# MARINE BIOLOGY IN WALES

*Inaugural lecture of the Professor of Zoology delivered at the College on December 4, 1956*

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B.Sc. (WALES), D.PHIL. (OXON.)

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WHEN I first thought that I might talk to you under this title, I hoped to start by dispelling any idea that a narrow and peculiar branch of biology was to be dealt with in a parochial way. I knew that I could produce one of those pictures which shows the main groups of animals from the lowest to the highest, and point out that if one draws a line across it in the right place, at quite a high level, one finds that below that line the groups of organisms are predominantly marine. Their non-marine representatives may be more familiar to people who have been more interested in pond life or parasites, but the marine forms are generally more numerous and several large groups are exclusively marine. In fact, there is a wider variety of animals in the sea than outside it, and certainly the seas are the last extensive refuge of wild life which cannot yet be controlled by man.

I knew also that if I could tell you something of all the marine research that has gone on in this country and around it, we could cover this wide field quite thoroughly, and I honestly intended to try to do so. But I have since realized that this could not be done clearly in an hour, so I now propose, under this misleadingly general title, to try to convey only some information and ideas picked up at just two Institutions in Wales at which I have worked, the Fisheries Experiment Station at Conway and the University's Marine Biology Station which is at Menai Bridge.

The Fisheries Experiment Station has been for thirty years the main centre of shellfish research in Britain, under the successive Directorships of the late Dr. R. W. Dodgson and of Mr. R. E. Savage. The present Director of Shellfish Research, Dr. H. A. Cole, has moved his centre of operations to the new Fisheries Laboratory at

Burnham-on-Crouch, in order to study the problems of the Essex oyster industry, but he still directs expanded research activities at Conway.

The scheme for the new Marine Biology Station of the University of Wales was due largely to the initiative of Dr. F. W. Rogers Brambell, F.R.S., Professor of Zoology at the University College of North Wales, Bangor. It received a serious setback in 1950 through the sad death of the first Director of the Station, Dr. Fabius Gross, within a year of his appointment. Since then it has made great strides forward under the Directorship of Dr. D. J. Crisp.

## Nutrients and Plant Production

Life in the sea, away from the coastal fringe, depends on the small plant organisms in the plankton, which drift about and which can grow only near the surface, where there is enough light for them. They are the basis of all the food chains which ultimately support the fish. Like all plants they need, besides carbon dioxide and water, compounds of nitrogen and phosphorus, and these are often deficient. There are great stores of these nutrients in deeper water, where it is too dark for plant growth, and some are constantly reaching coastal waters in land drainage, but in the open sea near the surface there are often insufficient nutrients during summer to support the growth of the plants. The whole system needs stirring, to bring the nutrients to the surface, as tends to happen during the big tides of the autumnal equinox, which are often followed by renewed growth. Clearly the distribution of these nutrient compounds is important to everyone who is interested in the fertility of the sea.

Now most of us were introduced at school to the idea of the nitrogen cycle. Nitrogen is an essential part of living material. Animals get their nitrogen from the plants



which they eat. Excretion and decomposition of animals release it again in the form of ammonium nitrogen, and certain bacteria oxidize this to form nitrites and nitrates. Similar bacterial oxidation of ammonia occurs readily in water from coastal sea areas, but much less readily in water from offshore. So it has been thought that these nitrifying bacteria do not occur freely in the main body of water away from land.

Dr. C. P. Spencer, Microbiologist at Menai Bridge, has recently been going into this. He took similar water samples from near the land, in the Menai Straits, and from away from the land, at international station E. 1 near the Eddystone Lighthouse, and he sterilized both of them. Then he inoculated both in a similar way with nitrifying bacteria, added some ammonium chloride for them to work on, and a little phosphate which they also need for growth, and left them, withdrawing samples every two days to see how much nitrite they had formed. Those in the inshore water produced plenty of nitrite at an increasing rate, which showed that they grew and multiplied rapidly until they had used up nearly all the ammonium nitrogen. Those in the offshore water produced very little nitrite, at a constant rate, which showed that they were unable to grow and multiply. Apparently the offshore water was deficient in some material which the bacteria needed for growth.

It has recently been shown that nitrifying bacteria on land need a good deal of iron for growth and certainly the offshore water contained very little iron, whilst the inshore water contained a lot. Dr. Spencer found that this was the critically deficient material. By adding enough iron to the offshore water, he was able to make it even more favourable for nitrite production than was the inshore water. It seems that little nitrifying activity is to be expected away from the land, basically because of the lack of iron in the water there. This may not be important to the plants, since they can use ammonium nitrogen just as well as nitrites and nitrates, but it is interesting to oceanographers, who need to know for what substances they should test when they are investigating the sea's fertility.

## Diatoms and Flagellates

Turning now to the all-important planktonic plants, we find that only the diatoms are at all well known. These are protected by being enclosed in little glassy cases, which are often spiny. Planktonic crustacea can chew them up but many plankton animals are unable to use them as food, if only because they are comparatively large. That is the reason that they are well known, since many of them are large enough to be filtered off by the nets which are used for plankton sampling.

The finest plankton nets have meshes which measure about 0·05 mm across. These retain many diatoms, but let others through and one of the problems when rearing oyster larvae at the Fisheries Station at Conway, was to study the very small plants which would pass through these nets. Oyster larvae have mouths not much more than 0·01 mm across, so they cannot eat anything larger than this. To estimate the abundance of these very small organisms, we used to concentrate them fifty times by filtering the sea-water samples through collodion membranes, which would retain even bacteria. Then we would count the plant cells in a haemacytometer, like those used in hospitals for counting blood cells.

Most of these very minute plants are flagellates of undescribed species, so it was necessary to start cultures of them for study of their systematics. At Dr. Cole's suggestion, I tried inoculating test tubes of sterile culture medium with measured quantities of sea water. In a few weeks cultures would develop. In test tubes which had been



inoculated with 10 cubic mm of sea water there were generally mixed cultures of several species. In tubes with 1 cubic mm of inoculum the cultures which developed were often of one plant species, and some of the tubes were blank. Tubes with 0·1 cubic mm were generally blank. Evidently, the densities of plant organism in the sea-water samples were often about one per cubic millimetre or a million per litre. These are minimal estimates, based on the assumption that all the organisms introduced multiplied to form cultures.

Dr. R. W. Butcher, the Fisheries botanist (well known for his illustrations of British plants), has been studying and describing the new species in such cultures. The most generally abundant was a minute flagellate which he called *Chromulina pusilla*. It occurred in all the samples which we took from estuaries and the open sea, often at densities of about a million per litre of sea water. Considering how vast the seas are, this species must surely be about the most abundant on the British list. It is remarkable that it has not been described before, but the trouble has been that it is so very small, with a body only just over 0·001 mm in diameter. No details of its structure can be made out with the ordinary light microscope, but Professor Irene Manton has kindly taken a picture of it with the electron microscope, which shows that it has a head, a middle piece, and a tail, just like a human spermatozoon. It is relatively fast, travelling fifty times its own length in a second, which must compare favourably with the relative speeds of birds and aeroplanes. Liquid viscosity is unimportant on such a small scale, and *Chromulina* is so small that it could not move more than about 6 metres per day, under its own power. We still know very little about its distribution, for since it is smaller than some bacteria, it is difficult to identify with any certainty.

The broad outlines of the distribution of plankton plants in space and time can be guessed at from various lines of evidence. The large placid diatoms are the dominant plants in colder seas, where growth nutrients are abundant but light energy is limiting, whilst little flagellates dash about in greatest numbers in warm seas, squandering the energy which they can get from sunshine, their movements and relatively large surface areas presumably helping them to find and mop up the sparse nutrients, which they need just for growth. In warmer latitudes it is generally scarcity of nutrients which limits growth. In temperate latitudes, where it is largely the overlapping in distributions of northern and southern forms that results in seasonal successions, diatoms produce a great crop in spring, when the seas are cold, nutrients are abundant, and light still tends to be limiting. Later in the year, when growth nutrients are scarce, the flagellates increase in importance.

Some plankton workers who catch diatoms are reluctant to concede much importance to the flagellates which escape their nets, since these are so small. In dealing with marine plants our difficulties are similar to those which would face an imaginary race of shortsighted giants, who lived in the clouds and had some knowledge of botany, but whose only way of learning about conditions on the earth's surface was to let down huge grapnels occasionally, and drag them about. They would catch a lot of trees and might reasonably suppose, rightly or wrongly, that these produced most of the food on the earth. It would be easy for them to overlook the importance of grasses. Until recently the flagellates have been overlooked in a similar way. It is not likely that they are of much importance in colder seas, but they probably form a fair proportion of the standing crop in temperate and tropical latitudes, and a much greater proportion of the yield. *Chromulina pusilla* is certainly a good food for oyster larvae, as Mr. P. R. Walne has shown at Conway.



## Rearing and Behaviour of Oyster Larvae

The experimental tanks, which are used for oyster-rearing at Conway, are on a sloping site by the estuary near the Castle. Sea water is pumped up at high tide, into storage tanks on the upper part of the site, and mussels are brought in daily during the winter, for cleansing in the lower tanks. This is necessary because there is some danger of sewage pollution in the river and this was the primary reason for the construction of the tanks and the foundation of the associated Fisheries Experiment Station. During the summer the mussel fishery closes and the deep storage tanks are then used for oyster-rearing experiments.

The swimming larval stage is a most critical period in the life-history of molluscs, and indeed of most marine animals. Several hundred thousand larvae are liberated from each mother oyster. The larvae measure about 0·2 mm long and, if it is warm enough and if there is enough food for them, they grow until within a week they are 0·3 mm long, having more than trebled their volume. They swim suspended in the water through the activity of little hair-like cilia which form thick fringes round their heads. At this stage they are not much like oysters and it needs practice to distinguish them from the larvae of similar bivalve molluscs which are common in the sea. It is a help in distinguishing them to look at the movements of the cilia. The cilia show waves of activity moving round and round the head, of the type that is well known as giving the appearance of little wheels in, for instance, the rotifer or wheel animalcule described in Charles Kingsley's *Water Babies*. In larvae of most bivalves the waves move in an anti-clockwise direction, seen from above, but in oysters and mussels (which with the scallops are in a separate order of bivalves, the Anisomyaria) the waves move clockwise. The direction of movement of these metachronal waves of cilia is of systematic importance, for it is remarkably constant and nearly always the same in related animals. One sometimes finds that the general symmetry of a species is the reverse of what is found in allied species, the little marine snail, *Triphora perversa*, for instance, being built on a plan that is the mirror image of that found in snails generally, with its shell coiling to the left, whereas in most snails the coil is to the right. But even in this species the direction of movement of the waves, round the expanded head which forms the swimming organ of the larva, is just the same as in other snails. Looked at from above, the waves move clockwise in all larval gastropods.

The oyster larvae in the Conway tanks are kept safe from predators and from being swept away by currents, but two problems remain in rearing them. Above all, they have to be fed and, though growth of the flagellates which they need as food can be encouraged by adding organic fertilizers, these additions have to be carefully controlled. Secondly, they have to be given surfaces to which they can attach themselves, as oyster larvae must do when the time comes to metamorphose. If they were to set on the sides and bottoms of the tanks, they would virtually be lost, for young oysters are firmly fixed and cannot be detached from hard surfaces without damage. Luckily the tank walls get too slimy for the setting of many oyster larvae, and special collectors are provided, of a type used in French and Dutch systems of oyster culture. These consist of bunches of tiles, wired together and coated with a mixture of lime and sand. After setting on them, the oyster spat can be transported easily to the sea, where they will have plenty of food brought to them by tidal currents. Within a year the young oysters have reached a size at which they can be detached, by scraping away the lime and sand from the collectors.



When the oyster-breeding season at Conway is in full swing, the tanks are full of millions of larvae busily searching for surfaces to which they can attach themselves. Once they have set they cannot move again. Just before setting their sensory and locomotory equipment is best developed, which reflects the importance of choice of a suitable setting place in helping to ensure survival. The settlement, or spatfall, is very important to oystermen too, because the young oysters are then, for the first time, visible to the naked eye, can be handled, and can become articles of property. The setting behaviour of the larvae is therefore well worth studying.

When they are searching for a favourable substratum the larvae crawl about over any shells or other objects which they happen to encounter. They withdraw the swimming organ (the head) into the shell and crawl about by means of the foot. Initially, they crawl in straight lines, generally upwards if the surface is sloping. Often they swim off again, to find some other place on which to crawl. Eventually they start turning round and round in a small area, which they thus reconnoitre very carefully, and finally they attach themselves in that area. During attachment, each larva takes a smart turn to the right and presses its left valve against the substratum. It has previously squeezed out a little patch of byssus cement, which fixes the left valve within a few minutes.

The Conway tanks give excellent opportunities for experiments on the setting behaviour of oyster larvae. The larvae set mostly in shady places and on the undersides of objects. They seem to need the surfaces to be slightly filmed with algae or bacteria. They prefer to set gregariously in places where there are already settled oysters. Gregariousness turned out to be particularly important on oyster grounds in Essex. The spatfall there was always much heavier on grounds that were already well stocked with oysters, than on grounds which were sparsely stocked. The oystermen knew this to be so and thought that it was due to the larvae setting immediately after they had been released by their parents, but in fact they swim for several days and are carried many miles by tidal currents.

### Gregariousness in Tube-worms

Several species of the genus *Spirorbis* are very common near Menai Bridge. The adults form white tubes, which are coiled in close spirals a few millimetres across, and the larvae pass through their early development in these tubes or in special brood chambers borne on the heads of the parents. The larvae of *Spirorbis borealis* are liberated regularly in large numbers at about the moon's quarters. This means that, since they settle after a few hours, their early settled life coincides with neap tides; so those which settle low down on the shore, where most of the adults live, are not exposed to drying by the ebb, until a week's growth has given them larger and thicker tubes to protect them. Whilst swimming, larvae live on yolk reserves, so they do not have to be fed. They first seek the light and swim about at the surface. Then they begin to search, finding dark objects, crawling about on them and often swimming off to seek new ones. Eventually they start turning round in a small area, where they are to set. Like oysters, they set once and for all time. They stop crawling, wriggle, squeeze out the secretion of a large gland situated in the middle of the back, and roll over repeatedly, first on one side and then on the other. The secretion is sticky and forms the initial tube. Within a few minutes the settled larvae have metamorphosed, quickly growing tentacles and adding to the tube. Within a few hours the first coil of the tube has been carried through 90°.

Two species of *Spirorbis* are particularly common on the shore. *Spirorbis borealis*, mostly on seaweed, has a



clockwise tube and *Spirorbis pagenstecheri*, mostly on stones, has an anti-clockwise tube, so they are distinguishable at a glance. If a mixture of larvae of the two species is given the choice between paired blocks of slate, one bearing *Spirorbis borealis* and the other *Spirorbis pagenstecheri*, the larvae tend to sort themselves out gregariously, a large majority choosing the block which already bears their own species.

It is possible to show that this gregariousness is due to earlier setting, by larvae which are associated with others of their species, than by isolated larvae. It must be that difference which allows choice of a previously colonized substratum. If larvae have been prevented from setting for a few hours by being kept in clean glass vessels, they become less discriminating in experiments involving choice, which is probably due to the fact that there is then less difference between associated and isolated individuals, in their readiness to set. Such less discriminating individuals will readily set in new, uncolonized places and, if larvae are abundant, others will follow them to form new breeding communities. But if larvae are few, gregariousness leads a high proportion of them to return, after their planktonic life, to places which have proved suitable for the species, where they help to maintain the old stocks.

### Setting Behaviour and Distribution of Barnacles

Larvae of barnacles are also suitable for experiments on gregariousness. They are very small when they are liberated by their parents and they must spend a long time, feeding in the plankton and growing, before they reach the final stage of their larval development, as cypris larvae about 1 mm long, when they attach themselves to rocks, piers, or ships. Their searching and attachment behaviour is very like that of oysters and tube-worms. When they find a surface they explore it, eventually turning round and round in a small area and then fixing themselves permanently by cement glands. They retain the torpedo-shaped larval form for a few hours, then moult and metamorphose into the adult form.

If cypris larvae of the common shore barnacle, *Balanus balanoides*, are presented with a smooth slate already bearing settled barnacles, the majority of the larvae will settle within a few hours, but if the slate has never borne barnacles, the larvae will not settle for days, and will often die rather than settle, unless some individual is so abnormally undiscriminating as to begin colonization of such a smooth bare surface. If one takes a slate bearing a little patch of adults of *Balanus balanoides*, scratches a line round the edge of the patch, scrapes off the adult barnacles and then offers the slate to larvae of the same species, one finds that the larvae settle very readily and that practically all settle within the area, bounded by the scratched line, that was previously occupied by the adults. This area contains only the almost invisibly transparent, membranous bases of the adult barnacles, which remained attached to the slate when the rest of the barnacles was removed. Evidently there is something in bases that encourages setting.

Slates like this, bearing the bases of recently detached barnacles, can be raised to 200° or treated with a variety of chemicals, without removing whatever it is that encourages the larvae to settle on them. They have to be heated to temperatures which cause charring or boiled for a long time in acid before they become unfavourable for setting. Boiling with caustic alkali has to be quite prolonged before it is effective. Sodium hypochlorite removes the stimulating substance, quickly dissolving the entire bases. Probably it is the cuticular material in the bases



which encourages setting in such experiments. The epicuticle of barnacles is known to be formed of quinone-tanned proteins, which are very resistant, but are attacked by hypochlorites. It is rather surprising, however, to find evidence that such inert substances are involved in a process of specific recognition. It seems to be necessary for the larvae to make contact with them before they can be recognized. Perhaps the suckers on the ends of the legs by which the larvae walk bear proteins capable of reacting *in situ* with proteins on the surfaces of cuticles with which they come into contact. These might be lock and key reactions, such as those postulated to occur between antibodies and antigens.

It may be of some interest to yachtsmen that the cleaning off of small barnacles, before a regatta, leaves the invisible bases behind to stimulate fresh fouling. A coat of paint or a thin film of celloidin, however, will prevent barnacle larvae from making contact with these bases, and this will remove the stimulating effect. It is unnecessary to boil one's yacht in strong acid. Once barnacle larvae have sensed the presence of their own species by contact with settled individuals, they will settle more readily on clean surfaces nearby, even if they have to swim to find them. It is therefore not advisable to tie up a yacht alongside a heavily fouled wharf.

Barnacle gregariousness is not entirely specific. In a series of experiments, twenty larvae of the common shore barnacle, *Balanus balanoides*, were presented with a stone in a little dish. In some experiments the stones were bare, in others they bore pieces of barnacles from other families not closely related to the larvae. In other experiments they bore pieces of barnacles of the same family as the larvae, and in yet others, of the same species as the larvae. Larvae never settle very readily in experiments such as these, which involve loose pieces of cuticular and other materials, but when these materials were of the same species, considerable numbers of larvae settled and, when they were of allied species, a smaller but still significant number settled. Pieces of barnacles from other families had little or no stimulating effect, their cuticles presumably being too different.

So much for one aspect of the setting behaviour of barnacles. This and their general biology is being studied at Menai Bridge with most interesting results by Dr. D. J. Crisp. Barnacles are the most important of the organisms which foul ships. The summer fouling at Swansea must have become more severe within the last ten years because of the introduction of the Australian barnacle, *Elminius modestus*, which is now by far the most common barnacle on the shores of Swansea Bay. It is easily distinguished since there are only four plates around the body, whereas there are six in British barnacles. It breeds throughout the summer, more prolifically than British barnacles do. It was first noticed in Britain in 1946, but by that time it was already abundant in the south-east. Perhaps it was introduced at the beginning of the war into the Thames Estuary from ships laid up there, for it is quite common on ships from the Southern hemisphere. Indeed, it is surprising that it did not establish itself in this country a long time ago. In 1951 it was abundant in Milford Haven, but less so at Swansea and still less so in the upper Bristol Channel. Since it thrives in estuaries and has recently become much more common at Swansea, its distribution in 1951 suggests that Milford Haven was the point of introduction into this area. It entered North Wales from the direction of Morecambe Bay. Since 1949 it spread along the North Wales coast at about 20 miles a year, helped there by the westward residual drift of the tides. The larvae swim for at least a week, so may get carried a long way.

Now larvae of most species are spread about in this



way, yet there are often striking gaps in the distribution of some. There are, for instance, many species common on the west of Anglesey which are never found to the east. All these western forms are also southern forms, so probably the winters are too cold for them to the east, to judge from the arrangement of the winter isotherms. As one comes south into Cardigan Bay, one finds additional southern forms. The worm, *Sabellaria alveolata*, which forms such conspicuous sandy reefs near Swansea, is also common in Cardigan Bay, but does not occur on the north coast of Wales. The purple barnacle, *Balanus perforatus*, which is so common near Swansea at low water and so liable to lacerate bathers, is still more southern in its distribution, for it does not extend north of Pembrokeshire. These are all Mediterranean forms approaching their limits in Wales. The points at which they disappear so sharply are peninsulas, were strong currents disperse the planktonic larvae, stopping the species from spreading at all into the less favourable areas beyond.

## Underwater Observations

Now let us go down below tide marks with the help of the aqualung. The poor visibility makes it difficult to map the underwater scene except in such a place as the Menai Straits Narrows, beneath the suspension bridge, where a submarine telegraph cable runs to connect Anglesey with the mainland. Marks were tied to this cable every 10 metres, the distance across at this point being nearly 200 metres. Dr. Clifford Jones and Miss Doreen Lucas, both of the Zoology Department at Bangor, kindly helped to identify the animals collected from the marked stations.

This narrow channel is rocky, swept by currents which reach six knots when the tide runs. The Straits here bend through almost a right angle. Entering the water on the outside of the bend, by the Caernarvonshire shore, one finds a thick jungle of *Laminaria hyperborea* and the shallow-water animals usually associated with attached algae. The water is rather turbid and the *Laminaria* penetrates no farther than 4 metres below low-water mark, but red algae are common down to 6 metres. Deeper down the slope, which looks like a roof, though it is only one in four, vast sheets of sponges cover the rocks, where the light is insufficient for plants to grow. The dominant sponge is *Halichondria panicea*. Colonies of the hydroid, *Tubularia indivisa*, sprout out of it abundantly. The heads of the *Tubularia* are cropped by numerous large sea slugs, *Dendronotus frondosus*, but the stems are left and these grow new heads quite quickly. The channel is 15 metres deep, appearing gloomy or sometimes entirely dark. Many of the animals common here are much admired for their pink or red colours when they are brought to the surface, but these colours are inconspicuous or unseen at the depths where the animals usually live, to which red light does not penetrate.

In the channel towards the inside of the bend, there are gravel banks with plenty of starfish. The sea anemone, *Tealia felina*, some nearly 6 inches across, occurs at densities of forty per square metre, attached to stones and rocks amongst the gravel. Ascending the slope above, one comes upon a well-lit shelf covered with colour, particularly with blue *Botryllus*, red weeds, and yellow or white sponges. This shelf is protected from strong currents by a promontory which bears one of the piers of the suspension bridge, and it is the home of a variety of fish. In summer one can guarantee to find shoals of pollack there, beautifully streamlined fish about a foot long, which flock round curiously if one stays still.

The landward side of the shelf is bounded by a submarine cliff crowned with *Laminaria*. Above it, at depths of 3 metres or less, we again encounter shallow-water animals, such as *Aglaophenia pluma* and *Amathia lendigera*. The vertical distribution of these is probably governed by the light gradient, for at Bardsey Island, where the water is clear and where the attached algae extend much deeper than in the Menai Straits, the limits of these shallow-water animals are correspondingly lowered. But it is quite uncertain whether they are governed directly by light, through its influence on the behaviour of the swimming larvae, or whether they are affected chiefly by the presence or absence of algae.



The comparative scarcity of fish in the channel of the Menai Straits Narrows is probably due to the currents and to the stinging cells of the hydroids and anemones which grow so abundantly there. It is certainly not due to shortage of food, for a kilogram of the sponge, *Halichondria*, collected from the tide-swept area, bears thousands of small crustacea. The majority are the ghost shrimp, *Caprella linearis*, which stands in jostling crowds on the surface of the sponge, waving its claws to catch particles that are being swept past. Where *Tubularia* is scarce and fish are common, the *Caprella* are less so, and their place is taken by another amphipod, *Tritaeta*, which lives protected in little holes which it digs out of the surface of the sponge.

Male *Caprella* are strikingly larger than the females and more conspicuously pushing in their habits. They seem to shoulder the females aside as they grab particles of food. On the surfaces of the sponges the females, which carry their young in brood pouches, outnumber the males, but in fishes' stomachs the males outnumber the females, so perhaps there is true nobility in their self-assertive behaviour.

### Biology of Fishes

Most of what I know about fish was learned from Dr. S. Z. Qasim, who recently returned to Aligarh, after working at Menai Bridge for three years. One of the species which he studied was the shanny, *Blennius pholis*, which is so common on rocky shores. During the breeding season in early summer the mature male becomes black, selects a space under a rock, and drives away all intruders except ripe females, which visit this nest from time to time and attach their eggs to the surrounding walls. Whilst a female is laying her eggs, which sometimes takes her all day, the male dithers about excitedly but not very usefully. He fertilizes the eggs, however, and when the female has finished, he chases her off, just as he chases everybody else off, until the next ripe female comes along.

Dr. Qasim also studied another of the Blenniidae, the butterfish, *Centronotus gunnellus*, which is also common on the shore. It is like a flattened eel with spots down each side. Its eggs form a mass like a golf ball, which is guarded first by both parents, and then by the female alone.

Now Dr. Hickling, who carried out that valuable research on the hake fished by the South Wales steam trawlers, has remarked that in some fish, hake included, the eggs in a maturing ovary are of various sizes, obviously destined to be shed in a succession of spawnings, spread over a long period; whilst in others, as you can see in a kipper, the eggs are all the same size and are presumably all spawned about the same time.

Qasim found his species were of those two types, and he collected from the literature details about the other British fish, the breeding habits of which are well known. Some of these could be called Mediterranean-boreal forms, since they breed in the Mediterranean but not north of the Arctic Circle. The others are northern, Arctic-boreal forms, breeding in the Arctic but not in the Mediterranean. Off western Europe their distributions overlap and the interesting thing emerges that all the southern



forms seem to mature their eggs in successive batches and have breeding seasons lasting at least five months of the summer. There must be plenty of food about then for the females to put into their next batch of yolky eggs, and any egg-guarding is done by the males, leaving the females free to feed. All the northern forms, on the other hand, have eggs of one size, probably shed all at once, as is certainly so in the butterfish. Their breeding seasons last no more than three or four months, and occur at the coldest time of the year. That is when they occur in the Arctic, too, in most of these species. The adaptive advantage of this behaviour must be that Arctic plankton production is intense for only a few months in summer. The fish larvae must hatch then, so as to feed on the plankton. Spawning must occur much earlier, before this favourable time, since there is a long incubation period between spawning and hatching. During spawning temperature and food supply are at about their annual minimum, so presumably conditions of life, for the adults, are too poor to support growth of further batches of eggs. Each fish therefore puts all its reserves into one batch. Egg-guarding can be done either by the females, as it is in the northern crested blenny, or by the males, or by both sexes, as in the butterfish. When the weather is so bad, one might just as well stay at home.

The growth of the shanny was followed by the usual fishery methods. The rings on the little ear stones, or otoliths, proved to be annual, as in many other fishes. In shannies the transparent zones, which appear dark in reflected light, just anticipate their owner's birthdays, generally appearing at the beginning of the spawning season, in spring.

Growth can be followed, at least in the younger fish, simply by measuring large samples, collected at the successive seasons of winter, spring, summer, and autumn, and examining the size groups into which they fall. A large, well-defined group of the smallest shannies, mostly measuring 4 or 5 cm long in winter and spring, were 6 or 7 cm long in summer and 8 cm in autumn, when the fishes of the next year class appeared. These were the next batch of little fish, a few months old, arriving back on the shore, after a brief period of feeding in the plankton. They had already reached a length of about 4 cm.

When all the evidence was put together, to give the growth curve of the shanny during its normal life of six years, it was clear that growth in length after the first year is confined exclusively to the three summer months of June, July, and August. In the autumn, when the water is still warm and the fish are feeding and fattening after the breeding season, they do not seem to grow in length at all. With growth so localized seasonally, it is not surprising that the otoliths show such distinct annual zones.

## Responses of Animals to Changes in Hydrostatic Pressure

Dr. Qasim reared the larvae of these fishes, finding that periodic spells of darkness were essential for their health, which suggested that they needed their night's rest. He also found that shanny larvae had air bladders for regulating buoyancy, as in so many fishes, whereas butterfish larvae lacked any gas-filled vesicles. Yet larvae of both species alike were sensitive to changes in hydrostatic pressure, swimming up if the pressure was artificially increased and swimming (or sinking) down if it was decreased. So the air bladder of fishes is not essential to their perception of pressure changes.

Now Professor Hardy and Dr. Bainbridge recently showed that planktonic crab larvae respond to pressure increases by swimming upwards. We confirmed this and



found that it is true for a variety of marine plankton invertebrates. Many can perceive changes equivalent to 5 or 10 cm of water, which are the same as 5 or 10 millibars. The response certainly helps them to regulate their depth, though they are not slaves to it in the sense that they will automatically perform vertical movements to compensate for any pressure change imposed artificially upon them. Most animals of high specific gravity, such as crab larvae, seem to be prevented from doing this by the fact that they are in the habit of swimming upwards at a rather constant speed, which is generally equal to their rate of sinking. They seem reluctant to depart very far from this constant level of activity. Though they swim more strongly at higher pressures, their increased activity does not generally last long enough to raise them sufficiently far to cancel a large increase in pressure, of, for instance, one atmosphere. It is well known, too, that light plays a part in regulating the depth at which many plankton animals swim. They shun strong light but swim towards weak light, so come up to the surface at dusk and return to deeper levels next day as the sun begins to ascend again. The pressure sense is only one of several mechanisms affecting their behaviour. Indeed, many animals show no response to pressure changes.

Anyone can observe a pressure response by getting one of those transparent comb-jellies, *Pleurobrachia pileus*. They are the size of gooseberries and are very common in summer, often becoming stranded at the water's edge in vast numbers. If you put a healthy buoyant one in a bottle of sea water and fix a piece of pressure tubing to the mouth of the bottle, so that you can reduce the pressure by sucking with your mouth, you will find that every time the pressure is reduced the *Pleurobrachia* will contract its tentacles, which it uses for fishing, and will swim downwards.

In *Pleurobrachia* the orientation of the pressure response is to gravity, but in some animals the orientation is to light. It is possible, by lighting young barnacle larvae from below (in reverse of nature), to delude them into swimming downwards more strongly when the pressure is increased. Older barnacle larvae, which are ready to settle, are excited by pressure changes and then more readily find suitable substrata. If they are kept constantly at high pressure they remain too intent on swimming towards the light, whilst at constant low pressure they are too inactive. But at fluctuating pressures they alternately swim up and sink down, and occasionally become negative to light, so that they quickly find dark stones placed in their aquaria. In a similar way the pressure changes caused by the waves probably help these larvae of the shore barnacle, *Balanus balanoides*, to find the rocks on which most of the adults live.

The problem of how such animals perceive small changes in hydrostatic pressure is very mysterious. Their insides should be as incompressible as the surrounding water and their body walls are not rigid, so the pressure inside them should always be the same as that outside. Small changes in pressure should cause no deformation if no gas vesicles are present. It seems unlikely that there are minute gas bubbles in the animals' bodies, because such bubbles would be in a very unstable state. There would be great forces of surface tension tending to make the bubbles dissolve, and the conditions suitable for bringing bubbles into being against these forces should lead them to expand quickly to an easily visible size, as you can see happening in any vessel of water plants that has been well lit. Many of these pressure-sensitive animals are perfectly transparent, yet no gas vesicles can be seen within them. If any were there, they should be easily visible under the microscope.



Now I have talked long and too fast, yet I have mentioned very little of the work that has been going on at these two Marine Stations in North Wales. I have certainly not left much time to talk about Swansea. Here Zoology has a traditional bias towards the marine side, thanks to the teaching of Dr. P. A. Little and to his research on the parasites of fish. I am hoping very much that my other marine biologist colleague, Dr. Naylor, and I will be able to follow in Dr. Little's wake. Dr. Naylor has an international reputation for his work on the marine Isopoda. He is also interested in shore ecology and the fauna of artificially warmed docks. My remaining colleague, Mr. Macfadyen, is of terrestrial habits, but his great ingenuity will be a tremendous help in all our work. He has devised, for his soil researches, a continuously recording respirometer, and it will be particularly interesting to use this for following the rhythmic changes in metabolic activity shown by marine animals, for these may vary not only diurnally, but also with the tidal cycle.

Our opportunities here are immense. In the Swansea docks the fouling and shipworm damage is tropical in character and intensity, since the water is warmed by being passed through a power station. I need scarcely mention the importance of the district's fisheries, or the use which we will be able to make of the Dale Fort Field Centre, where Mr. John Barrett holds genial sway. The Field Centre also caters for visitors to the nearby island of Skokholm, where steep rocks go down into deep clear water, promising good visibility for diving. In the Bristol Channel the water is generally rather turbid, largely because of the strong tides, but these tides expose vast areas of rock, sand, and estuarine mud, with a richly varied littoral fauna.

I am afraid that I have said practically nothing about the other Colleges of the University. I should certainly have said a lot about Aberystwyth, where Professor Lily Newton and Professor T. A. Stephenson, F.R.S., with their staffs, have directed so much marine research. I should have said much more than I did about the Zoology Department at Bangor, which is so well known for marine studies and for the annual vacation course in marine biology which draws students from all over Britain. There is much to be said about Cardiff, too, where the late Professor W. M. Tattersall worked and where so much marine biology is taught today, under Professor James Brough. I should have said something of the past and something of the many marine biologists who have gone from this University to work in various places throughout the world. The very fact that I have had to omit so much shows that marine biology is a subject that we, in the University of Wales, are especially well situated for studying.



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