periods which make it possible for their prey to survive their most critical age. We know that different starfish stop feeding during the month just before spawning only to be the more voracious afterwards (Galtsoff and Loosanoff, 1939). Even if such passive periods are significantly shorter than those of brittle stars (for instance, one month only), in the long run their presence may be of fundamental significance to the survival of prey populations.

For similar observations in other ophiurans, see Glaser (1907) and Wintzell (1918).
As is well known, growth increase in newly-settled bottom invertebrates will often take place rapidly. A mussel, *Mytilus edulis*, about 0.35 mm long at settling, will grow during the following month to about 10 mm in length (Coe, 1945), which means that its content of organic matter expressed in nitrogen will increase about 2,000 times (Joergensen, 1952). Several other lamellibranchs and gastropods will grow at a similar rate, but even if we take into consideration the more slowly growing young of some species, we can certainly assume an average increase of organic matter of about 500 times for all prey animals during their first month on the level bottom. This means, furthermore, that a predator which has been passive for one month during the season of settling and rapid growth of its prey may obtain as many calories by swallowing a single prey animal as it might have obtained one month earlier by swallowing 500 prey animals of the same batch. Under natural conditions such passive periods often seem to occur during the right season for the initial rapid growth of their prey, and a passive period of one month’s duration during the right season may reduce the waste of prey specimens to only 0.2 % of what would have been needed one month earlier, without reducing the caloric content ingested by the predator. In this way a lot of prey animals are saved from destruction.

To oyster-, cockle-, clam-, and scallop-farmers, who cultivate in their beds stocks or species imported from other localities and who suffer much when their cultures are attacked by starfish, it might be useful to find out the passive seasons of the starfish populations. They could then select stocks of lamellibranchs for their culture which would, at the prevailing temperatures, spend their first month on the bottom during these passive periods of their enemies.

Summarizing the main features of the marine level-bottom communities, we find that: the structure and composition of the substratum is the most essential single factor influencing the composition of the community; in the open sea the substratum is, in general, a common denominator for several other ecological factors; the passive periods among predators just at the time of settling and early growth of their prey animals guarantee that a species which has been attracted by the substratum and settled voluntarily on a level bottom is not likely to be fully exterminated; in most cases the final species composition of a level-bottom community is thus determined at the moment when the larvae settle there permanently.

I hope I have chosen the right examples to convince you that the ecological conditions prevailing in marine level-bottom communities are simple and well suited for research. The chains of parallel communities, comprising species of the same genera inhabiting the same
types of substratum in all latitudes, directly invite us to start a world-wide investigation.

We have come together here to open a new laboratory and to plan future research. Why not use this opportunity to start fruitful teamwork on marine level-bottom communities?

REFERENCES

BANSE, KARL

BERG, KAJ

BULLOCK, T. H.

COE, W. R.

DAVIS, F. M.

FOX, H. M.

GALTSOFF, P. S., AND V. L. LOOSANOFF

GLASER, O. C.

HYMAN, LIBBIE H.

JOERGENSEN, C. B.

JONES, N. S.
Knight-Jones, E. W.

Knight-Jones, E. W. and J. P. Stevenson

Mead, A. D.

Muller, S. W. and Alison Campbell

Orton, J. H. and J. H. Fraser

Petersen, C. G. Joh.

Pratt, H. S.

Scholander, P. F., W. Flegg, V. Walters, and L. Irving

Smidt, Erik

Spärck, Ragnar

Thorson, Gunnar


WILSON, D. P.


WINGFIELD, C. A.


WINTZELL, J.