PARASITES OF BENTHIC AMPHIPODS: MICROSPORIDANS OF *AMPELISCA AGASSIZI* (JUDD) AND SOME OTHER GAMMARIDEANS

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ABSTRACT

Microsporidan infections were found in individuals of 11 species of benthic amphipods collected during a 2½-year survey of populations on the continental shelf of the northeastern United States. *Ampelisca agassizi* (Judd) was the most numerous and broadly distributed species of amphipod. A microsporidan confined to the abdominal muscles was common in most populations of *A. agassizi*. It is provisionally assigned to the genus *Thelohania*. There were prevalences up to 37% depending upon the population surveyed, but the microsporidans did not seem to contribute to mortality in *A. agassizi* populations, with the possible exception of adult males. Microsporidans in other amphipod species parasitized various organs and tissues according to the amphipod species and type of microsporidan. The relationships of the microsporidans with the genera *Thelohania*, *Stempellia*, and *Nosema* are discussed.

In the late 1970's, a monitoring program was developed within the National Oceanic and Atmospheric Administration (NOAA) to assess the presence of pollutants and their effects on the fauna and flora of the continental shelf of the United States. As a part of this plan, the Northeast Monitoring Program (NEMP) has been conducted on a seasonal basis from the Gulf of Maine to Cape Hatteras by the Northeast Fisheries Center, National Marine Fisheries Service. In connection with NEMP, studies have been made of types and prevalences of parasites, diseases, and other abnormalities of various populations of benthic gammaridean amphipods. Samples were mainly from stations on the Georges Bank and Mid-Atlantic Bight.

The results of the survey will be presented in a series of papers. This, the first report, discusses microsporidan parasites, particularly those of *Ampelisca agassizi* (Judd).

Published information on parasites and pathological conditions of gammaridean amphipods is limited and concerns mainly the parasites of selected estuarine and freshwater species, particularly the microsporidan parasites (Bulnheim 1975). Data collected during the present survey concern a broad array of species of marine amphipods. Communities of benthic amphipods are unlike most animal communities because they are composed of numerous individuals of several to many related species that live in very close proximity to one another. Indeed, it is common for a population to contain two or more species of a single genus. It is also common for a thousand or more individuals of a single species, together with varying numbers of other species, to be crowded onto one-tenth of a square meter of the bottom (Dickinson et al. 1980). This unique population structure makes studies of parasites and diseases of the amphipods of great general biological interest.

The methods used for collecting and preparing the benthic amphipods are satisfactory for study of many facets of the host-parasite relationships that exist in these animal communities: effects of parasites on their hosts, host specificity of parasites, seasonal prevalence, and modes of passage of parasites through host populations. On the other hand, paraffin-embedded sections seldom allow specific identification of parasites. Depending on the parasite group, this may require examination of live animals or of whole specimens fixed and stained by special methods.

It is hoped that the data presented here and elsewhere will serve as a framework for more definitive studies on the taxonomy, life history, and other aspects of the various parasite species.

MATERIALS AND METHODS

Amphipods were sampled 11 times over a 2½-yr period from July 1980 to December 1982 on NEMP cruises (Table 1). The 35 stations where benthic amphipods were collected are shown in Figure 1. Not all stations were visited on each cruise, being sampled from 1 to 10 times each during the survey. The 11 stations indicated by solid circles on Figure 1 had

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TABLE 1.—Sampling cruises for benthic amphipods, July 1980-December 1982.

Date	NEMP cruise no.	Cruise designation
July 1980	AL80-07	A
September 1980	AL80-09	B
December 1980	DE80-09	C
April-May 1981	KE81-04	D
July 1981	AL81-07	E
August-September 1981	AL81-10	F
November 1981	DE81-07	G
January-February 1982	AL82-01	H
March-April 1982	AL82-03	I
August-September 1982	AL82-10	J
November-December 1982	AL82-12	K

consistent, and usually numerous, amphipod populations and were sampled five or more times. They yielded the majority of data presented in this paper.

Collections of bottom sediments and accompanying biota were made with a 0.1 m^2 Smith-McIntyre[2] grab. Generally a single grab was taken at each station sampled. If the first grab contained few amphipods but was from a station where they usually were abundant, a second and sometimes a third grab was taken. Sediment contained in the grab was washed through a 1.0 mm sieve, and amphipods were either collected with forceps or gently scraped from the sieve and placed in a jar of 10% seawater Formalin. On cruises A, B, and E (see Table 1), supplemental specimens were collected at some stations by use of an epibenthic sled or scallop dredge.

Storage of samples was in Formalin except that amphipods were transferred temporarily into 30 ppt artificial seawater for identification and enumeration, inspection for various gross lesions, and for determination of life-history stages and microsporidan infections of the muscle in the case of *Ampelisca agassizi* (Judd). A stereomicroscope was used for these procedures. Up to 30 and occasionally more individuals of each species in the sample, depending on numbers present, were processed for histological examination by standard means. Finished tissue sections were stained with hematoxylin and eosin. Depending on size and number to be embedded, 1 to 12 amphipods of a single species from a single station were embedded on their sides in each paraffin block. Several serial sagittal sections were taken, first laterally and then near the midline of the amphipods. Because of unavoidable variations in size and depth of the amphipods in the block, not all were sectioned at the same levels. Parts of the hemocoel, skeletal muscle, and appendages of all amphipods were present in sections. Usually, parts of the gills, hepatopancreas and other parts of the gut, heart, brain, and gonads were also present. Other tissues and organs, particularly the antennal gland, hemopoietic tissues, eyes, and ventral nerve cord, often were not included.

Measurements of microsporidan spores were based on fixed material, either whole or embedded, sectioned, and stained.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

The amphipod population sampled at any one time at a particular station was a mixture of up to 14 different species. Commonly five to eight species were collected in a single grab except at station 23, which was strongly dominated by *Ampelisca agassizi*. Of eight samples from station 23, three contained only *A. agassizi*, and *A. agassizi* made up 94 to 99% of the remaining samples. Totals of the eight samples from station 23 were 2,788 individuals of *A. agassizi* and 23 individuals of other species (99% *A. agassizi*).

Ampelisca agassizi was the most numerous and broadly distributed of the species investigated, and occurred at 17 stations including the 11 major ones. Certain information on the life history of this species is pertinent. It is an annual, tube-building species that produces a single brood of young (Bousfield 1973). Overwintering is in the juvenile stage. Gonads of both sexes develop during the subadult stage. Breeding begins in the spring, and newly ovigerous females are found from spring through autumn. Postovigerous females tend to remain in the population for an unknown period after the young are released from the brood pouch. Adult males are pelagic or epibenthic, probably short-lived, and usually were missing from samples collected with the Smith-McIntyre grab. Only the adult male has strongly developed transverse pleosomal muscles (muscles of the first three abdominal segments) (Fig. 2). Presumably, these muscles aid in swimming. The transverse muscles lie lateral to the longitudinal muscles and are developed during the subadult stage. They can be seen in various stages of development through the translucent cuticle of subadult males.

Females of the gammaridean, tube-dwelling amphipods so far studied leave their tubes to molt to the adult stage. Mating and egg extrusion take place in the water column (Mills 1967). Population dispersal is presumed to occur either by ovigerous females settling away from their original location

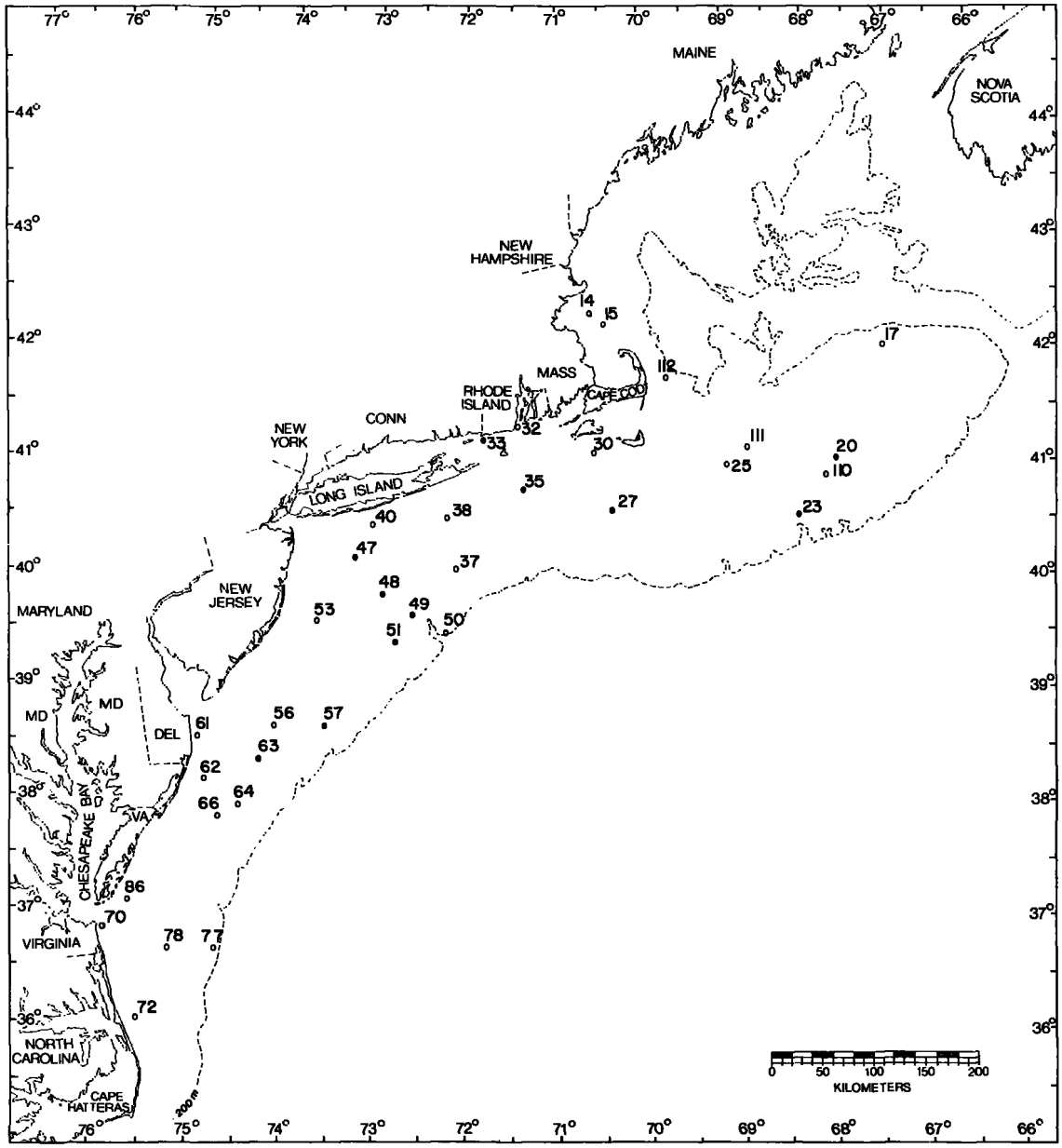

FIGURE 1.—Benthic stations of Northeast Monitoring Program at which populations of gammaridean amphipods were sampled during the survey, 1980-82.

and probably in a less populated area (Mills 1967) or by emigrating juveniles (Bousfield 1973). Thus, juveniles and perhaps ovigerous and postovigerous females of *A. agassizi* and other species could at times be immigrants into locations with already established populations of older juveniles and subadult males and females.

Microsporidans of *Ampelisca agassizi*

Most of the populations of *A. agassizi* sampled were regularly infected by a species of microsporidan that attacks the longitudinal pleosomal muscles (Figs. 3, 4). Infected muscles were chalky white in fully developed infection, and easily visible through

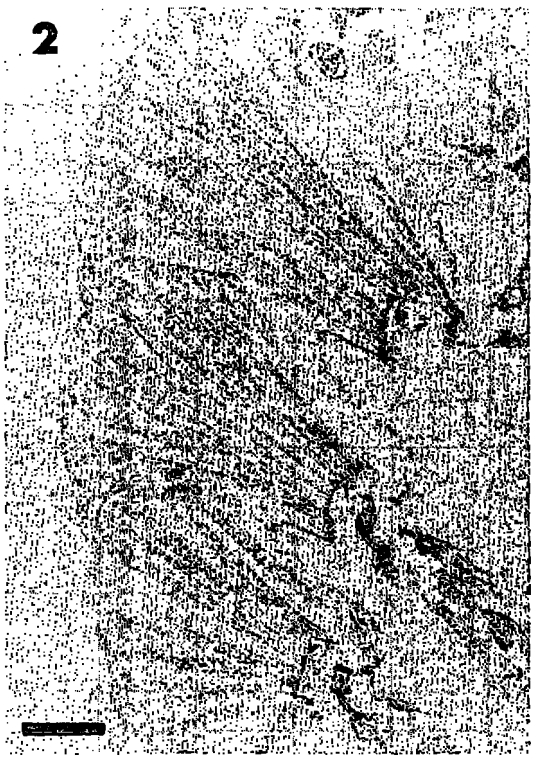

FIGURE 2.—*Ampelisca agassizi*: Transverse pleosomal muscles of an adult male. Bar = 0.2 mm.

FIGURE 3.—*Ampelisca agassizi*: Longitudinal pleosomal muscles infected by microsporidans (open arrows). Normal muscle is also present (closed arrow). g, midgut. Bar = 0.2 mm.

the translucent cuticle. Usually, only one to three muscles were infected. Inspection of 150 microsporidan-infected amphipods showed that in eight cases transverse pleosomal muscles were also involved, and in three cases, only the transverse muscles were infected. One postovigerous female, with microsporidan infection in muscle, also had what appeared to be the same organism in one of the ganglia of the ventral nerve cord.

On the basis of a tissue section she examined, A. Cali[3] determined that this microsporidan is a pansporoblastic organism with the clusters appearing to be in groups of eight. However, she said further that possibly some clusters contained more than eight spores. This is a point difficult to determine in sectioned material. Spores are oval and of fairly uniform size. Ones dissected out singly from infected muscle (not paraffin embedded) measured approximately 3 μm × 1.5 μm. In Cali's opinion, the *A. agassizi* parasite is best provisionally placed in the genus *Thelohania*, without specific designation.

[3]A. Cali, Rutgers University, Newark, NJ 07102, pers. commun. 1983.

Numerical information on this microsporidan is based on samples taken on cruises D-K, because determination of microsporidan infection was by study of sectioned material only from cruises A-C, and infections can be missed by this method. Considering all stations on cruises D-K, juveniles had a lower prevalence of grossly visible infection than did male and female subadults and ovigerous females (Table 2), but this was not invariably the case in individual samples. In 5 of the 38 samples with micro-

TABLE 2.—Prevalence of microsporidan infections in *Ampelisca agassizi* by life-history stages. All stations, cruises D-K.

Life-history stage	No. infections/ total collected (% prevalence)
Juveniles	517/4,868 (11)
Subadults	1,335/5,293 (25)
Ovigerous females	111/501 (22)
Postovigerous females	82/413 (20)
Adult males	1/55 (2)
Totals	2,046/11,130 (18)

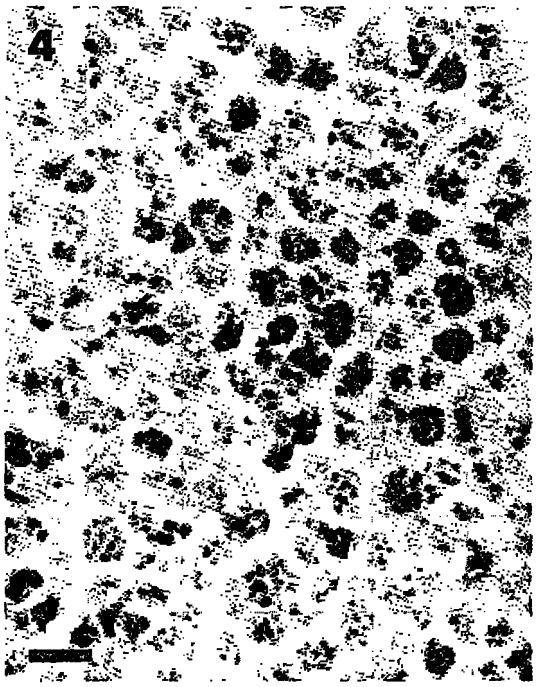

FIGURE 4.—*Ampelisca agassizi*: Groups of spores and prespores of the muscle-infecting microsporidan. Bar = 10 μm.

sporidan-infected *A. agassizi*, prevalence was equal to or slightly higher in juveniles than in subadults or ovigerous females. Prevalence was very low in the small sample of adult males, but varied considerably in individual samples of both males and postovigerous females (Table 3). The three stations with the most consistently numerous populations of *A. agassizi* also had the highest prevalences of microsporidan infection. These were stations 23, 33, and 48, with overall prevalences of 30%, 37%, and 22%, respectively. Overall prevalence at other stations ranged from 0 to 14%.

The majority of infected hosts showed no reaction to the presence of the microsporidans. However, there was occasional melanization in heavily infected muscle, with invasion of hemocytes into the mass of spores, some encapsulation of spores and infected muscle, and lysis of many spores. In these cases, it appeared that the muscle had lost its integrity; that is, the sarcolemma probably was no longer entire. Often, other infected muscle near the necrotic mass of spores and muscle showed no evidence of attack by host defense mechanisms.

The second microsporidan of *A. agassizi* parasitized epithelial cells of the posterior half of the midgut. Juveniles, male and female subadults, and ovigerous and postovigerous females were infected. The parasite resembled *Nosema*, the spores being single and free in the cytoplasm of the host cell (Fig. 5). Spores were slightly oval and about 2 μm in the greater dimension. Infected cells were hypertrophied (Fig. 6). In one heavy infection, many spores were free in the gut and apparently most infected cells had ruptured. There was no host reaction to infection. This parasite occurred twice in individuals with microsporidan infection in abdominal muscle. Based on sectioned material, overall prevalence of the gut microsporidan was < 0.1% (25/2403). Prevalence in samples with one or more infected *A. agassizi* was 3.7% (25/678), range 1-6%. Amphipods with microsporidans in the gut epithelium were from stations 23, 33, 47, 48, 49, 50, and 51.

Microsporidans in Species Other Than *A. agassizi*

Males and females of *Unciola* species (probably all *U. irrorata* Say and *U. inermis* Shoemaker) were hosts to a microsporidan that infected longitudinal muscles of the pleosome. In three instances, a similar or the same microsporidan was found in a ganglion of the ventral nerve cord, and not in muscle. Spores appeared similar to those of the *A. agassizi* parasite; they measured about 3 × 1.5 μm; and there were eight or more spores per envelope. Unlike the *A. agassizi* parasite, vegetative stages were often present along with developed and developing spores. *Unciola* species have an opaque cuticle, and infected muscle cannot be seen grossly. Based on sectioned

TABLE 3.—Prevalence of microsporidan infections in *Ampelisca agassizi* by life-history stages. Stations 47 and 48, cruises E and F.

Life-history stage	No. infections/ total collected (% prevalence)	No. infections/ total collected (% prevalence)
	Cruise E	Cruise F
Station 47	(depth 48 m)	(depth 62 m)
Juveniles	29/851 (3)	130/1,124 (12)
Subadults	45/258 (17)	12/53 (23)
Ovigerous females	14/84 (17)	11/53 (20)
Postovigerous females	0/24 (0)	6/29 (21)
Adult males	0/34 (0)	1/3 (33)
Totals	88/1,251 (7)	160/1,262 (13)
	Cruise E	Cruise F
Station 48	(depth 72 m)	(depth 68 m)
Juveniles	2/33 (6)	5/29 (17)
Subadults	66/246 (27)	28/111 (25)
Ovigerous females	0 (—)	11/51 (22)
Postovigerous females	0 (—)	3/27 (11)
Adult males	0/1 (0)	0/4 (0)
Totals	68/280 (24)	47/222 (21)

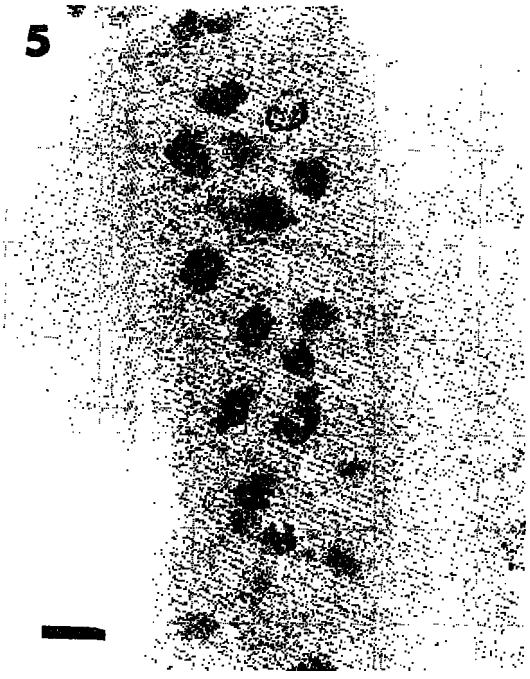

FIGURE 5.—*Ampelisca agassizi*: *Nosema*-like microsporidan in the midgut epithelium. Bar = 10 μm.

FIGURE 6.—*Ampelisca agassizi*: Hypertrophy of midgut epithelial cells infected by a *Nosema*-like microsporidan. Infected epithelium to left, normal epithelium to right. Bar = 60 μm.

material, prevalence was 8.3% (23/277), considering only samples containing infected *Unciola* spp. Prevalence was 1.7% when considering all *Unciola* spp. that were sectioned and examined (Table 4). There was no host reaction to infection in the ganglia, but animals with muscle infection often showed some melanization and encapsulative response (Fig. 7). Scattered small melanized nodules were common in the hemocoel of infected *Unciola* spp., but it was not evident whether they had formed in response to microsporidans.

Other amphipod species with microsporidan infections are listed in Table 4. Prevalence was usually very low. Most of the parasites appeared like the muscle-infecting microsporidans of *A. agassizi* and *Unciola* spp. A *Nosema*-like parasite similar to the gut microsporidan of *A. agassizi*, but smaller (0.7 μm), occurred in the hepatopancreatic epithelium of a specimen of *Leptocheirus pinguis* (Stimpson). Another *L. pinguis* harbored a larger *Nosema*-like species in oocytes and heart muscle. Infected oocytes were necrotic and encapsulated by hemocytes. The generalized muscle parasite of *Melita dentata* (Krøyer) *s. lat.* was also *Nosema*-like.

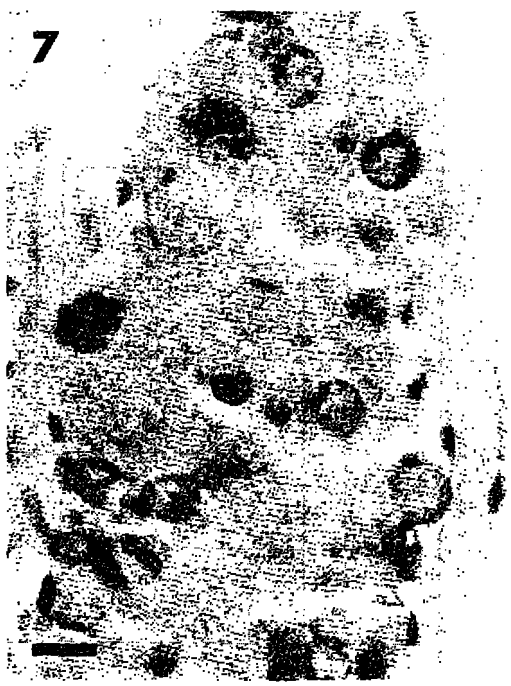

FIGURE 7.—*Unciola* sp.: Host reaction to microsporidans in abdominal muscle. Some groups of degenerating spores and prespores are surrounded by melanized material. A few nuclei of encapsulating host cells are visible around the mass of microsporidans. Bar = 10 μm.

TABLE 4.—Microsporidans in amphipods other than *Ampelisca agassizi*.

Amphipod species	No. infections/ total examined (% prevalence)	Positive stations	Tissues infected	Type of microsporidan
Unciola spp. (*irrorata* Say and *inermis* Shoemaker)	23/1,365 (1.7)	33, 35, 38, 47, 48, 51, 110, 112	Abdominal muscle, ganglia of ventral nerve cord	"*Thelohania*"
Ampelisca vadorum Mills	4/448 (0.9)	57, 66	Muscle, tegmental glands, oocytes	"*Thelohania*"
Ampelisca verrilli Mills	1/48 (2.1)	62	Connective tissue, muscle	"*Thelohania*"
Ericthonius rubricornis Smith	1/436 (0.2)	38	Abdominal muscle	"*Thelohania*"
Eriopisa elongata (Bruzelius)	1/29 (3.4)	47	Ganglia of ventral nerve cord	"*Thelohania*"
Leptocheirus pinguis (Stimpson)	1/913 (0.1)	47	Abdominal muscle	"*Thelohania*"
	1/913 (0.1)	15	Oocytes, heart muscle	*Nosema*-like
	1/913 (0.1)	20	Epithelium of hepatopancreas	*Nosema*-like
Melita dentata (Krøyer) *s. lat.*	2/44 (4.5)	51	Generalized in muscle	*Nosema*-like
Monoculodes edwardsi Holmes	1/110 (0.9)	40	Abdominal muscle	"*Thelohania*"
Photis dentata Shoemaker	4/301 (1.3)	33	Abdominal muscle, ganglia of ventral nerve cord	"*Thelohania*"

The microsporidan of *Ampelisca vadorum* Mills resembled that of *Unciola* spp., but fully developed spores were not seen (Fig. 8). Muscle, tegmental glands, and oocytes were infected. Often, groups of microsporidans had "used up" the host tissue, and appeared like groups of extracellular, closely knit, vegetative and sporulating stages, but some of these groups were unmistakably in the shape of tegmental glands and oocytes and were in the correct anatomical positions. In one case, muscle fibers were still present adjacent to the mass of microsporidans and in another, microsporidans infected a recognizable tegmental gland. Host reactions to the microsporidans had not occurred in the few infected *A. vadorum* available for study.

FIGURE 8.—*Ampelisca vadorum*: Vegetative and prespore stages of a muscle-infecting microsporidan. Bar = 10 μm

More than 35 specimens each of the following species were sectioned and examined, but microsporidans were not found: *Anonyx sarsi* Steel & Brunel (36 specimens), *Byblis serrata* Smith (316 specimens), *Casco bigelowi* (Blake) (60 specimens), *Corophium crassicorne* (Bruzelius) (50 specimens), *Harpinia propinqua* Sars (116 specimens), *Orchomenella minuta* Krøyer (64 specimens), *Phoxocephalus holbolli* Krøyer (73 specimens), *Pseudunicola obliquua* (Shoemaker) (46 specimens), and *Rhepoxynius epistomus* (Shoemaker) (249 specimens).

DISCUSSION

Bulnheim (1975) and Sprague (1977) have listed and discussed the various microsporidans reported from amphipods. Most of the hosts are freshwater and estuarine forms, and depending on the species

of microsporidan, muscles, ovaries, connective tissues, and gut epithelia are infected. One of the microsporidans, a parasite of *Gammarus pulex* L., infects the longitudinal abdominal muscles of its host in the same manner as does the *A. agassizi* parasite, but is known to have a variable number of spores per envelope. It was named *Glugea muelleri* (Pfeiffer, 1895, in van Ryckeghem 1930), later named *Thelohania giraudi* (Léger and Hesse, 1917), and has been called *Stempellia muelleri* (Pfeiffer) by Bulnheim (1975) and *Microsporidium giraudi* (Léger and Hesse) by Sprague (1977). The relationship of "*Glugea muelleri* Pfeiffer" and the microsporidan from *A. agassizi* remains to be determined. Although "*Glugea muelleri* Pfeiffer" and the *A. agassizi* parasite are remarkably similar in being restricted to the longitudinal abdominal muscles of their hosts, the latter is probably significantly smaller. Fixed spores of the *A. agassizi* parasite are about 1.5 × 3 μm, and fresh spores of "*Glugea muelleri*" are 2.2 × 4.5 μm.

The method of transmission of the *A. agassizi* parasite is not known. Microsporidans are usually transmitted orally, but transovarial transmission also occurs in amphipods. Transovarially transmitted microsporidans of *Gammarus duebeni* Lilljeborg infect the ovary, and, depending on the species, cause complete or partial feminization of males (Bulnheim 1975, 1977). The parasite of *A. agassizi* did not infect the ovary, and because it was regularly found in normal males, it apparently does not cause feminization of males. Bulnheim (1971) successfully transmitted "*G. muelleri* Pfeiffer" to several species of *Gammarus*, including euryhaline ones, by feeding of infected muscle.

Prevalence of the muscle parasite of *A. agassizi* apparently increases with age of the host, and it could be hypothesized that this microsporidan is transmitted orally, that the older the host the more chances it has had to become infected, and that the parasite does not contribute to increased mortality in the population. Adult males are active swimmers and might prove an exception because impaired muscle function could lead to increased predation. If this occurred, one would expect infected males to be preferentially removed from the population, leading to a lower prevalence of infection in this stage. Indeed, prevalence in adult males was only 2%. However, relatively few males were collected during the survey, and the low prevalence could prove to be sampling artifact. Note that in the sample from cruise E, station 47 (Table 3), both postovigerous females and adult males were uninfected, but 2 mo later, at the same station, prevalence in postovigerous females was 21% and the only infected adult male found during the survey was also collected at that time. The discrepancy in prevalence might be due to sampling of slightly different populations. As discussed below, there is no assurance that the same population was sampled spatially, and temporal differences conceivably might also have complicated the results.

Relationships of the microsporidans seen in the various species of amphipods could not be decided on the basis of material fixed and prepared as it was. It would be interesting to determine whether the parasites of *Unciola* spp. and *Ampelisca vadorum* are the same or different species, and what their relationship is to the *A. agassizi* parasite. There were some differences in the habits and the developmental stages present in the three amphipods. Vegetative stages were common in the case of the *A. vadorum* parasite and fairly common in *Unciola* spp., but usually rare or absent in *A. agassizi*. Several different tissues were infected in *A. vadorum*, but excepting a few infections in nervous tissue, only abdominal muscle was infected in *Unciola* spp. and *A. agassizi*. Previous investigators have found that microsporidan infection is well tolerated by amphipod hosts, and that defense reactions against these parasites generally are limited and may come into play mainly when host tissue becomes necrotic (reviewed by Bulnheim 1975). The muscle-inhabiting microsporidan of *A. agassizi* is obviously a primary parasite of that species and is seldom attacked by the host. However, the similar parasite of *Unciola* spp. often either provokes attack merely by its presence or damages the muscle so that a response occurs to the necrotic tissue. In either event, it is possible that this parasite is not fully adapted to *Unciola* spp., because arthropods are known to be less tolerant of non-adapted parasites (Salt 1970; Unestam and Weiss 1970)

With exception of the muscle-infecting species from *A. agassizi*, microsporidans are not common parasites of benthic amphipods in the areas sampled, even considering that some infections must have been missed because not all would be seen in the limited number of sections examined from each amphipod.

Sampling methods used in the survey do not lend themselves to precise studies on progression of parasitic infections through particular populations. Sampling cannot be done often enough to show if and when additions to populations (with perhaps different prevalences of parasites) are provided by immigrating juveniles or other stages of these short-lived animals. Further, populations may not be

homogeneous over the area sampled at a single station. Sediment sampling with a grab is imprecise, as the different depths of samples taken at stations 47 and 48 on cruises E and F testify (Table 3). It is probable that return to an exact location was never accomplished. Even if populations were homogeneous, predation by fish, and other short-term disturbances, may cause local impoverishment of populations or differences in population composition that would not be detected in the necessarily blind sampling done with a Smith-McIntyre grab.

A general pattern does emerge. In the area surveyed, microsporidans are dominant parasites of the most numerous and ubiquitous species, *A. agassizi*, but are rare in all other species. This may be a reflection of the fact that only *A. agassizi* consistently occurred in dense populations at certain stations at all sampling times, a circumstance that would promote spread of a host-specific and horizontally transmitted parasite.

ACKNOWLEDGMENTS

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