Special Lecture

THE ECOLOGY OF PARASITISM IN THE INTERTIDAL ZONE

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The tidal rhythm is reflected in a biological rhythm of activity and quiescence of the animals in the intertidal zone, and the ecosystem so built up there provides scope for varieties of animal communities with unfamiliar patterns of food chains, and favourable opportunities for the spread of parasites. These phenomena are exemplified by the opisthorchid *Cryptocotyle jejuna* and *C. lingua* developing in *Littorina littorea* and inshore fish ; microphallid trematodes in *Littorina* spp, and *Carcinus maenas* or *Gammarus* sp.; species of *Transversotrema* parasitising marine, brackish-water and freshwater fish in the gastropod *Melanoides* spp; the heterophyid *Galactosomum* of bird hosts *Sterna fuliginosa* and *Larus argentatus* in marine gastropods and clupeoid fishes; and, the schistosome *Microbilharzia variglandis* of gulls and other shore birds in the mud-snail *Nassa obsoleta*. Swimmers, fishermen and clam-diggers are vulnerable to the attacks of the cercariae of *M. variglandis* in low tide and sunny weather.

The tides enable freshwater, estuarine, littoral, planktonic and benthic organisms to congregate in the intertidal areas, in diverse patterns of food-chains, when predation and parasitization reach their maximum potential, and the classical migration of andromous and catadromous fishes would further accentuate the dynamics of parasitism. A species of parasite could thereby be used as an 'ecological label' to unmask the food habits, migratory behaviour, or the habitat of a host or group of hosts.

The tidal zone comprises the upper portion of the littoral zone, and is classified as an amphibious situation. Plants and animals living on the seashore between tide-marks are subject to alternating droughts and flood twice each day. Organisms living in the central area of the tidal zone must be able to be *aquatic* for about $6\frac{1}{4}$ hr when the tide is in, and *terrestrial* for an equal period when the tide has ebbed, and so on, day in day out. Each high tide is an advance of the sea on the threshold of the land, while the ebb is an expansion of the land into the sea, exposing the intertidal area that belongs alternately to sea and land.

The tidal zone is thus a very difficult habitat (with all the problems of a border area), complicated further by the differences in the timing and height of the tides. Since low tide and high tide occur about one hour later each day, the intertidal area comes to be exposed at all hours of the day and night. Because also of the fluctuations in the amplitude of the tides during spring tide and neap tide, an animal or plant in the upper extreme limit of the tide will be covered by sea-water for only a brief period about every two weeks, whereas an organism living in the lower extreme tidal limit will receive only a correspondingly short exposure of air and sun. When the tide is low, there is little or no food for most intertidal animals, and the essential life processes have to be carried on while the sea-water covers the shore. The tidal rhythm is therefore reflected in a biological rhythm of alternating activity and quiescence.

Despite these severe conditions, a dense population of a variety of plants and animals characteristically inhabits the tidal zone. The fauna and flora consist chiefly of sessile forms, such as the common sea-weeds, anemones, barnacles, mussels and clams. These, by their sedentary nature, must endure the full effects of the differences in the two media. In addition, certain active forms forage in this zone under favourable conditions and retreat.

At low tide, animals come from land and feed on the materials that have been exposed. Shore birds are the most dominant members of the area, but less common are the rats, mice and other small mammals that feed chiefly at night. During high tide, the situation is reversed ; fishes, crabs, worms, starfish and other active animals from deeper waters migrate for a few hours and retire. The alternating visitations of these forms make the shore a densely populated and intensely active habitat. The ecosystem so built up provides immense scope for varieties of animal communities, involving unfamiliar patterns of food chains, and in which the parasite finds the most favourable circumstances for spread. The study of the ecology of the parasites of the shore animals would undoubtedly be fascinating and rewarding, not only in unravelling their life-histories but also in understanding the biology of their hosts.

The ecology of such parasites can be explained by choosing a few outstanding examples of trematode infections, as given below.

Excellent habitats for the study of bird flukes are the mud-flats and saltings, consisting generally of flat stretches of mud and water, a no-man's land in a manner of speaking, which belong neither to the sea nor to the earth. Saltings are a paradise for wild birds such as waders, ducks, and gulls. A familiar bird in these surroundings is the Redshank, host of the trematode *Cryptocotyle jejuna* (Opisthorchidae). The fluke's eggs pass out with the droppings and become scattered over mud and brackish water pools. The mollusc, *Hydrobia ulvae,* another inhabitant of the same area, swallows the eggs and releases cercariae which utilize fish (freshwater, salt, or brackish-water species) as the second intermediate hosts.

A related species, *Cryptocotyle lingua,* parasitizes herring-gulls and many piscivorous birds and mammals in Britain and North America. The periwinkle, *Littorina littorea,* serves as the first intermediate host, and various inshore fish-like gobies (*Gobius*), blennies (*Blennius* spp), and butterfish (*Pholis*) as the second intermediate hosts. Stunkard (1930) had elucidated the development of the trematode in the U.S.A. He found the common tern (*Sterna hirundo*) of the Woods Hole region heavily infected with the parasite. Eggs discharged with the droppings are washed about by the tides, or deposited on the rocks and caught in the slime and moss, to be eaten by *Littorina littorea*, in which development progresses up to the cercarial stage. The actively swimming cercariae meet a fish, the Cunner (*Tautoglabrus adspersus*), a sluggish swimmer which lies almost motionless on the substratum, and bore into its skin on or near the fin, and encyst. Shore birds (gulls and terns) which feed on such fishes are exposed to infection resulting in the development of the adult flukes in the intestine.

Littorina littorea, a characteristic inhabitant of the littorine zone, was originally a European gastropod which was later introduced on the western side of the Atlantic. It was first found near the New Brunswick in 1855, and later on the coast of Nova

Scotia in 1868, whence it gradually spread southward to become one of the most abundant snails in the Woods Hole area. Gulls are always seen dipping into pools, fishing in little gullies on the saltings, or sitting in small flocks along the water waiting for the turn of the tide. No group of birds seems more heavily infected with worms: at least 20 species of trematodes have been recorded from the Black-headed Gull alone.

Other flukes occurring in these birds are representatives of the Plagiorchidae and Microphallidae. Several of the latter utilize *Hydrobia* and *Littorina* as the first intermediate host, and the Shore-Crab *Carcinus maenas* and the amphipod *Gammarus* as the second intermediate hosts. Consumption of these crustaceans, at low tide, would lead to certain parasitization by the flukes.

Another habitat, not quite on the shore, is the estuarine brackish-water influenced by tidal fluctuations in nearly identical manner. Predominant among the fauna in the brackish-water pools is the melaniid gastropod, *Melanoides tuberculatus*, other species *M. terebra* and *M. scabra* being less common. Its distributional range extends from freshwater tanks, lakes, canals, streams and creeks of rivers to brackish-water mud-flats, and its tolerance to salinity is high (3 parts of fresh water, 2 parts of sea-water), though it cannot survive in sea-water. *M. tuberculatus* and other species harbour over 30 kinds of cercariae, as single or multiple infections, which are widely representative of trematode groups. Among them is the morphologically unique progenetic cercaria, *Cercaria patialensis* recorded first from Punjab (Soparkar 1924), and later from Nellore (Anantaraman 1948), from Belgian Congo (Brien 1954), Ceylon (Crusz 1956), and Waltair (Rao and Ganapati 1967), while a similar cercaria, *C. koliensis*, is known from *M. terebra*(?) in the Solomon Islands (Oliveir 1947), all freshwater sources. The first record of an adult worm, that of *Transversotrema haasi*, was from a Red Sea fish (Witenberg 1944); that of *Transversotrema* sp., from scorpid marine fishes in the Pacific, near Queensland, Australia (Manter 1965); and the metacercaria of *T. laruei* from a Philippine marine and brackish-water fish, *Lates calcarifer* (Velasquez 1958, 1961). But, the post-cercarial stages of *T. patialensis* are known from the freshwater fish, *Macropodus cupanus* in Ceylon (Crusz and Sathananthan 1960), and *Panchax panchax*, *Catla catla* and *Esomus danricus* in India (Rao and Ganapati 1967), while its adult is on *Panchax panchax* (Murthy and Rao 1968).

It is to be expected that since *Melanoides* does not enter the sea, marine fishes brought by the tide into the estuarine region and brackish-water pools would acquire the infection in that habitat when the free-swimming larvae emerge from the snail. The cercariae infest the fish hosts under the scales, and as they develop into adults in the same location, the tolerance of the developmental stages to salinity changes should accordingly be high. The importance of *Transversotrema* as a 'biological indicator' would be referred to later in the lecture.

Studies on helminth parasites from hosts on the Madras coast were made by Anantaraman (1961, 1963), as a result of which several trematode, cestode and nematode larvae were reported from ctenophores, medusae, gastropods, copepods and crabs, and adults in fishes and fish-eating birds (snipe, tern, gulls, etc.). Brief reference may be made to the three species of the Heterophyid *Galactosomum* found to infect *Sterna fuliginosa* and *Larus argentatus*, and a larval form of the same

genus in *Matuta victor*. A magnacercous cercaria believed to be the larval form of one of them was subsequently encountered (Reimer and Anantaraman 1968) from the gastropod *Turritella attenuata* on the same coast. Workers at Waltair (Madhavi and Rao 1968) have added valuable observations, as in the case of *Transversotrema,* to the studies in Madras, in reporting the metacercaria of *Galactosomum puffini* of *Larus* spp, from four clupeoid fishes, thus linking the successive stages of the life-history. When sardines came ashore, sea-gulls gathered round the nets and consumed them voraciously.

For a change, let us now examine how human health is influenced by parasites in the tidal region. The syndrome 'Cercarial Dermatitis' has long been known to be caused by schistosome cercariae of non-human origin (i.e. of animals and birds) emerging from freshwater snails. A comparable reaction on the exposed skin of sea-bathers and clam-diggers has repeatedly been encountered on the Atlantic coast of the U.S.A. The cercariae of *Microbilharzia variglandis*, a schistosome of gulls, plovers, sand-pipers and other migrant shore-birds, are harboured by the gastropod intermediate host, *Nassa obsoleta*, and when liberated invade unprotected areas of the human skin provoking an allergic reaction known as Swimmers' itch or clam-diggers' itch (Stunkard and Hinchliffe 1952). Many shell fishermen had therefore had to resort to the use of hip-boots and gauntlet-gloves, while digging for the clams *Mya arenaria* and *Mercenaria mercenaria* on those shores.

Nassa obsoleta is the most abundant and widespread mud-snail in the infectious areas of Narragansett Bay and marine ponds on the beaches of Rhode Island, and is relatively tolerant to lowered salinity near the mouths of freshwater streams. Its intertidal habitat points atonce to shore-birds as the natural hosts of the schistosome. The dermatitis is contracted most often in periods of low tide, calm water, and sunny weather, and by persons who are relatively inactive in the water or exposed for a prolonged period. Swimmers are vulnerable to the attacks of the cercariae, and as the snail shares the same habitat with the two bivalves mentioned, this dermatitis develops into an occupational disease among clam-diggers. 'Sea-bathers' eruption' on the East coast of Florida is also attributed to similar cercariae.

The shore is again liable to pollution, as emphasized by Rachael Carson in *Silent Spring*, not only by organic and industrial wastes directly discharged into it but also by the large scale application of pesticides in agricultural and public health programmes. For instance, DDT dispersed over fields against plant pests, and in the swamps and marshes against mosquitoes, get washed into the rivers and ultimately into the sea. It has been estimated, in Long Island Sound, that a concentration of 0.000003 ppm in the run-off water in the fields builds up about 10 million times (i.e. 25 ppm) in fish-eating shore birds (cormorants, ospreys), through zooplankton (0.4 ppm), plankton-feeding small fish (minnows with 0.5 ppm), and large Needle-fish (2.0 ppm) which devour the minnows.

A detailed analysis of the ecological relationships involved in these infections is obviously difficult in the time available to us. But, these examples show how closely are the life-histories and transmission of the parasites tailored to the habits and habitats of their hosts. External parasites, such as the monogenean trematodes,

copepods and isopods would evidently be subject to changes in the environment (light, temperature and salinity) in much the same manner as their hosts are, and this would be true of the free-living stages of the internal parasites too. The tides enable freshwater, estuarine, littoral, planktonic and benthic organisms to congregate, though for brief periods, in changing patterns of communities, when predation and parasitization attain their maximum potential. The complex and intricate food-chain is the main channel through which the parasite finds its successive hosts. The classical migration of anadromous and catadromous fishes would further accentuate the dynamics of parasitism and enlarge the scope for parasitization in a diversity of habitats. The salmon, for instance, is known to harbour different kinds of parasites in each of its developmental stages.

Host-parasite relationships lead to two kinds of specificity : ecological and physiological. Ecological specificity is decided by the host's behaviour and habitat to enable the parasite to reach it, whereas physiological specificity is dependent upon the physical and biochemical environment within the host being favourable to the establishment of the parasite. In many cases, the latter is so developed that parasites are highly host-specific. Such parasites serve as "ecological labels" (Biological tags or indicators) to reveal the habits and habitats of their hosts. The presence of a particular species of a parasite could unmask the food habits, migratory behaviour, or habitat of a host or group of hosts. The example of *Transversotrema* cercariae from a freshwater snail infecting marine fish has been mentioned earlier. Parasitization of any marine fish with the adult trematode should reveal its migration to the shore or a brackish-water habitat, where *Melanoides* would be the source of the cercariae.

Summing up then, it might be claimed that parasitological evidence has been arrayed to underline its importance in the study of the biology and zoogeography of marine organisms, more particularly those frequenting the intertidal zone. The tides of the sea exert a profound influence on life at the shore, may it be that of a parasite, bird, beast, or man. How biologically true are the words of Shakespeare :

"There is a tide in the affairs of men,
Which taken at the flood, leads on to fortune;
Omitted, all the voyage of their life
Is bound in shallows and miseries.
On such a full sea are we now afloat :
And we must take the current when it serves,
Or lose our ventures".

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