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Population Dynamics and Description of *Ptycholaimellus hibernus* n. sp. (Nematoda: Chromadoridae)[1]

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Abstract: *Ptycholaimellus hibernus* n. sp. from the muddy subtidal of North Inlet Estuary, Georgetown, South Carolina, is described and a key to the genus is provided. *P. hibernus* differs from all other species of *Ptycholaimellus* by the shape of the gubernaculum. *Ptycholaimellus* sp. 2 Hopper 1969 is synonymized with *P. ponticus.* The abundance of *P. hibernus,* measured over a 3-year period, is greatest from January to March, coinciding with minimal annual water temperatures (10–15 C). *P. hibernus* abundance was significantly (negatively) correlated with water temperature and (positively) with the depth of the anoxic sediment layer.

Key words: ecology, free-living marine nematode, South Carolina, new species, temperature, salinity, taxonomy.

As part of a project to monitor meiofaunal populations in the North Inlet Estuary, Georgetown, South Carolina, population dynamics of nematode species were noted from January 1980 through December 1982. The meiofaunal populations of this area, which is one of the national long-term ecological research sites, have been studied intensively for 10 years (3,4). Few long-term (2 years or longer) investigations of benthic free-living marine nematode populations at the species level have been conducted (1); consequently, little is known about the year-to-year variability in marine nematode populations, although long-term data are available for populations of terrestrial and phytoparasitic nematodes (19,20). This study describes the seasonal population changes of a previously undescribed species of *Ptycholaimellus* during a 3-year period and the correlation of that population with several physical factors.

MATERIALS AND METHODS

Two replicate cores (2.6 cm i.d.) were taken to the depth of the anoxic sediment layer (as estimated by the presence of a black line; mean depth 2.5 cm) below the level of low tide, at the time of low tide at monthly intervals in 1980 and fortnightly in 1981 and 1982. The cores were fixed in the field with 10% borax buffered formalin, and the organisms were stained with Rose Bengal. Nematodes were extracted from the mud by modified Ludox centrifugal flotation (5) and collected on a 63-μm-pore sieve. The residue was washed into a counting tray and all nematodes were counted under a stereomicroscope; every fourth nematode was removed and mounted in glycerine for identification. The proportion of each species in the aliquot of identified individuals was multiplied by the total number of nematodes in the core and a correction factor to calculate the number of individuals of each species under 10 cm^2 of surface area. Temperatures were measured at 1-cm depth in the sediment with a mercury thermometer, salinity was measured by refractometer, and the depth of the anoxic sediment layer below the sediment surface (redox potential discontinuity layer) was estimated by the depth of the black line below the surface of the core. SAS software (8) was used for all data manipulation and statistical procedures.

RESULTS

The genus *Ptycholaimellus* was first proposed by Cobb (2) (type species *Ptycholaimellus carinatus* Cobb, 1920). Gerlach (6) reduced *Ptycholaimellus* to a subgenus of *Hypodontolaimus.* Wieser and Hopper (17) reviewed the genus and noted that in their opinion *H. carinatus* sensu Timm, 1952 (14) was synonymous with either *H. ponticus* Fi-

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TABLE 1. Measurements of male paratypes of *Ptycholaimellus hibernus* (summary statistics). Width is the width at the base of the esophagus.

Feature	N	Mean	SD	Range
Head width	14	13.4	1.5	10.8–16.2
Esophagus	14	158.1	7.8	135.0–165.6
Width	14	48.1	3.5	41.4–54.0
Maximum width	13	53.2	6.6	41.4–61.2
ABD	14	36.0	3.3	28.8–41.4
Tail	14	99.9	12.0	83.0–120.6
Length	14	930.6	86.8	770.0–1,056.6
a	13	17.6	2.1	14.3–21.3
b	14	5.9	0.5	4.9–6.5
c	14	9.5	1.5	7.0–11.7
Spicule (l)	9	39.6	2.9	34.2–43.2
Spicule chord	10	31.7	2.3	27.0–34.2
Gubernaculum (l)	10	23.7	2.7	19.8–27.0

TABLE 2. Measurements of paratype females of *Ptycholaimellus hibernus* (summary statistics). Width is the width at the base of the esophagus.

Feature	N	Mean	SD	Range
Head width	21	14.7	1.6	10.8–16.2
Esophagus	21	168.7	9.7	147.6–181.8
Width	21	55.5	7.5	43.2–66.6
Maximum width	16	64.5	13.8	39.6–90.0
ABD	21	29.2	4.3	21.6–36.0
Tail	20	122.9	8.3	102.6–135.0
Length	21	939.9	114.9	630.0–1,080.0
a	15	15.5	2.1	11.3–20.3
b	20	5.6	0.6	4.3–6.6
c	17	7.6	0.8	6.0–9.0
Vulva (%)	8	49.0	1.0	47.0–51.0

lipjev, 1922 or *H. pandispiculatus* Wieser and Hopper, 1967. Hopper (10) emended the diagnosis and revalidated *Ptycholaimellus* as a genus with the characters described below.

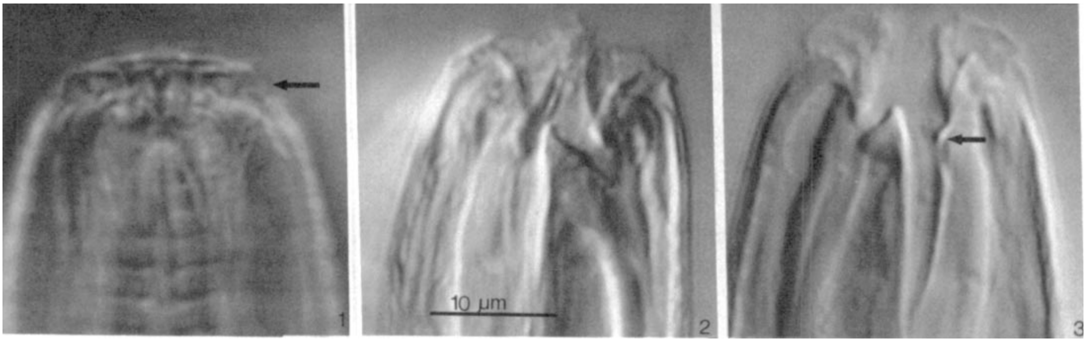
Ptycholaimellus Cobb, 1920

Type species: P. carinatus Cobb, 1920 (2).
Description: Hypodontolaiminae with cephalic setae inserted on protrusible vestibular region composed of labial rugae and enclosing membrane. Esophageal bulb double (except in *P. monodon*). Male without typical chromadorid supplements.

Family Chromadoridae Filipjev, 1917
Subfamily Hypodontolaiminae de Coninck, 1965
Genus *Ptycholaimellus* Cobb, 1920
Ptycholaimellus hibernus n. sp.
(Figs. 1–6)

Measurements are given in micrometers. Width is the width at the base of the esophagus; a is calculated using maximum width.
Holotype (male): Head diameter = 14.4, width (at base of esophagus) = 52.2, length of esophagus = 156.6, anal body diameter = 45.0, length of tail = 75.6, length = 984, a = 18.9, b = 6.3, c = 13.
Allotype (female): Head diameter = 14.4, width = 55.8 (at base of esophagus), length of esophagus = 180.0, anal body diameter = 36, length of tail = 120.6, length = 1,015, a = 18.2, b = 5.6, c = 8.4, vulva = 49%.
Paratypes: Tables 1 and 2.
Description: Four cephalic setae 4.8 μm in length attached to membranous cone enclosing stomatal vestibule. Cone consists of membrane seemingly supported by 12 spatulate labial extensions (i.e., rugae), with roots extending posteriorly below base of vestibule (Fig. 1); membranous portion extends anteriorly beyond labial extensions. Amphid not discernible. One large dorsal sigmoid tooth (Figs. 2, 4). Lining of the esophageal lumen strongly cuticularized for 14.4 μm (= 3.6 tooth lengths; apophysis of stoma sensu Timm, 1961; 15), then weakly cuticularized thereafter. Sclerotized thickening (minute tooth) situated opposite large tooth (Figs. 3–4). Esophagus swollen anteriorly by large muscles which operate dorsal tooth (2). Esophagus cylindrical between anterior swelling and posterior esophageal bulb. Bulb double, divided into approximately anterior one-third and posterior two-thirds (Fig. 4). Females didelphic with antidromous ovaries, anterior ovary to right, posterior ovary to left of gut; vagina neither strongly muscular nor heavily cuticularized. Spicules arcuate, slightly obtuse, uncephalated. Gubernaculum moderately cuticularized, longer than the distal portion of spicule, and enlarged, club-like at its distal end (Fig. 5). Terminus of tail with spinneret; terminal setae absent. Cuticle laterally differentiated by longitudinal row of enlarged punctations on each site of lateral alae, consisting of transverse bands between rows of enlarged punctations. Bands composed of transverse rows of smaller paired punctations. Size and spacing of rows of punctations varies along body (Figs. 6, 4c).

Analysis of variance revealed significant



FIGS. 1–3. Anterior of *Ptycholaimellus hibernus.* 1) Cone around stoma (arrow). 2) Stoma with sigmoid tooth. 3) Stoma with dorsal apophysis of tooth and small tooth (arrow). Scale in Figure 2 applies also to Figures 1 and 3.

differences ($P < 0.05$) between males and females for all comparable measurements except length ($P = 0.798$) and the ratio b ($P = 0.072$).

Type locality: Bread and Butter Creek, North Inlet, Georgetown, South Carolina (33°20′N; 79°10′W). Subtidal fine mud.

Geographical distribution: Penzance Point, Woods Hole, Massachusetts, salt marsh (B.E.H., pers. obs.).

Located in the U.S. National Museum. Holotype: male, U.S.N.M. #76371. Allotype: female, U.S.N.M. #76372. Paratypes: 10 males, U.S.N.M. #76373–76382;

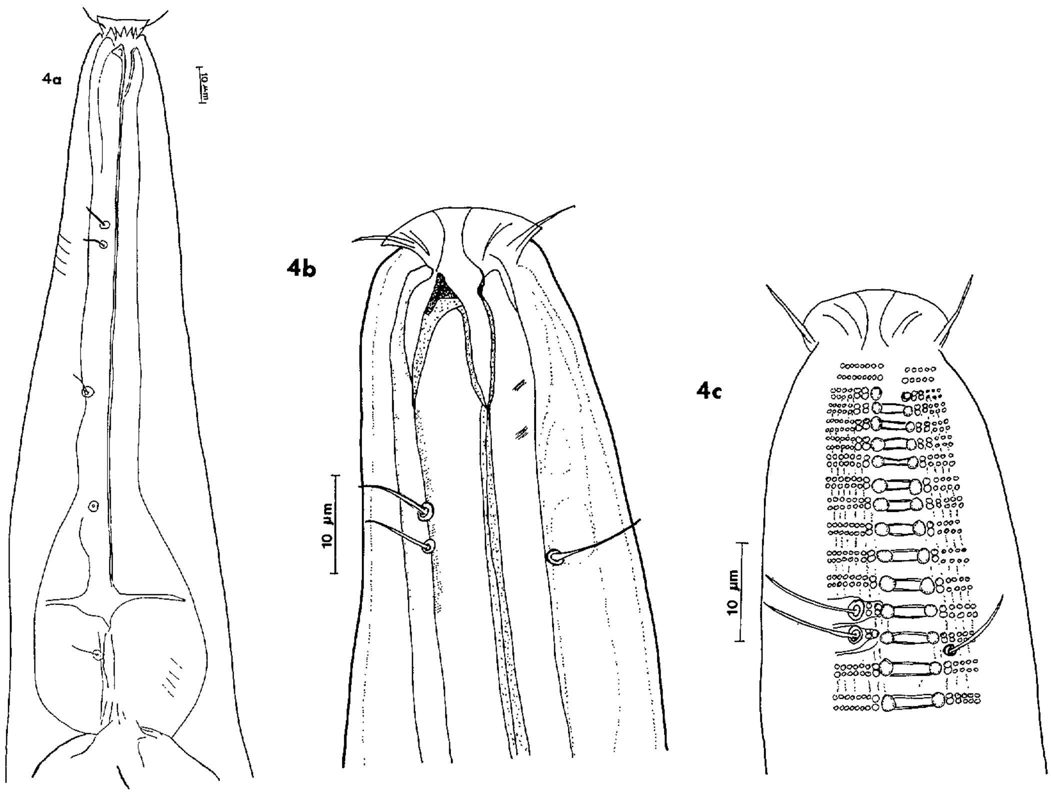


FIG. 4. Anterior of *Ptycholaimellus hibernus.* a) Outline of buccal region and double bulbed esophagus. b) Detail of head region. c) Detail of anterior cuticular ornamentation (slightly sublateral view).

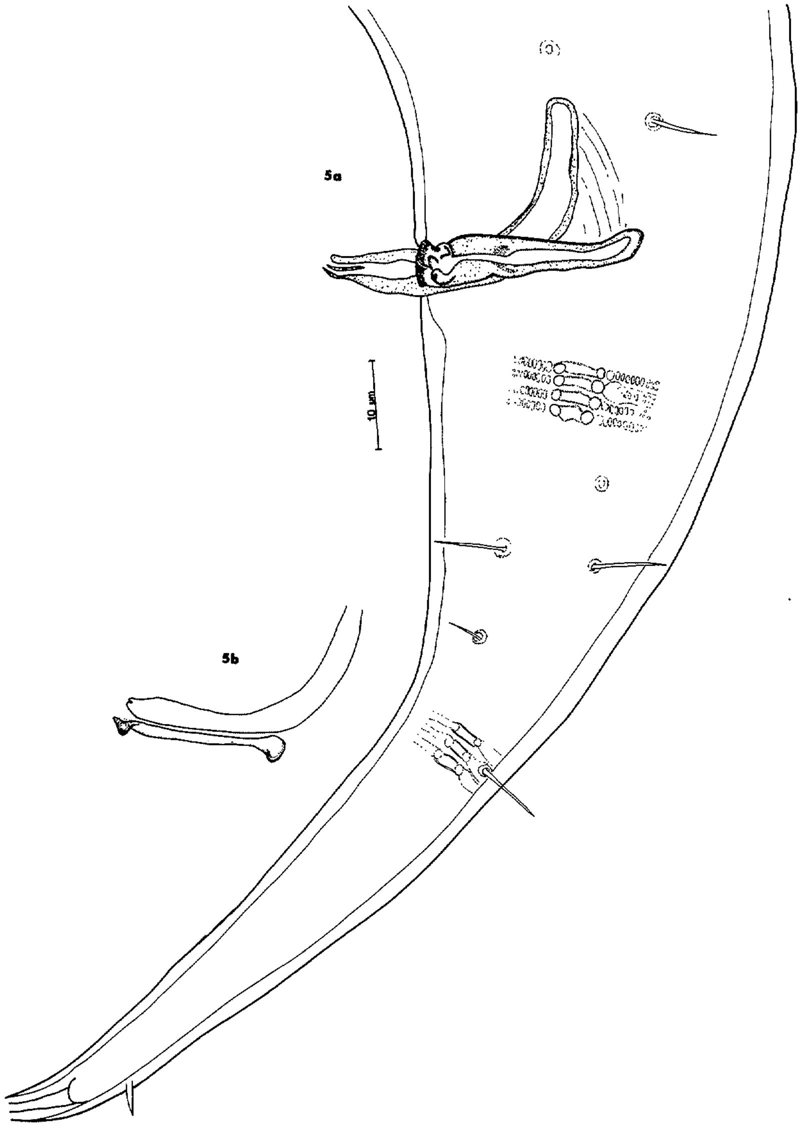


FIG. 5. Tail, spicule, and gubernaculum of *Ptycholaimellus hibernus* (a) with spicule and gubernaculum of *P. pandispiculatus* (b) for comparison.

4 females, U.S.N.M. #76383–76386. Twelve additional paratypes are retained in the author's collection.

Etymology: (Latin) *hibernus* for "of winter," because the species abundance is highest at the time of lowest water temperatures in South Carolina.

Differential diagnosis: P. hibernus is most similar to *P. pandispiculatus* (Hopper, 1961) in general form, but the males are readily distinguished by the morphology of the gubernaculum (Fig. 5a, b). *P. hibernus* n. sp. has a thick gubernaculum enlarged distally while *P. pandispiculatus* has a very thin gubernaculum with a proximal apophysis. No character has been found to clearly distinguish the females of these two species, which both occur in our South Carolina site (13). However, *P. pandispiculatus* seems to prefer brackish water (9; R.A.E., pers.

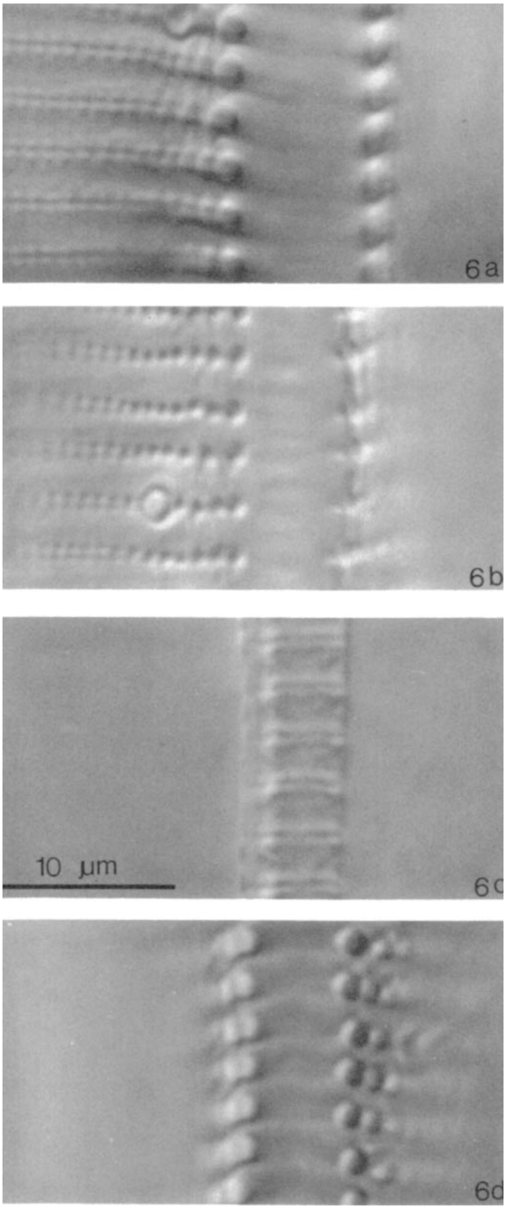


FIG. 6. Cuticular patterns along body of *Ptycholaimellus hibernus* (slightly sublateral view). a) Over esophageal bulb. b) Midbody. c) Lateral ala at midbody. d) Tail. (Scale bar applies to a–d.) Note lateral ala is above plane of focus in a, b, and d and sublateral cuticular ornamentation is below plane of focus in c.

obs.) while the type habitat of *P. hibernus* is a well-mixed estuary with a mean salinity of 33 ppt. Judging from the presence of males, *P. pandispiculatus* is a rare visitor to the Bread and Butter site. Its frequency is insignificant in comparison to that of *P. hibernus* n. sp., although it can be common in a high marsh tidal creek and impounded rice paddies in the same estuarine system (13; Coull, unpubl.).

KEY TO THE SPECIES OF *PTYCHOLAIMELLUS*

1. Body stout (width ≥ 50 µm), with long (≥ 20 µm) cephalic setae 2
1. Body slimmer (width < 50 µm), cephalic setae less than 10 µm long 3
2. Lateral differentiation begins near head, gubernaculum thin, slightly curved, without lateral processes .... *P. carinatus* Cobb, 1920
2. Lateral differentiation begins mid-esophagus, gubernaculum with proximal lateral processes which lie over spicule .... *P. slacksmithi* (Inglis, 1969)
3. Knob-like swellings at base of tooth, cephalic setae = 8 µm = head diameter ..... *P. macrodentatus* (Timm, 1961)
3. No knob-like swellings at base of tooth, cephalic setae shorter than head diameter 4
4. Protoplasmic interruptions to form double esophageal bulb very weak or absent, no small subventral teeth, small species, L = 650 µm .. *P. monodon* (Schuurmans-Stekhoven, 1942)
4. Double esophageal bulb obvious, small subventral teeth present, larger species, L > 750 5
5. Length of excretory cell = length of esophagus *Ptycholaimellus* sp. 2 Hopper, 1969 n. syn. .... *P. ponticus* (Filipjev, 1922)
5. Length of excretory cell < length of esophagus 6
6. Gubernaculum as thick as distal portion of spicule, swollen and knobbed at distal end .... *P. hibernus* n. sp.
6. Gubernaculum very thin, with small apophyses at proximal end .... *P. pandispiculatus* (Hopper, 1961)

Species no. 2 Hopper, 1969 is synonymous with *P. ponticus*.

Population: A consistent seasonal population pattern was displayed by *P. hibernus* n. sp. during the 3 years of this study, with highest populations in January, February, and March and lowest in July, August, and September. The winter highs consistently reached 150–200 animals 10 cm² and the lows usually reached zero (Fig. 7a). When

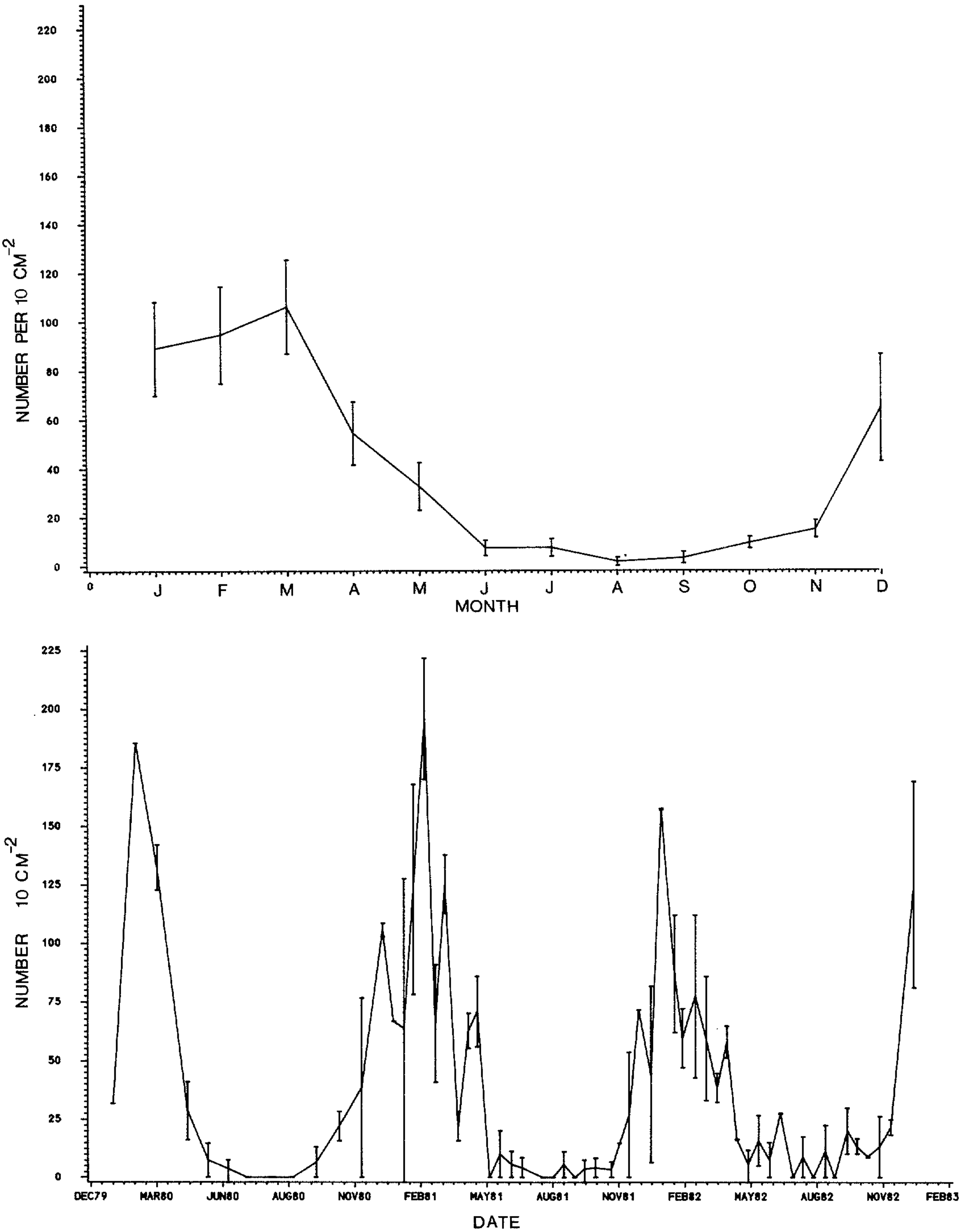


FIG. 7. Population of *Ptycholaimellus hibernus* (mean number 10 cm^2 ± 1 standard error) at Bread and Butter Creek. a) From January 1980 to December 1982. b) Mean by month for 3 years (1980–82).

data for 3 years were averaged by month to give an average year, there was a sharp increase in December, followed by a slow increase during January, February, and March and a sharp drop in April (Fig. 7b). Pearson product moment correlations of populations and physical environmental factors were significant for sediment temperature ($r = -0.68$, $P = 0.0001$) and for the depth of the anoxic layer ($r = 0.71$, $P = 0.0001$), but not for salinity ($r = -0.19$, $P = 0.18$). Temperature and depth of the RPD layer are also significantly correlated ($r = -0.61$, $P = 0.0031$), and therefore we cannot determine whether the effects of temperature alone or the potential reduction in habitat caused by the movement of the anoxic, sulfide laden layer toward the surface was responsible for the variation in the nematode population.

The ratio of males to females in the population examined was 0.56:1 (N = 500); 47% of all females were gravid. Juveniles composed only 7.4% of the population, suggesting that possibly some were lost during the extraction from the mud and that our absolute population estimates may be low. However, several samples were sieved with both 63- and 44-μm-pore sieves, and the smaller pore size did not collect a significant number of juveniles; therefore, we know they were not passing through our sieve.

Discussion

Temperature and the presence or absence of oxic sediment are known to influence reproductive rates, metabolism, abundance, and distribution of marine nematodes (7,11,16,18). Typically such studies have been performed in the laboratory. In the field, temperature can interact in a complex fashion with other physical variables such as the presence of sulfides, the lack of oxygen, and low pH. Our field study has verified such interactions, again confirming the necessity to exercise caution in extrapolating laboratory results to the field.

Diatom abundance data are available for 1981; diatoms are most abundant in March and display a second peak in summer (12). It is possible that the abundance of diatoms in spring provides ample food for rapid growth of nematodes, but in summer detrimental physico-chemical conditions prevent such population growth. Our sampling design did not permit us to determine the cause of the population fluctuations, which may have been caused by die-off followed by recolonization, or by the nematodes going into a resistant stage (perhaps egg) which survived the summer.

The fact that *P. hibernus* is abundant for predictable periods of the year suggests that it may serve as a model organism to experimentally test hypotheses regarding the interaction of nematode life history strategies with environmental factors demonstrated in this study to be important—in particular, the role of the depth of the anoxic layer in determining seasonal abundance and the trophic habits of this species.

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