

with rotenone over a 2-yr period at intervals of 1 mo, 3 mo, and 6 mo. She found rapid recolonization but with lower densities of recolonizers in winter than in summer. During 26 monthly samples, only one of the original species did not recolonize the pool, while 13 additional species were found. In Pool 2, which was sampled in 3-mo intervals, 14 species were taken in the initial sample, 7-12 in subsequent samples. Three of the original 14 species failed to recolonize, but 8 additional species were taken. During four repeat visits to Pool 3, the number of species varied between 9 and 14, all but 1 species recolonized the pool, and 5 additional species were recorded.

My study and those of Thomson and Lehner (1976), Grossman (1982), and Beckley (1985) indicate great resilience of species of tidepool fishes in tropical and temperate waters. Recolonization is quite rapid, within a matter of weeks.

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PARASITES OF BENTHIC AMPHIPODS: CILIATES

Benthic gammaridean amphipods were sampled during a 2½-yr period as a part of the Northeast Monitoring Program (NEMP) of the Northeast Fisheries Center, National Marine Fisheries Service. The amphipod survey was designed to determine the kinds of parasites and pathological conditions occurring in amphipod populations that live in and on the sediments of the continental shelf from Maine to North Carolina. Microsporidians of the sampled amphipods have been discussed by Johnson (1985), and this paper presents and discusses data on host distribution, prevalence, effects on the host, and probable relationships, of ciliates parasitizing amphipods from the same samples.

Materials and Methods

Benthic amphipods were collected from 35 stations, mainly on the Georges Bank and Mid-Atlantic Bight (Fig. 1). Amphipods were sampled during 11 cruises, July 1980-November 1982 (Table 1). Each station was sampled from 1 to 10 times during the survey. The 11 stations indicated by solid circles on Figure 1 had the most consistent and numerous populations of amphipods, were sampled at least five times each, and yielded the majority of data presented here. A Smith-McIntyre grab and occasionally an epibenthic sled or scallop dredge were used to obtain the samples. Up to 30 individuals of each species present in a sample, and sometimes more depending on numbers present, were prepared for histological study. Details of collecting procedures and preparation of the amphipods for study are given by Johnson (1985).

Results

Host and geographic distribution of ciliate infection is given in Table 1. Ciliate-infected amphipods were taken in samples from at least one station on every cruise. There was no indication that prevalence was influenced by the season of the year or location of the positive stations. The majority of infected specimens were *Ampelisca agassizi* (Judd), but prevalence of ciliate infection was lower in *A. agassizi* than in the other species found infected (*Pontogeneia inermis* Krøyer, *Phoxocephalus holbolli* Krøyer, *Harpinia propinqua* Sars, and unidentified haustoriids) (Table 2). In three instances, at station 33, cruise G; station 48, cruise I; and station 57, cruise E, individuals of *H. propinqua* or *P. holbolli* were infected

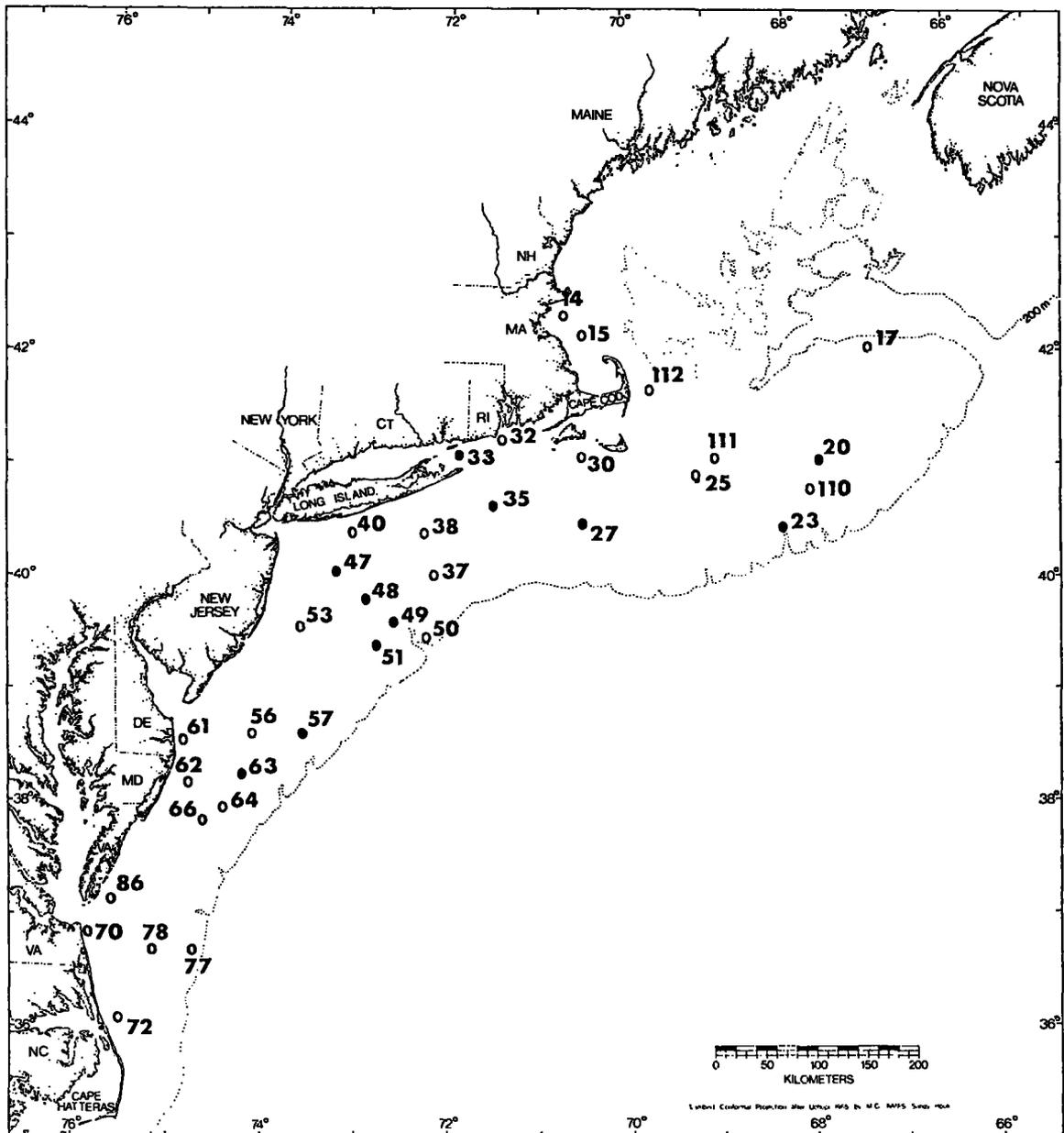


FIGURE 1.—Number designations and positions of Northeast Monitoring Program (NEMP) benthic stations where gammaridean amphipods were sampled during the survey.

but *A. agassizi* collected at the same times were not.

Except for *A. agassizi*, all the species with ciliate infections were rare (Table 2). The most numerous species collected, after *A. agassizi*, were *Leptocheirus pinguis* Stimpson, which made up 11% of the total collected (2,655/24,244), and *Unciola* species (probably all *U. irrorata* Say and *U. inermis* Shoe-

maker), which made up 10% of the total (2,356/24,244). Despite their abundance, these species were never found infected with ciliates. Considering all amphipods sectioned and examined, overall prevalence of ciliate infection was 0.6% (41/7,363).

Light infections consisted mainly of large ciliates. Heavier infections had medium to small ciliates, but

TABLE 1.—Stations with ciliate-infected amphipods, by cruise and host species.

Station	Cruise ¹										
	A	B	C	D	E	F	G	H	I	J	K
20	PI ²	— ³	—	—	—	—	—	—	—	—	—
23	AA ²	AA	AA	—	—	AA	—	—	—	—	—
25	—	—	—	—	PH ²	—	—	—	—	—	—
33	—	AA	AA	AA	AA	AA	HP ²	—	—	—	—
35	—	AA	—	AA	—	—	—	—	—	AA	—
37	—	—	—	AA	—	—	—	—	—	—	—
38	—	—	—	—	AA	—	—	—	—	—	—
48	—	—	—	—	AA	—	—	—	HP	—	—
49	—	—	—	—	—	—	—	—	AA	—	—
50	—	—	—	AA	—	—	—	—	—	—	—
51	AA	—	—	—	—	—	—	—	AA	—	—
57	—	—	—	—	AA	PH	—	—	AA	—	AA
62	HAU ²	—	—	—	—	—	—	—	—	—	—
76	—	—	—	—	—	—	—	HAU	—	—	—

¹Dates of cruises: A, July 1980; B, Sept. 1980; C, Dec. 1980; D, Apr. 1981; E, July 1981; F, Aug. 1981; G, Nov. 1981; H, Jan. 1982; I, Mar. 1982; J, Aug. 1982; K, Nov. 1982.

²Infected amphipods present at the station: PI = *Pontogeneia inermis*; AA = *Ampelisca agassizi*; PH = *Phoxocephalus holbolli*; HP = *Harpinia propinqua*; HAU = unidentified haustoriids.

³— = station sampled, no ciliate infections found.

sometimes large forms were also present. The largest ciliates were in the gill of a specimen of *Pontogeneia inermis* (Fig. 2). Measured in paraffin sections, they were about 17 $\mu\text{m} \times 80 \mu\text{m}$. Large forms in other infected amphipods were 16-20 $\mu\text{m} \times 40$ -50

μm . The majority of small- and medium-sized ciliates were 17-30 μm in the greater dimension; none were less than 14 μm (Fig. 3). Ciliates were elongate-spindle-shaped, with pointed or sharply rounded ends in *P. inermis*, and oval to subspherical in the other amphipods. The macronucleus of the large ciliates in *P. inermis* was sometimes ribbonlike (Fig. 2), and macronuclei of the smaller ciliates in *P. inermis* and those from the other amphipod species were elongate cylinders or elongate ovals in section (Fig. 3).

None of the infections showed recent evidence of host reaction against the ciliates. The melanized nodules and small hemocytic encapsulations occasionally seen in infected amphipods did not contain recognizable ciliates, and may have been due to other causes.

Few pathological effects were visible in ciliate-infected tissues. Two infected subadult males of *A. agassizi* had karyorrhesis and probable lysis in the transverse abdominal muscles, and one heavily infected female of *A. agassizi*, which had a few early embryos in the brood pouch, also had retained necrotic, mature ova in the ovaries. All infected amphipods had material in the gut, indicating that feeding was continuing. Hemocytes were present in



FIGURE 2.—*Pontogeneia inermis*: large and small ciliates in the gill. L, large form; S, small form. Bar = 10 μm .

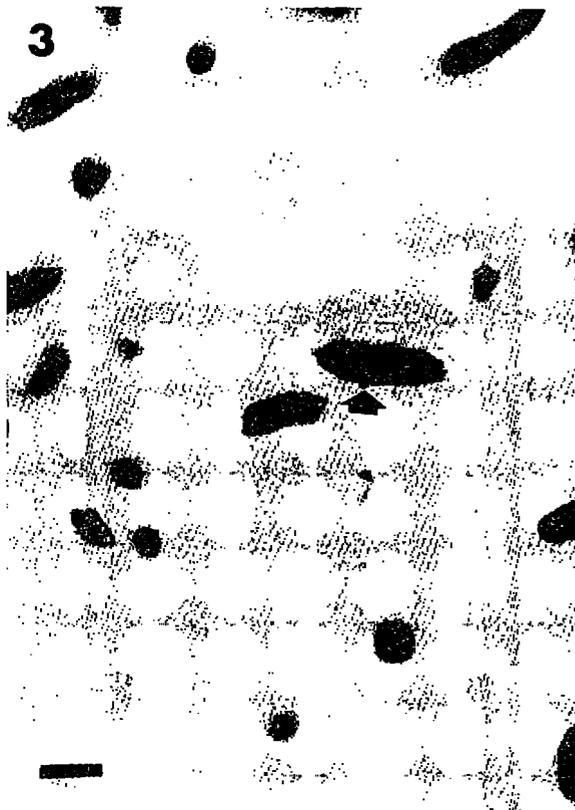


FIGURE 3.—*Ampelisca agassizi*: medium-sized ciliates. The small, pale micronucleus is visible close to the macronucleus in one of the ciliates (arrow). Bar = 10 μ m.

light to medium infections, but essentially missing in heavy infections. None of the ciliates were positioned in such a way that they appeared to have been phagocytizing hemocytes or other cells at the time of fixation. The granular inclusions commonly present in the cytoplasm of the ciliates bore no resemblance to food vacuoles or phagocytized material.

Discussion

Two groups of ciliates contain species that parasitize crustaceans. *Paranophrys*, in crabs, lobsters, and possibly isopods, and *Parauronema*, in penaeid shrimp, belong in the class Oligohymenophora, order

Scuticociliatida (Corliss 1979). They are apparently opportunistic parasites (Bang 1970; Sindermann 1977; Couch 1978; Armstrong et al. 1981; Hibbits and Sparks 1983). The remaining parasites are members of the class Kinetofragminophora, order Apostomatida (Corliss 1979). Typical apostomes are obligate commensals of aquatic crustaceans and have a life cycle geared to their hosts' molting cycles (Bradbury 1966, 1973), but some apostomes have become internal parasites of various invertebrates, including polychaetes, cephalopods, ophiurans, coelenterates, tenophores, and isopod, amphipod, and decapod crustaceans (Corliss 1979).

Because specialized fixation and staining of whole

TABLE 2.—Species of amphipods infected by ciliates: proportion of the amphipod population and prevalence of ciliate infection.

Species of amphipod	Percent prevalence at positive stations	Proportion of the total amphipods collected
<i>Ampelisca agassizi</i>	3.8% (31/812)	54.3% (13,165/24,244)
<i>Harpinia propinqua</i>	18.2% (2/11)	0.6% (146/24,244)
Hauatoriidae spp.	5.4% (3/56)	0.9% (225/24,244)
<i>Phoxocephalus holbolli</i>	9.5% (2/21)	0.5% (125/24,244)
<i>Pontogeneia inermis</i>	10.3% (3/29)	0.7% (164/24,244)

ciliates is necessary for firm identification (Corliss 1979), the amphipod ciliates can be only provisionally assigned to a ciliate group, as is true in other studies based on fixed and embedded material (Sparks et al. 1982; Hibbits and Sparks 1983). On the basis of similarities in hosts and morphology, the amphipod ciliates discussed here are like the apostome genus *Collinia*, whose members parasitize amphipods (Summers and Kidder 1936; de Puytorac and Grain 1975). Like *Collinia*, size of individual ciliates from the benthic amphipods varied greatly and there was no indication that the ciliates were phagocytic *Paranophrys* and *Parauronema*, on the other hand, belong to a group that ingests particulate material. *Paranophrys* is known to ingest hemocytes and other cells of its hosts, and does not exhibit major size differences (Bang 1970; Sparks et al. 1982; Hibbits and Sparks 1983). Provisionally, the ciliates of benthic amphipods are being considered apostomes.

Whether more than one species of ciliate was involved in the infections is uncertain, but probably the ciliate of *Pontogeneia inermis* represented a species apart from the others. Its very large forms with the ribbonlike macronucleus were not duplicated in other infections.

Although more *A. agassizi* were found infected with ciliates than any other species of amphipod, this was apparently because it was the most abundant and widespread of the susceptible species sampled. *A. agassizi* had the lowest overall prevalence of ciliate infection and sometimes was not parasitized when other species in the same samples were parasitized. There are at least two possible explanations for the odd host distribution of the amphipod ciliates. First, the ciliates might be highly host specific, each amphipod species having its own species of ciliate. Second, the ciliates might be either primary parasites of some other member(s) of the benthic community, or incompletely adapted to a parasitic existence, and thus only occasionally parasitizing the least resistant species of the sampled amphipods. *Unciola* species and *Leptocheirus pinguis* were often the most abundant amphipods at certain stations, but ciliates were never found in individuals of these species, suggesting that they are resistant to ciliate attack. Conversely, the relatively high prevalence of ciliates in the rare species of amphipods could indicate less resistance than is exhibited by most of the species of amphipods sampled.

Presumably, infected amphipods would eventually die of their ciliate infections because of the massive loss of hemocytes. The infrequency of ciliate infection, except in certain rare species, indicates that

these parasites are not important in regulating the general amphipod populations they infect.

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FECONDITY OF THE PACIFIC HAKE, *MERLUCCIUS PRODUCTUS*, SPAWNING IN CANADIAN WATERS

Previous studies on the fecundity of Pacific hake, *Merluccius productus*, have been concentrated on the coastal stock in Baja California (MacGregor 1966, 1971; Ermakov et al. 1974), although large-scale spawning events have been recorded as far north as lat. 38°N, near San Francisco, CA (Stepanenko 1980). The present work was undertaken in conjunction with ichthyoplankton surveys, aimed at estimating the released egg production and spawning biomass of the Pacific hake stock resident in the Strait of Georgia, a semi-closed marine basin in British Columbia (Thomson 1981). The spawning season extends from February through June, peaks in early April, and is 90% complete by mid-May (Mason et al. 1984).

In comparison with the coastal stock of some 1-2 million metric tons (t) (Bailey et al. 1982), this inshore stock, of about 140,000 t, is subject to modest annual exploitation (1-500 t) and resides in a semi-estuarine environment on the known northernmost edge of the reproductive range. The coastal stock undertakes a northward feeding migration after the spring spawning and reaches the southwest coast of Vancouver Island by late summer (Bailey et al. 1982). There is no evidence of intermingling between these two stocks, based on their distributional patterns. The inshore stocks in the Strait of Georgia and Puget Sound may undergo some exchange, possibly due to surface transport of larvae produced in the central Strait of Georgia (Mason et al. 1984). The Puget Sound and coastal stocks have been identified as genetically distinct by Utter and Hodgins (1971), but the two inshore stocks in Puget Sound and

the Strait of Georgia have not been similarly compared.

Histological analysis has indicated that only one mode of oocytes develops in Georgia Strait hake. However, like the Baja, California form and hake species elsewhere, some Strait of Georgia hake show evidence of ovarian resorption following spawning (Foucher and Beamish 1980). The quantitative significance of resorption relative to individual and stock fecundities, or to their potential physiological and environmental correlates have not yet been examined. This report considers the "apparent fecundity" as an annual expression of reproductive potential applicable to the stock in the Strait of Georgia, determines that fecundity, and concludes that ovarian resorption is of minor consequence in the stock.

Materials and Methods

The ovaries of 97 Pacific hake females 39-82 cm FL were collected during late February and early March of 1980 and 1981, 71 of which were collected in 1981 (McFarlane et al. 1983). Unspawned females were selected in maturity stages R^2 and R (Foucher and Beamish 1977) when the ovary is yellow and opaque, has prominent blood vessels, and fills one-third to one-half of the coelomic cavity. No ovaries contained translucent oocytes which signify imminent spawning. Fresh ovaries were preserved in 10% formaldehyde solution. In the laboratory, the preserved ovaries were transferred to modified (Simpson 1951) Gilson's fluid for several months to allow breakdown of connective tissue.

Ovaries were then washed thoroughly in cold water over a series of stainless steel screens of 40 μ m and larger aperture, and gently broken up by hand when necessary to separate the hardened eggs from the ovarian tissue. The mesh size of the finest screen was determined by the difficulty encountered in separating oocytes <40 μ m diameter from ovarian tissue. The cleaned eggs were then stored in 5% formaldehyde solution in preparation for analysis.

Eggs from a single ovary were transferred to a 20 L glass reservoir filled to either 10 or 15 L. While the reservoir was being stirred vigorously with a wooden paddle in a rotating figure-eight pattern, a second worker extracted 50 1-2 mL volumetric subsamples using Stempel pipettes and transferred them to petri dishes. Under the dissecting microscope at 50 \times magnification, all eggs in five subsamples were sized and counted in 20 μ m intervals of oocyte diameter. These results were then combined to construct oocyte size-frequency histograms and