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Studies on oyster scavengers and their relation to the fungus Dermocystidium marinum

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STUDIES ON OYSTER SCAVENGERS AND THEIR RELATION TO THE FUNGUS *DERMOCYSTIDIUM MARINUM*[1]

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ABSTRACT

Dermocystidium marinum, a parasitic fungus of oysters, was demonstrated from the stomach of the snail, *Urosalpinx cinerea*, from the stomach, intestine, and body of three fishes, *Gobiosoma bosci*, *Chasmodes bosquianus*, and *Opsanus tau*, and from the body, especially setae, of two crabs, *Neopanope texana* and *Rhithropanopeus harrisii*. All animals containing *D. marinum* had scavenged oysters infected by the fungus. A few oysters became lightly infected when kept in aquaria with fishes that had been fed infected oyster tissue. In one tidal inlet of Chesapeake Bay, Virginia, *Eurypanopeus depressus* was the most abundant scavenger, followed by *Nassarius vibex*, *Gobiosoma bosci*, and *Panopeus herbstii*. Killed oysters on this reef were consumed by scavengers in less than one day in temperatures over 24 C. At temperatures above 18 C, dead oyster tissue never remained long enough to decay. Theoretical methods of transmission of *D. marinum* by scavengers are discussed. It is concluded that nearly all dying oysters are consumed by animals during periods of normal mortality, so their parasites must pass through the digestive systems of scavengers.

INTRODUCTION

Within the past decade there have been several studies on the biological structure of oyster reefs. These studies, however, have given little insight into the dynamics of oyster communities. The extensive studies of Hedgpeth (1953), Gunter (1955), and Parker (1955, 1959) in Texas, Wells (1961) in North Carolina, and Korringa (1951) in Holland were largely concerned with sedentary forms, and the highly motile fishes went little noticed. The concept of the oyster biocoenosis is known widely, but has received little expansion.

The present study was not concerned with the whole community, but with the role of fishes, crabs, and a few other scavengers in the community, especially in their relationship to the oyster, *Crassostrea virginica* (Gmelin) and its parasitic fungus, *Dermocystidium marinum*

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Mackin, Owen, and Collier, 1950. Knowledge of D. marinum has been reviewed very recently by Johnson and Sparrow (1961) and by Mackin (1962).

This study started from observations of fishes living in close association with oysters, and progressed to observations on the relationship of mortality of oysters with activity of other species in the community. Mortality of oysters in the study area occurs predominantly in the warmer months, and most of this mortality is due to Dermocystidium marinum. Some of the oyster associates that are active in summer are scavengers of dying oysters and consequently ingest cells of oyster parasites. This suggested that the scavengers might transmit infections to other oysters.

METHODS

Data on scavengers were collected incidental to studies of oyster mortality on the Eastern Shore of Virginia. Studies were largely confined to a small embayment off Chesapeake Bay called The Gulf, just north of Cape Charles, Virginia. Life history data on scavengers gathered here and in other areas of Virginia will be presented elsewhere.

The presence of Dermocystidium marinum was determined by Ray's (1952) thioglycollate culture method. After culture the enlarged fungus cells were stained (blue) with iodine. Oysters and the digestive tracts of fishes were cultured by the standard method, but feces were originally cultured in petri dishes with 10 cc of medium added to about 5 cc of water containing fecal material. This method has the advantage of not disturbing the feces, but enhances the growth of molds. Since this proved generally unsatisfactory, feces were later placed in test tubes with the medium, and dilute oyster serum from uninfected oysters was added. Uninfected oysters came from the Seaside of Virginia where D. marinum has not been found (Andrews and Hewatt, 1957; also unpublished studies). Fishes and crabs were fed in aquaria or small bowls with pieces of meat, or with whole oysters that died with heavy Dermocystidium infections. The fish were then washed in three or more separate dishes and placed in dishes with Seaside water of a salinity near 30 parts per thousand; or they were placed in aquaria for infection experiments. Later, after it seemed that the fungus was killed by Seaside water, Chesapeake Bay water of salinity near 20 ppt was substituted. Feces were collected with a sterile pipette and placed in culture. After two to five days these cultures were examined under monobjective and stereoscopic microscopes.

At approximately monthly intervals from 9 June through 7 November 1961, groups of 10 oysters were made into "gapers" by cutting adductor muscles. Each month, these artificial gapers were placed in individual trays (10 per tray) made of one-inch-mesh rat wire, with a cover of the same material. These permitted small scavengers to enter while preventing large crabs from removing the oysters. Ten control oysters with adductors cut were placed in a cage of 1/8-inch hardware cloth, which eliminated most scavengers other than very small recently metamorphosed gobies and mud crabs (which ate very little meat). The experimental and control cages were placed on the top and edge of an oyster reef at The Gulf. This reef is located near the lower edge of the intertidal zone just inshore from extensive eelgrass (Zostera marina) flats. The amount of meat taken by scavengers was calculated from wet weights of experimental and control oysters, after 10 minutes drying in the shade. Direct observations were made on the activities of scavengers on killed oysters in the shallow, clear water on and near the reef.

Several crude infection experiments were conducted by feeding fish pieces of infected oyster tissue and then placing them in aquaria with disease-free Seaside oysters. The habits of oyster fishes were observed in aquaria for a two-year period (1960-61).

DEMONSTRATION OF D. MARINUM IN SCAVENGERS

On 12 October 1959 an adult goby, Gobiosoma bosci, from the hinged shells of a dead oyster from Messongo Creek, was cultured in thioglycollate medium for Dermocystidium. After culturing and staining, numerous fungus cells were observed covering most of the caudal myomeres; most of the remainder of the fish had disintegrated. Since this observation, Dermocystidium has been demonstrated in the stomach, feces (Fig. 1), and on the skin of fishes, in the digestive systems of mud crabs and drills, and covering the body and among setae on the legs of crabs (Table 1). All of these had just come from oysters recently killed, or had been fed infected tissue. Nearly all scavengers from gaping oysters were positive.

Goby feces consist of highly digested remains of oyster tissue and more definite fecal "pellets" which are apparently the remains of small animals and scattered sand grains. In a few cases, Dermocystidium cells seen in the digestive system were in eroded oyster tissue recognizable as gill or mantle, but most fungus cells were found with numerous colorless fat globules suspended in the liquid intestinal contents, or in mucus. Dermocystidium was always found abundantly,

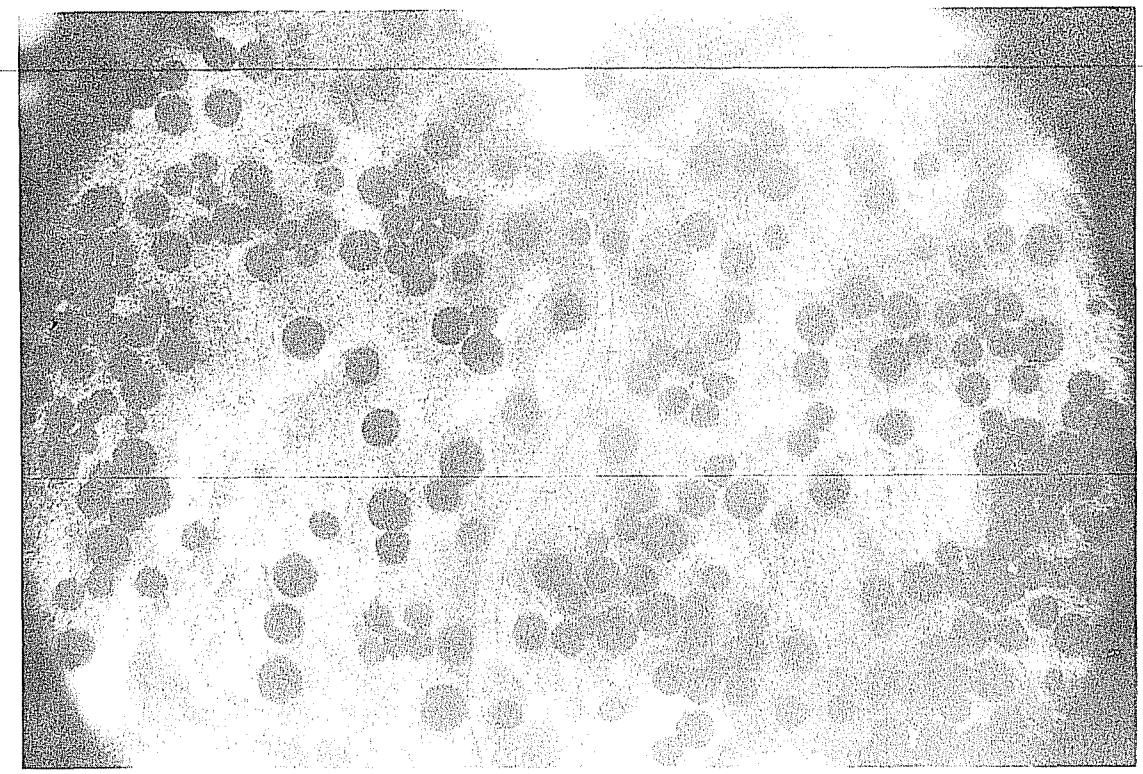

Fig. 1. Dermocystidium marinum in feces of Chasmodes bosquianus. Thioglycollate culture after three days. Iodine stained.

if present at all, in what appeared to be the remains of oyster tissue, but it was usually scarce in the fecal "pellets."

These observations showed that Gobiosoma bosci, Chasmodes bosquianus, and Opsanus tau ingest and defecate cells of D. marinum that respond to the thioglycollate test, and that pieces of infected tissue or mucus may attach externally to fishes and crabs. Since the fungus enlarged when cultured properly, and took the iodine stain, it must have been alive. Mackin and Boswell (1955) concluded that all stages were infectious.

When small fish were fed Dermocystidium-infected oyster meat and then placed in aquaria with disease-free oysters, some of the oysters developed Dermocystidium infections (Table 2). In experiments 1 through 5 only G. bosci was used, but C. bosquianus and Hypsoblennius hentzi were added in experiment 6. In spite of the small number of fish used and the small amounts of infected tissue they had eaten, the results indicate that G. bosci, at least, can transmit infection to oysters.

Table 1. Records of *Dermocystidium marinum* in scavengers. Animals from aquaria had been fed heavily infected oysters; those from natural waters had been found in recently dead infected oysters.

Species	Locality	Location of fungus	Number positive for *D. marinum*
Gobiosoma bosci	Messongo, Chesconessex	Skin, stomach	5
	Occahannock, Cherrystone	Intestine	
	Gulf		
	Aquarium	Feces	3
Chasmodes bosquianus	Gulf	Digestive system	1
	Aquarium	Feces	4
Opsanus tau	Nandua	Stomach	1
	Aquarium	Stomach, feces	2
Urosalpinx cinerea	Gulf	Stomach	1
Neopanope texana	Gulf	Covering body & legs	2
Rhithropanopeus harrisii	Occahannock	Covering body & legs	1

Table 2. Experimental infection of oysters by D. marinum from fishes. Temperatures were 20-24 C. All experiments were terminated after approximately 1 month except no. 3 which lasted 6 weeks. All infections were light.

Exper. no.	Number of fish added	Experimental oysters			Control oysters		
		Number alive	Number dead	Number infected	Number alive	Number dead	Number infected
1[a]	5	23	2	0	25	4	0
2[a]	5	21	4	2	21	4	0
3[a]	38	35	12	2	19	3	0
4[a]	36	5	18	0	17	2	0
5[b]	34	0	21	3	0	25	0
6[c]	44	4	21	2	20	5	0

a Seaside water, salinity 29-33 ppt.

b Evaporated Bayside water, 32-34 ppt.

c Bayside water, 22-24 ppt.

OBSERVATIONS ON SCAVENGING

One of the most ubiquitous and conspicuous scavengers is the blue crab, Callinectes sapidus. A single adult crab can consume a whole oyster. Both blue crabs and large Panopeus herbstii can carry or drag a whole killed oyster or one valve with the meat. Large Panopeus were capable of moving clumps of oysters they were hiding under. Whenever these two crabs were present, they dominated scavenging. Eurypanopeus depressus was reluctant to enter killed oysters while larger crabs were feeding.

Sometimes snails, mainly Nassarius vibex, would enter and begin feeding on killed oysters in experimental wire cages. They seemed to consume small amounts of meat and were usually the last scavengers to begin feeding. When killed oysters were placed around the periphery of a reef, large numbers of N. obsoletus from the nearby flats would feed on them. Both Urosalpinx cinerea and Eupleura caudata were found feeding on recently dead oysters. Although they are widely studied

predators their scavenging is little mentioned. Demonstration of living Dermocystidium in the digestive systems of crabs, drills, and fishes caught in the study area indicates that they had recently scavenged oysters.

Although most species in the proximity of a reef would eat oyster meat, it may be significant that several would not. Fundulus heteroclitus, F. majalis, and a species of Palaemonetes showed interest in killed oysters but none were observed to eat. However, F. heteroclitus ate loose meat when the shells were pulled apart and Palaemonetes has eaten meat in aquaria. Fundulus seems afraid to enter partly closed shells.

Although crabs and snails feed quietly, observations showed that fishes were the most voracious of scavengers. Due to their mobility they are often the first scavengers to enter killed oysters. While feeding, G. bosci tears off pieces of tissue; often several individuals simultaneously twist, spin, and turn, scattering bits of meat. A single killed oyster never failed to attract a few of these gobies, and often they were very numerous.

All species known to scavenge on the Eastern Shore of Virginia are listed below. These are included on the basis of direct observations in natural waters and circumstantial evidence such as the presence of Dermocystidium. This list is obviously incomplete and probably all motile animals living with oysters scavenge. However, it seems certain that a few species (Gobiosoma bosci, Chasmodes bosquianus, Opsanus tau, Eurypanopeus depressus, Panopeus herbstii, Rhithropanopeus harrisii, Callinectes sapidus, Urosalpinx cinerea, Eupleura caudata, Nassarius vibex, and N. obsoleta on native reefs and these plus closely related species on planted bottoms) account for most tissue consumed in the study area. Fishes, crabs, and snails came to the vicinity of killed oysters within minutes, regardless of the hour of the day or night. Most studies, however, were conducted during afternoon hours.

ABUNDANCE OF SCAVENGERS

There is very little information on the density of oyster associates. As previous authors have noted, relatively few species on oysters are very abundant. In fact, only Nassarius vibex and Eurypanopeus depressus were abundant at The Gulf on native oysters, but Gobiosoma bosci and Panopeus herbstii were not uncommon. The only other scavengers on the reef were Gobiesox, Opsanus, and Chasmodes, which were comparatively rare. Other reefs nearby and at other localities varied somewhat but the

dominance of snails, mud crabs, and gobies was apparent everywhere on native oysters. Oysters planted on subtidal bottoms acquire a more varied fauna, but the scavengers are similar. Annelids, which were not studied, are much more abundant on subtidal oysters.

The reef studied at The Gulf is situated at about low tide level, but it is a rare tide that exposes all of the reef. Such a tide occurred on 6 October 1961 and afforded an opportunity to measure the abundance of G. bosci. Apparently most of the fish in the reef migrated to the edge and to small pools in the reef. This migration is common on Seaside reefs also, during ebb tide. Most fish were then left behind by the tide; relatively few abandoned the reef for the nearby flats. The fish were easily captured, and a total of 184 was taken on half of the reef, an area about 40 feet long and 10 feet wide, by picking up clumps of oysters along the periphery. All fish were not captured due to rising tides, but it is believed a majority were. Later observations after the tide inundated the reef showed no fish attracted to killed oysters as had always before been the case. Since that part of the reef sampled was estimated to have 400 square feet of oysters, an estimate of 0.46 fish per square foot is made. During the low-water period the fish were concentrated in a narrow band a few inches wide, a concentration of 6.6 fish per linear foot. As many as 17 gobies were taken under a single clump of oysters. These figures are probably a fair minimum index of goby concentrations in autumn.

Nine square-yard samples on 6 and 19 October yielded counts of 15, 16, 16, 18, 18, 19, 24, 25, and 29 2-to-4-inch oysters, an average of 20 oysters per square foot or a total of 17,000 on the reef. Six square-yard collections of mud crabs, E. depressus, from The Gulf on the same dates yielded counts of 4, 6, 8, 8, 13, and 14. This gives an estimate of 7,830 E. depressus on the reef. Estimates of abundance of macro-associates of the reef are given in Table 3. These estimates closely match observations on scavengers, the most abundant forms appearing to consume the most meat proportional to size. Other than a few barnacles, there were no other animals found associated with these oysters.

SCAVENGING RATES AND DETERIORATION OF OYSTERS

A rough idea of the amount of oyster tissue consumed by scavengers can be computed from data obtained from trays of live oysters maintained at a number of stations on the Bayside of the Eastern Shore and examined at intervals averaging 20 days from May through November 1960. This encompasses the Dermocystidium mortality season in the area. Of 1338 dead oysters taken, only 156 (11%) had any meats left.

Table 3. Estimated abundance of oysters and scavengers on intertidal reef at The Gulf, October 1961.[a]

Species	Average number per ft^2	Total number on reef	Biomass, kg
Crassostrea virginica	20	17,400	700[b]
Eurypanopeus depressus	9	7,830	4.4
Nassarius vibex	1	> 600	?
Gobiosoma bosci	0.5	> 400	0.2
Panopeus herbstii	0.3	> 261	?

a The fishes Chasmodes bosquianus, Gobiesox strumosus, and Opsanus tau were too few to estimate. The blue crab, Callinectes sapidus, and the mud snail Nassarius obsoletus were not regular inhabitants of the reef but invaded it sporadically in unpredictable numbers.

b Shell weight accounts for 600 kg.

Assuming that oysters die randomly between examinations and that deterioration of oysters tends to be linear, then the tissue of an average oyster lasted a little over two days after death. Actually only 2% of the dead oysters were taken immediately after death (based on condition of meats), indicating that an average tray oyster lasted only 0.4 days before it had lost some meat. This seems too fast to explain by bacterial activity alone, and the destruction probably resulted from a combination of scavenging and decay. These figures agree with those of Gunter et al. (1957) who found that oyster meats disappeared in about two days in the summer at 28 C. Their studies, like these tray observations, were not made on natural oyster reefs.

Finding recently killed oysters with intact meats on natural bottoms is difficult. In fact, in all our scavenger studies on oyster beds we never encountered a gaping oyster, although oysters were dying.

The results of experiments conducted with killed oysters on a natural reef at temperatures of 24 to 30 C are shown in Fig. 2. Oyster meat exposed to scavengers was always consumed in one day, and

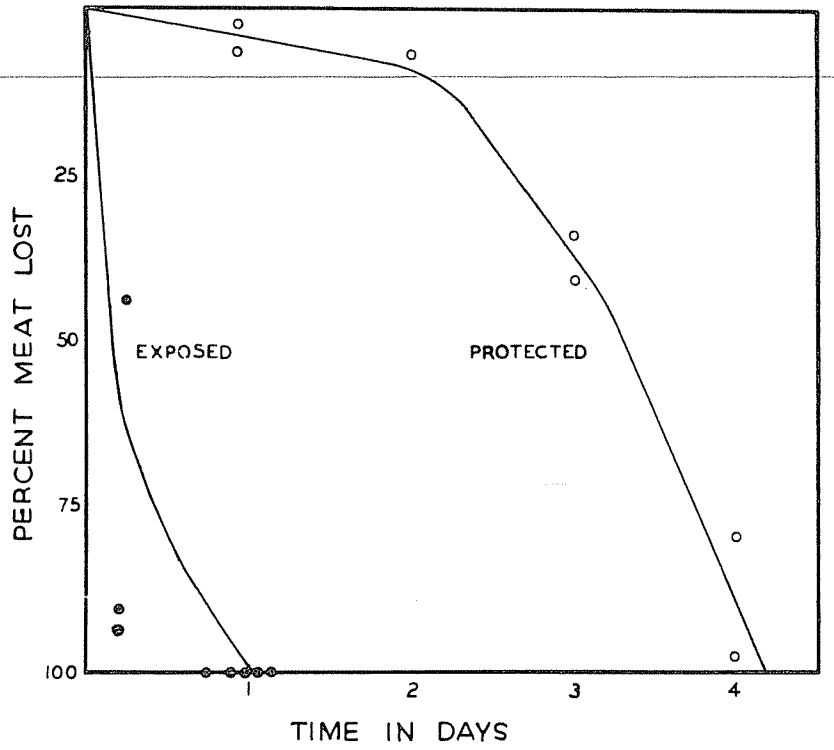

Fig. 2. Comparison of meat losses from bacteria in protected oysters and from scavengers plus bacteria in exposed oysters.

half or more was consumed in a few hours. In the controls bacterial decay destroyed most of the tissue in four days or more, and half in three days, the curve correlating with many culture growth curves of bacteria. Within one day oysters kept from scavengers showed no evident deterioration and weights indicated little had been lost. Brief studies at 18 to 24 C indicated that both curves shift to the right, but most meat was still consumed by scavengers within one day and all within two days. Groups of killed oysters exposed to scavengers on open bottom, uninhabited by oysters, lost little more meat than controls, presumably because scavengers were not present there.

The figures obtained from these experiments have two sources of error: (1) Killing ten oysters saturated a small area with a large amount of meat. Whenever a single oyster was killed, its consumption, at least to the muscle, was measured in minutes rather than hours. (2) Dying oysters probably are invaded by decay bacteria some hours prior to death, so perhaps the decay curve should be shifted to the left to represent what actually occurs.

The death point of oysters needs further study, using naturally dying oysters. Oysters die gradually and scavenging (sensu lato) may begin before the oyster is technically dead. Small gobies (G. bosci) often enter gaping oysters in aquaria and feed on gill tissue while these oysters still have the power of complete closure. An oyster sometimes closes on a goby, rarely catching it at mid-body and killing the fish, but more often temporarily trapping the fish inside. Pathogens such as D. marinum which cause lysis of tissue may speed up deterioration, although Ray et al. (1953) did not believe this accounted for decay of the oyster after death.

In any case, it seems significant that all meat was always eaten by scavengers in a relatively short time. Observations showed that the meat was actually eaten, not just removed from the shells. It is difficult to demonstrate 100% consumption, but the motivation obviously exists.

DISCUSSION

Since oysters form the basis of an extensive estuarine community with many dependent organisms, any pathogen of oysters is significant to numerous plants and animals. A certain amount of oyster mortality seems to be normal and is of considerable value to the community. The absence of oyster mortality would limit feeding and spawning of some associated species. On the other hand, excessive mortality may provide more food than can be absorbed by the community, and it removes the oysters which are the most important member, the dominant species on which the existence of the community depends.

Hopkins (1957) stated that a common effect of marine parasites is to increase the host's susceptibility to predators. Menzel and Hopkins (1956) noted that blue crabs, Callinectes sapidus, destroyed many spat, but ate only weak and dying adult oysters. The same is true of mud crabs (McDermott, 1960). This was also true of oyster drills, Urosalpinx and Eupleura, and other snails in the study area. The scarcity of recently killed oysters with intact meat on natural bottoms, and the observations on artificially killed oysters, indicate that nearly all oyster tissue infected with D. marinum is consumed by scavengers, at least during normal or less extreme mortalities. This would force almost all oyster tissue parasites to pass through animals other than oysters.

Spawning of G. bosci in recently killed oysters on the bayside of the Eastern Shore occurred largely from 15 June to 15 August

(unpublished data). This is when infections of Dermocystidium build up in live oysters (Andrews and Hewatt, 1957). Ray (1954) noted that oysters in Louisiana placed in endemic waters in June suffered higher mortality than those placed there in late August. This is also true of transplants of highly susceptible Seaside oysters into Chesapeake Bay.

As an oyster has more fungus cells available for release, it presumably will be more susceptible to attack by other animals. Andrews and Hewatt (1957) believed that disintegrating gapers account for most infective material, and Ray (1954) showed that infection by live oysters was much slower than other methods. Although it is not certain that live oysters can release large numbers of infective spores, dead oysters do, and subsequent transmissions could be due, at least in part, to scavengers, by means hypothesized in Fig. 3. The very least that scavengers may do is to speed up release of oyster parasites and prevent production of bacterial metabolites.

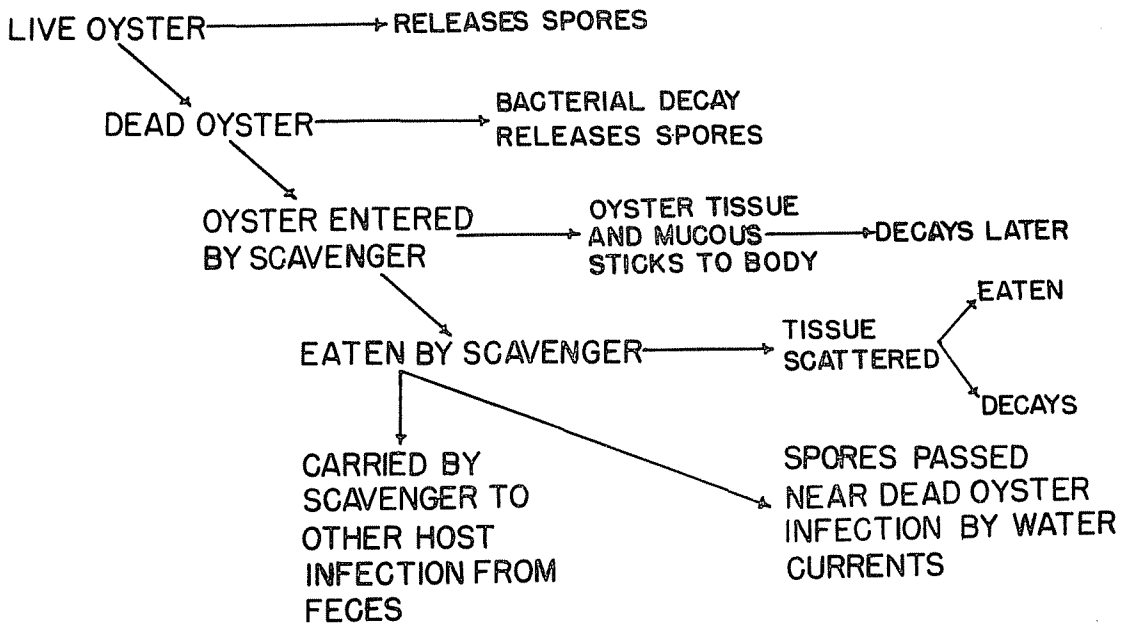

Fig. 3. Theoretical routes traveled by D. marinum in natural waters.

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