Marine Biology 101, 401–409 (1989)

Marine Biology
International Journal on Life in Oceans and Coastal Waters

Spatial and temporal occurrence of the parasitic dinoflagellate *Duboscquella cachoni* and its tintinnine host *Eutintinnus pectinis* in Chesapeake Bay

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Abstract

Eutintinnus pectinis (Kofoid, 1905) Kofoid and Campbell is a seasonally important component of the Chesapeake Bay, USA, microzooplankton. During the summers of 1986 and 1987, *E. pectinis* populations commonly reached densities well above 10^3 cells l^{-1} and were often heavily infected by *Duboscquella cachoni* Coats, 1988, a lethal parasitic dinoflagellate. The temporal and spatial occurrence of *D. cachoni* suggests that this parasite has a significant impact on *E. pectinis* populations and may, under appropriate conditions, regulate host abundance. Infection levels above 10% were frequently encountered and epizootic events with 20 to 50% of host individuals parasitized by dinoflagellates were observed over broad areas. Epizootic infections were usually recorded in regions of the Bay that had high concentrations of *E. pectinis*, and data for vertical profiles, when integrated with depth, showed a significant positive correlation ($p \ll 0.01$) between host abundance and parasite prevalence. However, peak *E. pectinis* density and maximum levels of parasitism were often not vertically coincident at stations, and a clear relationship between host abundance and parasite prevalence was not evident for data from discrete samples. These vertical distributions and the absence of a correlation between host density and parasite prevalence for discrete samples may reflect death of *E. pectinis* as epizootics spread through the host population. Bay-wide infection levels averaged 10.4% (± 1.73 SE) for eight cruises in 1986 and indicate that parasite-induced mortality removes 7 to 24% of the *E. pectinis* standing stock per day. Comparison of these values to ingestion rates for copepods on tintinnine ciliates reveals that parasite-induced mortality of *E. pectinis* is comparable to predation pressure by the dominant mesozooplankton grazers in Chesapeake Bay.

Introduction

Since the late 1970's, progressively greater attention has focused on microbial activities of marine pelagic ecosystems. Recent studies have emphasized trophic pathways within the microbial community and implicated phagotrophic protozoa as a prominent link of the pico- and nanoplankton to the larger zooplankton (Conover 1982, Porter et al. 1985, Sherr et al. 1986). These investigations have also promoted the realization that trophic relationships among protozoa constitute a complex and poorly understood food web (Sherr et al. 1988) that includes host-parasite as well as more classical predator-prey interactions (Laval-Peuto et al. 1986).

The wide variety of parasites known to infect marine organisms is believed to play an important role in the ecology of the oceans, yet they are the least known components of food webs (Rohde 1982). This is particularly true for microparasites of protozoa, as most studies have been limited to investigations of parasite morphology and life history. While bacteria, fungi, and protozoa are known to infect planktonic protists, data on the abundance, distribution, and ecology of these parasites is sparse. However, protozoa appear unable to mount a response to parasitic invasion or to develop acquired immunity, and recovery from infection is unlikely in these organisms (Anderson and May 1981). Thus, parasitism may have a significant effect on protistan populations.

Dinoflagellates of the genera *Dubosquella, Duboscquodinium,* and *Amoebophrya* are endoparasites of planktonic protozoa including ciliates, radiolaria, and other dinoflagellates (Cachon and Cachon 1987). Species of *Duboscquella* most frequently parasitize tintinnine ciliates and act much like predators as they usually kill and consume the host. *Duboscquella* spp. infestations of ciliates are passively transmitted when dinospores, a flagellated dispersal stage, are ingested by susceptible hosts (Cachon 1964). Once inside the host, the spore differentiates into a vegetative stage, the trophont, that enters an extended growth phase and eventually occupies much of the ciliate's cytoplasm. In several species of *Duboscquella,* maturation of the trophont involves an elaborate morphogenetic process that results in the ingestion of most, if not all, of the infected organism, however

other species consume the host without forming a food vacuole. In either case, the parasite is liberated from the host and passes through a series of rapid cell divisions to produce several hundred to many thousand infective spores.

Previous studies have suggested that parasitic dinoflagellates have a strong influence on the population dynamics of host species. For example, Cachon (1964) reported that in some Mediterranean samples nearly 100% of the tintinnine ciliates were infested with dinoflagellates and argued that death due to parasitism may have caused abrupt declines in host abundance. This argument is supported by the observation that *Duboscquella* sp. was most prominent in tintinnine ciliates of Narragansett Bay during periods of declining host abundance (Verity 1986). In a comparison of in situ and in vitro growth of microzooplankters, Stoecker et al. (1983) attributed the lower net growth of *Favella* sp. in field samples, in part, to parasitism by *Duboscquella*. sp. Most recently, an experiment on a natural assemblage of *Eutintinnus pectinis* and *D. cachoni* showed a marked increase in parasite prevalence coupled with a rapid disappearance of host organisms (Coats 1988). In this paper we provide additional data on the relationship between *E. pectinis* and *D. cachoni* by considering temporal and spatial aspects of host abundance and parasite prevalence in Chesapeake Bay.

Materials and methods

Observations on the temporal and spatial occurrence of the parasitic dinoflagellate *Duboscquella cachoni* Coats, 1988 and its tintinnine host *Eutintinnus pectinis* (Kofoid, 1905) Kofoid and Campbell in Chesapeake Bay, USA were made during 16 cruises aboard the R. V. "Ridgely Warfield". Eight to ten stations along the major axis of the Bay (Fig. 1) were sampled at biweekly intervals between May and October 1986 and less regularly in summer 1987. During July and August 1987, samples were also collected from stations on two cross-Bay transects in regions of high host abundances. CTDFO_2-Niskin bottle casts provided data and material for determining conductivity and temperature (Plessey-Grundy CTD), chlorophyll *a* (chl *a*) fluorescence (Q-Instruments in situ and Turner Designs model 10 fluorometers), dissolved O_2 concentration (Yellow Springs Instruments O_2 meter; Winkler titrations), host abundance, and parasite prevalence. The number and vertical position of Niskin samples varied among profiles and depended on depth and stratification of the water column. Typically eight to ten bottles were collected at each station with three to four samples from the surface mixed layer, two to three in the region of density discontinuity, two to three from subpycnocline waters.

Host density was determined by inverted microscopy (Utermöhl 1931) at 160 × using 50 ml aliquots of whole-water samples preserved with a modified Bouin's solution (Coats and Heinbokel 1982). For assessment of parasite prevalence, host cells were collected from 2 liter samples by screening onto 20 μm Nitex, fixed in modified Bouin's, and stained with acidulated alum hematoxylin (Galigher and

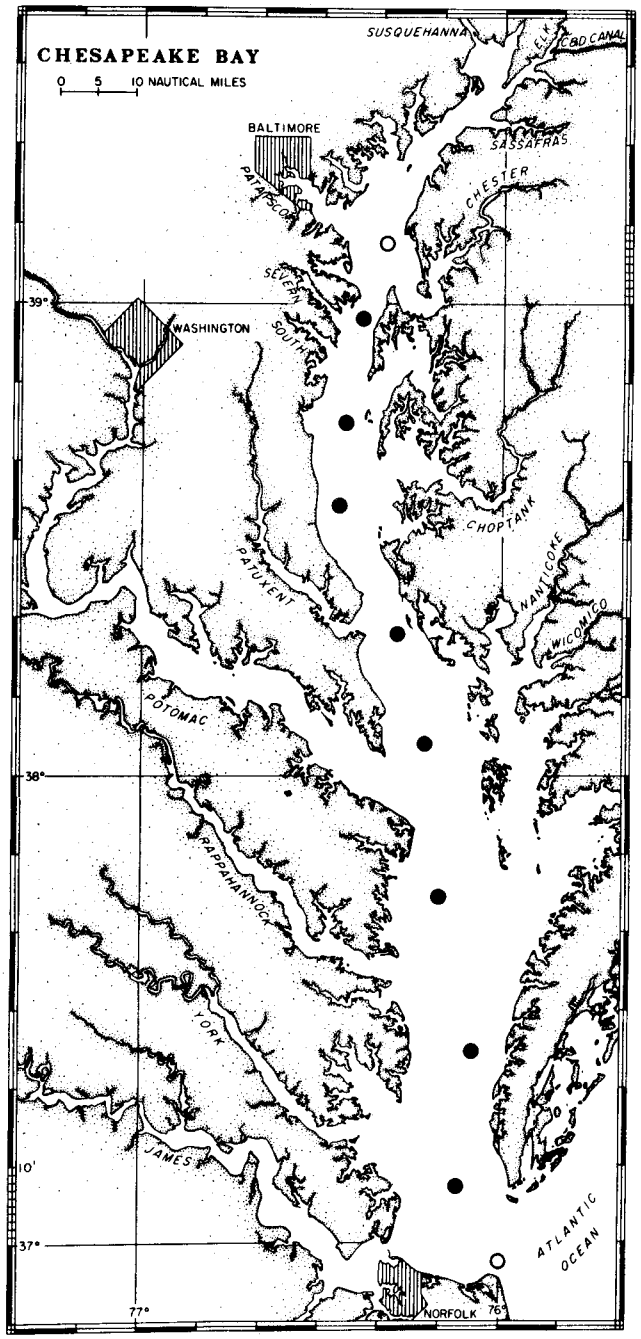


Fig. 1. Map of Chesapeake Bay, USA showing routine stations (•) for research cruises in 1986 and 1987, and stations (○) not sampled on all cruises. Stations are designated from north to south, 908, 858, 845, 834, 818, 804, 744, 724, 707, and 656. Station numbers reflect degrees and minutes N lat. (e.g., Station 858 was at 38° 58′ N lat.; 76° 23′ W long.)

Kozloff 1971). Infested hosts were recognized by identifying developmental stages of *Duboscquella cachoni*, using established morphological criteria (Coats 1988). Parasite prevalence at intermediate to high host densities (≥ 500 cells l^{-1}) were obtained by examining ≥ 100 *Eutintinnus pectinis* per sample. However, stained material collected from water with lower host concentrations often contained < 100 *E. pectinis* and sample sizes at very low host densities were occasionally too small to provide reliable data. In the latter

case, estimates of parasite prevalence were derived by pooling data from adjacent samples within vertical profiles. This procedure produced 224 determinations of parasite prevalence, only nine of which were based on observation of <50 host cells. Station averages for host abundance and parasite prevalence were obtained by integrating sample data against depth for the portion of the water column inhabited by *E. pectinis*. Bay-wide estimates of host density and parasite prevalence were calculated for 1986 cruises by integrating station data relative to transect distance.

Pearson correlation coefficients and significant probabilities (p) for parasite prevalence vs host density were calculated using individual sample data and integrated values for vertical stations.

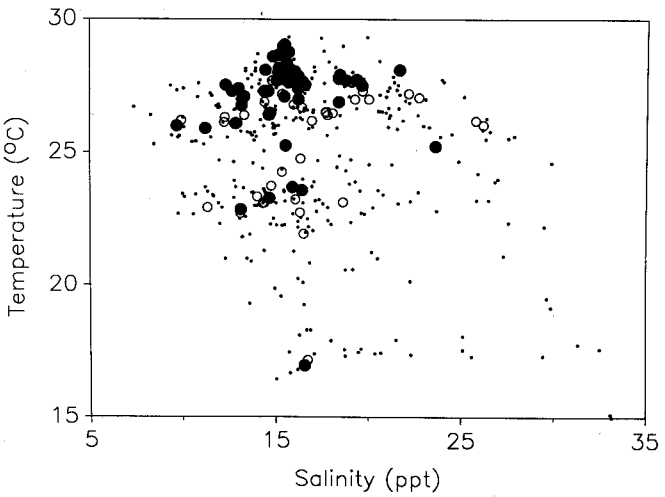


Fig. 2. *Eutintinnus pectinis*. Abundance plotted on salinity-temperature parameter space. (·) <500 cells l^{-1}, (o) 500 to 999 cells l^{-1}, (•) $\geq 1\,000$ cells l^{-1}

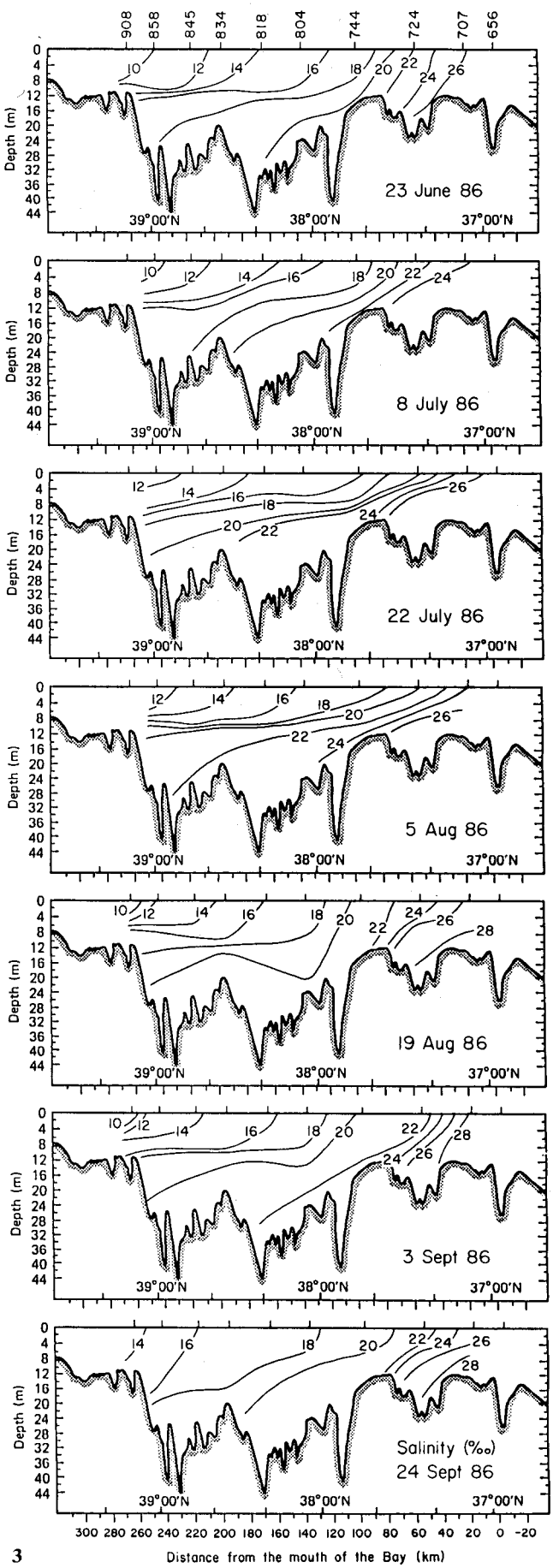
Results

During the summers of 1986 and 1987, *Eutintinnus pectinis* was present in detectable numbers (≥ 20 cells l^{-1}) from early June through September and reached maximum abundance in July and August with densities as high as 6 000 cells l^{-1}. *E. pectinis* was observed at all stations, but peak abundances ($\geq 10^3$ cells l^{-1}) were most frequently encountered at salinities of 12 to 20‰, when water temperature exceeded 22 °C (Fig. 2). Host populations were largely restricted to surface waters above the major density discontinuity and were seldom observed below a depth of 10 to 12 m. *E. pectinis* was rarely encountered in hypoxic waters (dissolved O_2 ≤ 1 ml l^{-1}), and cell densities showed no clear relationship to chl *a* concentration.

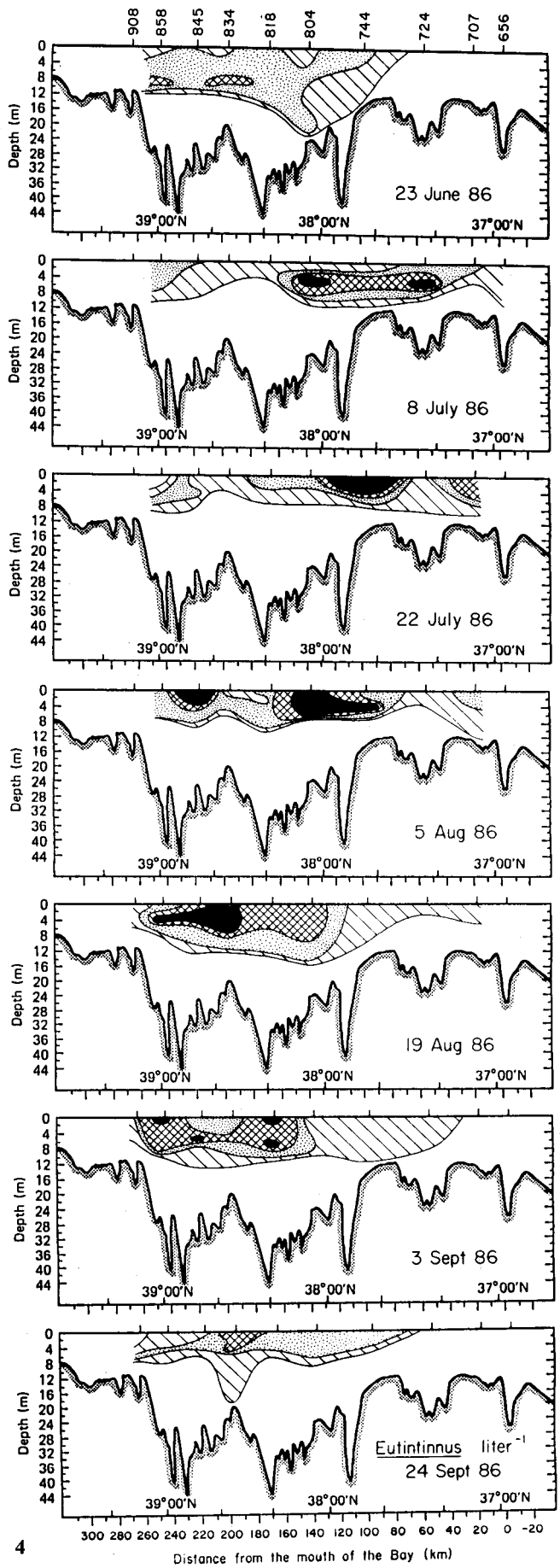
Data on salinity and the distribution of *Eutintinnus pectinis* for seven biweekly cruises in 1986 are summarized in Figs. 3 and 4. *E. pectinis* was present in relatively low numbers during June with densities of ≤ 500 cells l^{-1} broadly distributed from just below the Bay bridge at Station 858 to the southern Bay at Station 724. By early July, host abundance had sharply increased south of the Patuxent River (ca Station 818), and subsurface concentrations $\geq 10^3$ cells l^{-1} were associated with the 16‰ *S* isohaline at Station 804 and the 22 to 24‰ *S* isohalines at Station 724 (cf. Figs. 3 and 4). High concentrations of *E. pectinis* were also observed in this portion of the Bay during late July and early August, but peak densities ($\geq 10^3$ cells l^{-1}) were only associated with the 16 to 18‰ *S* isohalines and were more restricted to surface waters. In late August, host abundance was noticeably lower south of the Patuxent River, and cell densities in that region continued to decline in subsequent cruises. A second area of elevated *E. pectinis* abundance had developed near the Bay bridge by early August and was associated with the 12 to 14‰ *S* isohalines. Peak densities were still present north of the Patuxent River during late August, but appeared to disperse in the following two weeks. Only isolated patches of *E. pectinis* $\geq 10^3$ cells l^{-1} were present in the northern portion of the study area in early September, and peak concentrations were not encountered later that month.

Infestations of *Eutintinnus pectinis* by *Duboscquella cachoni* in the summers of 1986 and 1987 were common, widespread, and occasionally reached epizootic proportions (20 to 50%). Parasite prevalence was rather low during June 1986 with *D. cachoni* infesting well under 5% of the *E. pectinis* in most samples (Fig. 5). By early July, infestations were far more prominent and a zone of high parasite prevalence (>10%) broadly overlapped the dense host population in the southern Bay. Levels of infection approaching 50% were observed between the 16 and 20‰ *S* isohalines and at a slightly greater depth than the two peak densities of *E. pectinis*. Parasite prevalence remained elevated south of the Patuxent River through late July and early August. During this period, the percent of hosts infested by *D. cachoni* was highest (20 to 40%) in samples taken near the lower boundary and beneath peak concentrations of *E. pectinis*. In early August, a second zone of high parasite prevalence was located north of the Patuxent River and was associated with peak *E. pectinis* abundances between the 12 to 16‰ *S* isohalines. *D. cachoni* infestations above 10% were more widespread in this region during late August and encompassed a major portion of the host population. High levels of parasitism persisted into September, but appeared to be reduced in spatial coverage as *E. pectinis* abundance declined.

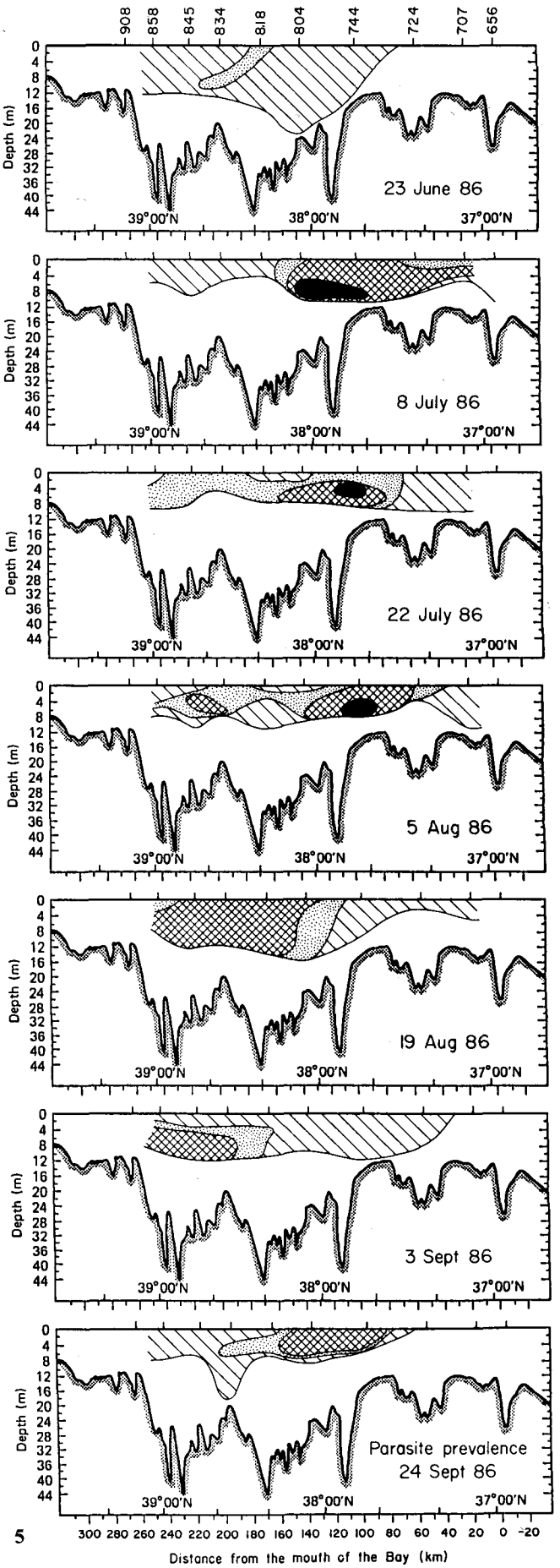
Fig. 6 summarizes data for cruises during late July and early August of 1987. In July, *Eutintinnus pectinis* concentrations above 10^3 cells l^{-1} were located upstream of the 12‰ *S* isohaline (Stations 908 and 858) and between the 14 and 20‰ *S* isohalines south of the Patuxent River. Parasite prevalence was very low north of the Patuxent River, with most samples having ≤ 2% of the hosts infested with dinoflagellates. However, *Duboscquella cachoni* infestations were common in the southern Bay and produced epizootic infections in subsurface host populations between the 16 to 20‰ *S* isohalines. Interestingly, peak concentrations of *E. pectinis* in surface waters at Station 804 were not heavily infected (<1%). Samples taken at stations along cross-Bay transects (Fig. 7) revealed that peak densities of *E. pectinis* were not restricted to the central portion of the Bay and showed that


908 858 845 834 818 804 744 724 707 656
Depth (m)
23 June 86
8 July 86
22 July 86
5 Aug 86
19 Aug 86
3 Sept 86
Salinity (‰)
24 Sept 86
39°00'N
38°00'N
37°00'N
300 280 260 240 220 200 180 160 140 120 100 80 60 40 20 0 -20
Distance from the mouth of the Bay (km)

3


908 858 845 834 818 804 744 724 707 656
Depth (m)
23 June 86
8 July 86
22 July 86
5 Aug 86
19 Aug 86
3 Sept 86
Eutintinnus liter⁻¹
24 Sept 86
39°00'N
38°00'N
37°00'N
300 280 260 240 220 200 180 160 140 120 100 80 60 40 20 0 -20
Distance from the mouth of the Bay (km)

4



high levels of parasitism were very widespread. By early August, distributional patterns of host and parasite populations had changed dramatically. *E. pectinis* concentrations between Stations 804 and 744, that portion of the Bay previously inhabited by heavily parasitized *E. pectinis*, were generally ≤ 300 cells l^{-1}, but peak abundances with low parasite infestations were present north and south of this region. Host densities upstream from the 12‰ *S* isohaline were also sharply reduced, and parasite infestations, which were infrequent in that region two weeks earlier, were at epizootic levels.

While parasite prevalence was often greater in regions of the Bay that were densely populated by *Eutintinnus pectinis*, high host abundance and maximum infection levels were often spatially separated along the axis of the Bay. Vertically, epizootic infections were occasionally coincident with peak host densities, but were frequently encountered either below or above high *E. pectinis* concentrations (Fig. 8). Thus, it is not surprising that estimates of parasite prevalence were not correlated with host abundance (Fig. 9A). However, a greater proportion of samples collected from regions of elevated host densities had high levels of parasitism. For example, $\geq 5\%$ of the hosts were frequently parasitized at all host densities, whereas the proportion of samples with $\geq 10\%$ of the *E. pectinis* containing parasites steadily increased with host abundance, and samples with $\geq 15\%$ of the hosts infested were twice as common at $\geq 10^3$ cells l^{-1} (Fig. 9B). The dependence of parasite prevalence on host density is also apparent in integrated station data where infection levels and host density showed a significant ($p < 0.01$) positive correlation (Fig. 9C).

A more synoptic view of host and parasite occurrence in Chesapeake Bay is provided by integrating station data along cruise transects (Fig. 10). These values clearly show the seasonality in *E. pectinis* abundance and generally demonstrate the dependence of parasite prevalence on host density. Curiously, the highest incidence of parasitism (18.4%) was recorded prior to the mid-summer peak in host density and reflected the occurrence of a heavily infected host population south of the Patuxent River when *E. pectinis* in the northern Bay was still in low numbers. Bay-wide values for parasite prevalence averaged 10.4% (± 1.73 SE; $n = 8$) from June through September 1986, with monthly averages ranging from 5.3% in June to 16.1% during July.

Fig. 3. Salinity distribution along the longitudinal axis of Chesapeake Bay. Station numbers from Fig. 1 are indicated at the top

Fig. 4. *Eutintinnus pectinis*. Abundance along the longitudinal axis of Chesapeake Bay. (▨) < 100 cells l^{-1}, (▩) 100 to 499 cells l^{-1}, (▩) 500 to 999 cells l^{-1}, (■) $\geq 1\,000$ cells l^{-1}. Station numbers from Fig. 1 are indicated at the top

Fig. 5. *Eutintinnus pectinis*. Percent infested by *Duboscquella cachoni*. (▨) < 5%, (▩) 5 to 10%, (▩) > 10% and < 20%, (■) $\geq 20\%$. Station numbers from Fig. 1 are indicated at the top

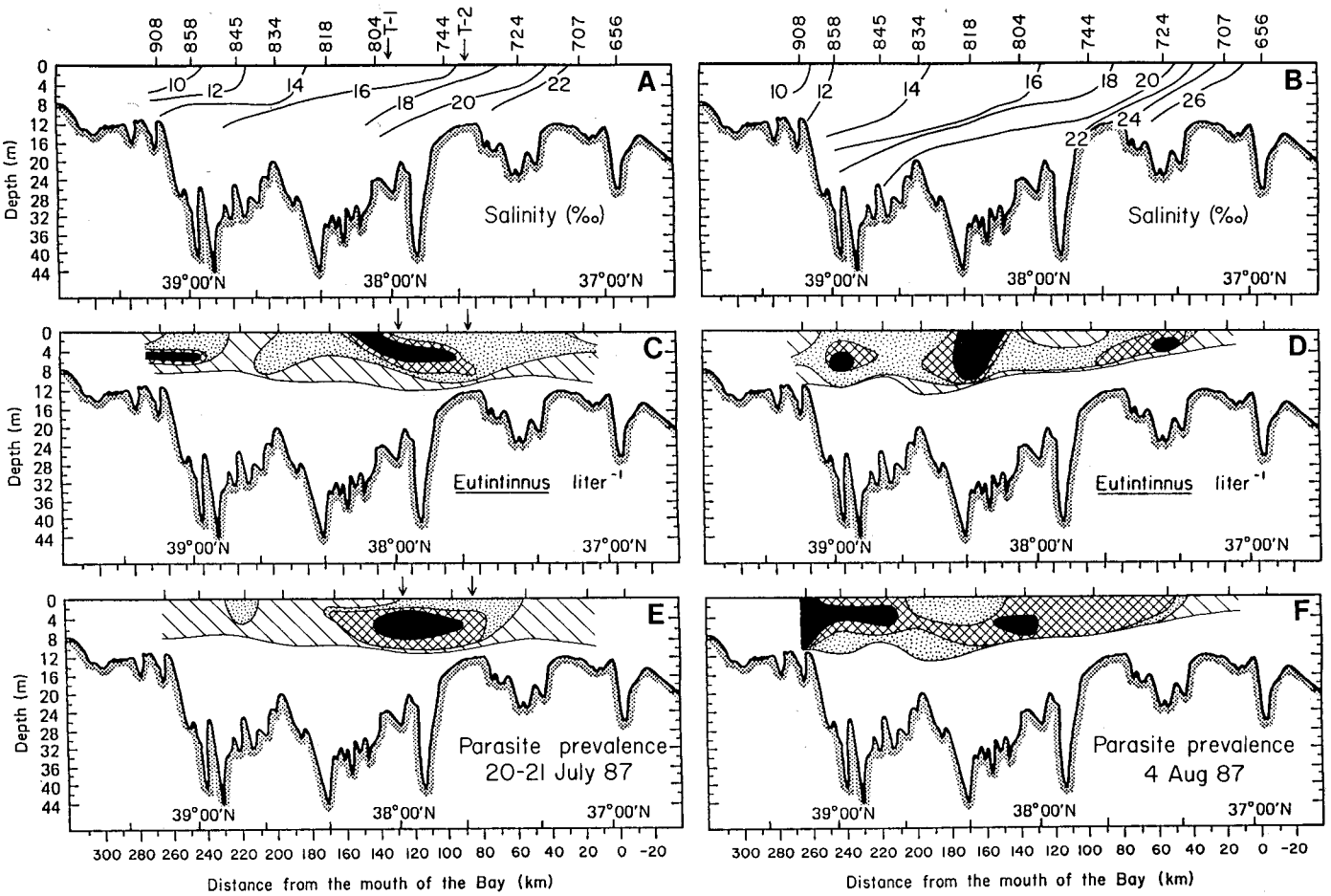


Fig. 6. Cruise data summary for 20 to 21 July and 4 August 1987. Arrows T-1 and T-2 indicate position of cross-Bay transects. A and B = longitudinal salinity distributions. C and D = *Eutintinnus pectinis* densities at central channel stations: (▨) < 100 cells l^{-1}; (▩) 100 to 499 cells l^{-1}; (▩) 500 to 999 cells l^{-1}; (■) ≥ 1 000 cells l^{-1}. E and F = percent hosts infected by *Duboscquella cachoni:* (▨) < 5%, (▩) 5 to 10%; (▩) > 10% and < 20%; (■) ≥ 20%

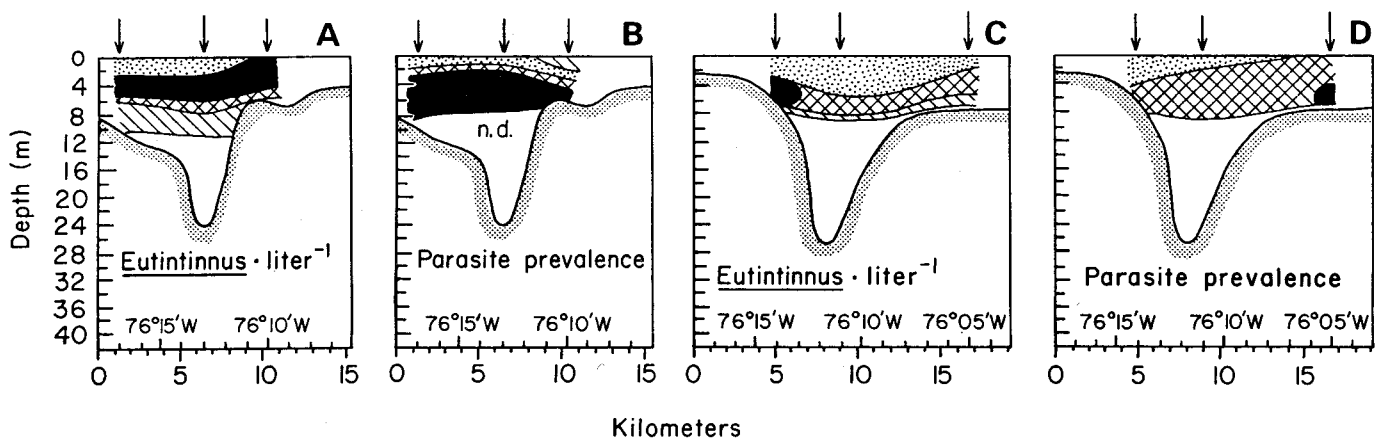


Fig. 7. *Eutintinnus pectinis.* Abundance (A, C) and percent infested by *Duboscquella cachoni* (B, D) on 21 July 1987 at cross-Bay transects T-1 (A, B) and T-2 (C, D). Arrows indicate station locations. Shaded areas are as in Fig. 6; no data (n.d.)

Discussion

Eutintinnus pectinis, originally described from waters off San Diego, California (Kofoid 1905), has been frequently observed in coastal waters along the east coast of North America (Gold and Morales 1975, Hargraves 1981, Verity 1986). This tintinnine ciliate can occur in very high densities and has been reported at concentrations $>10^4$ cells l^{-1} in protected estuarine environments (Stoecker et al. 1983, Turner and Anderson 1983). *E. pectinis* is a summer resident in

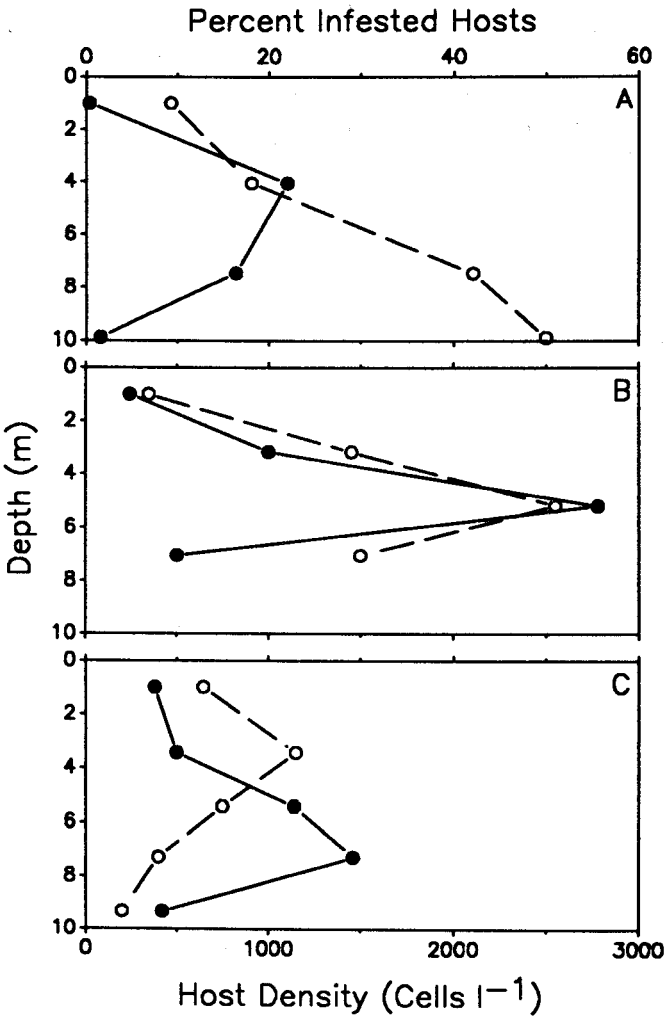


Fig. 8. *Eutintinnus pectinis*. Vertical distributions (•) and percent hosts infested by *Dubosquella cachoni* (○) at A: Station 804, 8 July 1986; B: the central station of cross-Bay transect T-1, 21 July 1987; C: Station 858, 4 Aug 1987

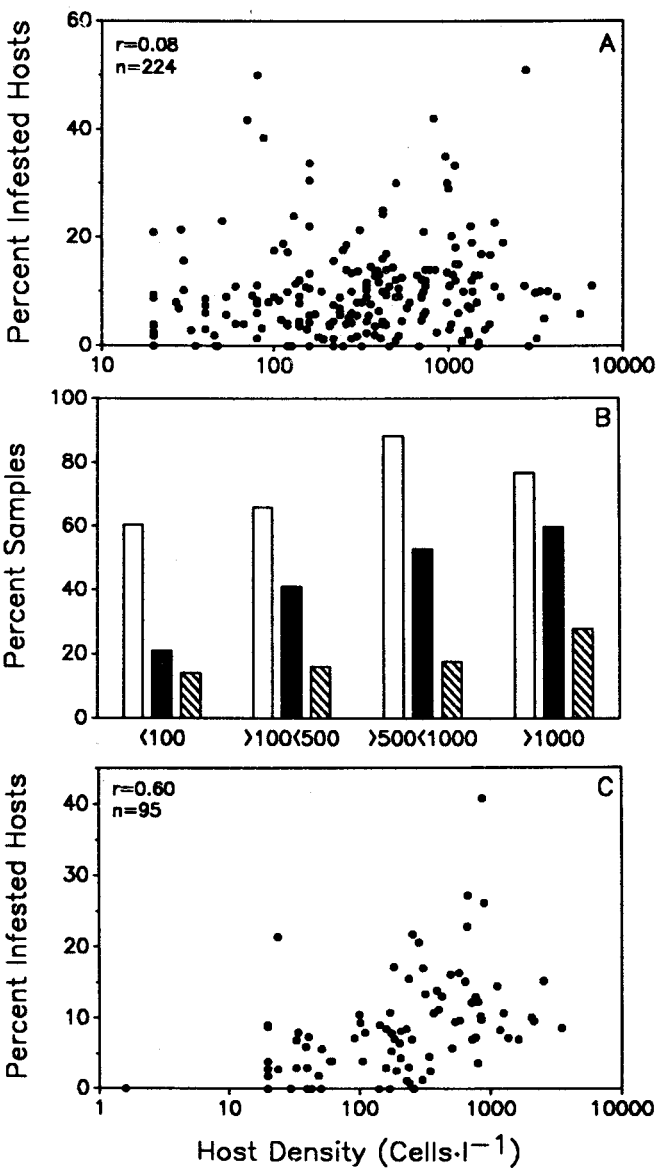


Fig. 9. *Eutintinnus pectinis*. A. Percent infested with *Duboscquella cachoni* plotted against host abundance for all samples taken in 1986 and 1987. B. Data grouped according to host abundance and showing the proportion of samples with (□) > 5%, (■) > 10%, and (▨) > 15% of *E. pectinis* infested by *D. cachoni*; sample size for the four categories of host density are ≤100, $n=43$; >100<500, $n=100$; ≥500<1 000, $n=34$; ≥1 000, $n=47$. C. Percent infested with *D. cachoni* plotted against *E. pectinis* abundance for station data integrated with depth. Correlation coefficients are given for samples of "n" determinations in A and B

Chesapeake Bay and reaches densities well above 10^3 cells l^{-1} in mesohaline waters.

During periods of peak occurrence in 1986 to 1987 (July to August), *Eutintinnus pectinis* populations in Chesapeake Bay were heavily infected by the parasitic dinoflagellate *Duboscquella cachoni*. Host populations commonly supported parasite prevalences ≥10%, and epizootic infestations (20 to 50%) occurred over large areas. Integrated station data showed a significant positive correlation ($p \ll 0.01$) between host abundance and parasite prevalence and indicate a density dependent relationship between *E. pectinis* and *D. cachoni*. The proportion of samples with high parasite prevalence (≥10%) was also directly related to host abundance, which supports a density dependent interaction. However, elevated levels of parasitism were often encountered outside peak host concentrations and parasite prevalence was occasionally low in areas of high host abundance. Consequently, parasite prevalence and *E. pectinis* density for individual samples were not correlated.

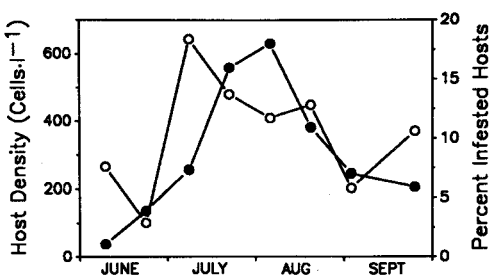


Fig. 10. *Eutintinnus pectinis*. Seasonal occurrence (•) in Chesapeake Bay during 1986 and prevalence of *Duboscquella cachoni* infestations (○)

While epizootic infestations were typically encountered at stations where host densities were $\geq 10^3$ cells l^{-1}, vertical profiles showed that highest infections often occurred adjacent to peak host concentrations. In most instances, parasite prevalence was highest in samples taken below those with maximum host abundance, indicating that parasitized cells might be sinking out of the host population. However, epizootic infestations were occasionally observed in shallower samples and in samples with peak host densities, and prior investigations have established that infected *Eutintinnus pectinis* continue to swim (Coats 1988). Since *Duboscquella cachoni* infestations are lethal, increased parasitism adjacent to peak *E. pectinis* densities may reflect reduced host abundance caused by the epizootic spread of parasites through the host population. If *D. cachoni* does regulate *E. pectinis* populations through periodic or cyclic epizootic events that cause mass martality of host organisms, then the absence of a correlation between host density and parasite prevalence in discrete samples, as observed here, is expected.

Previous observations indicate that *Duboscquella cachoni* infestations of 30 to 40% are sufficient to cause a significant decrease in *Eutintinnus pectinis* abundance (Coats 1988). However, parasitic infections alone can only cause a decline in host abundance if death due to parasitism exceeds reproduction of the host. Development time of *D. cachoni* from infection to death of the host is ca 18 h at 24 °C, and, once infected, *E. pectinis* appears unable to reproduce (Coats 1988). Thus, ignoring potential increases in parasite prevalence, a host population which has 50% of the cells infested must double more than once per day to offset losses due to parasitism. Heinbokel (1978) reported a maximum growth rate of 0.06 ($\sim$2 generations d^{-1}) for *E. pectinis* grown under optimum food concentrations at 18 °C. Verity (1986) observed in situ growth rates of 1.2 to 2.2 generations d^{-1} for *E. pectinis* in Narragansett Bay (temperature not specified, but between 18° and 24 °C). By contrast, Stoecker et al. (1983) obtained in situ growth rates ranging from -0.0058 to 0.0292 (≤ 1.0 generations d^{-1}) for apparently non-parasitized *E. pectinis* at 17.5 to 18.5 °C. Thus *E. pectinis* reproducing at maximal rates should be able to withstand high levels of parasitism. However, in suboptimal conditions (e.g. reduced food supply) and at the lower growth rates reported for field populations, *E. pectinis* abundance would be quickly reduced by epizootic infestations. Interestingly, host populations south of the Patuxent River in 1986 persisted in peak concentrations ($\geq 10^3$ cells l^{-1}) for several weeks even though parasite prevalence was high, whereas epizootic infestations in 1987 appeared to cause rapid declines in *E. pectinis* abundance.

Cruise averages for 1986 show that *Duboscquella cachoni* infested 5.3 to 18.4% (mean = 10.4% $\pm$ 1.73 SE; $n=8$) of *E. pectinis* Bay-wide. Adjusting these data by a parasite development time of 0.75 d, (i.e., % *E. pectinis* killed d^{-1} by parasitism = (% infected hosts)/(parasite development time) indicates that parasitic dinoflagellates removed 7 to 24% of the *E. pectinis* standing stock per day. The dominant metazoan grazer in Chesapeake Bay during the summer is the estuarine copepod *Acartia tonsa* (Heinle 1966, Brownlee and Jacobs 1987). Densities of this copepod in meso- and polyhaline regions of the Bay range from 4 to 20 l^{-1} between May and September (Brownlee and Jacobs 1987). Estimated clearance relates of *Acartia* spp. vary from 4.6 to 9.2 ml copepod^{-1} d^{-1} for *A. hudsonica* when feeding on natural populations of *E. pectinis* (Turner and Anderson 1983) to 72 to 289 ml copepod^{-1} d^{-1} for *A. tonsa* when fed monospecific cultures of larger tintinnine ciliates (Robertson 1983, Stoecker and Sanders 1985). Stoecker and Egloff (1987) showed that the clearance rate of adult *A. tonsa* for ciliates varied with prey size and species composition. Large ciliates were generally cleared at faster rates than small ciliates, but non-loricate species were preferred over tintinnine ciliates. In their study, clearance rates of adult *A. tonsa* for *Favella* sp. (65×150 μm) were 7 to 54 ml copepod^{-1} d^{-1} and for a moderate size *Tintinnopsis* sp. (32×65 μm) were 29–67 ml copepod^{-1} d^{-1}. Ayukai (1987) observed clearance rates of female *A. clausi* fed *Helicostomella fusiformis* or *F. taraikaensis* to be 7.4 to 21.5 ml copepod^{-1} d^{-1} and 47.3 ml copepod^{-1} d^{-1}, respectively, and concluded that *A. clausi* preferentially ingests large tintinnine ciliates to co-occurring phytoplankton and/or small tintinnine species. That *E. pectinis* and *H. fusiformis* are cleared at comparable rates by different species of *Acartia* is noteworthy as these tintinnine species have long slender loricae that are very close in size ($\sim 20 \times 150$ μm; Kofoid and Campbell 1929). Should filtration rates of *A. tonsa* on *E. pectinis* in Chesapeake Bay be similar to values reported by Turner and Anderson (1983) for *A. hudsonica,* then grazing by copepods would remove 2 to 18% of the *E. pectinis* standing stock per day. In that case, death of *E. pectinis* due to parasitism would approximate grazing by mesozooplankton. However, at clearance rates reported by Robertson (1983) and Stoecker and Sanders (1985) grazing by copepods would have a greater impact on *E. pectinis* populations than parasitism except during periods of epizootic infestations.

This study indicates that *Duboscquella cachoni* is capable of regulating *Eutintinnus pectinis* populations in eutrophic coastal settings where host densities are sufficiently high to support epizootic events. Data also suggest that these parasites may compete with mesozooplankton predators for tintinnine ciliates and, during epizootic infestation, may have a greater impact on host populations than the metazoan zooplankton. Parasitic dinoflagellates have been reported in a variety of planktonic protozoa including several tintinnine and non-tintinnine ciliate genera (Cachon and Cachon 1987). Whether parasitism has a significant influence on other estuarine species or on ciliate populations in the open ocean, where host densities are considerably lower, has yet to be determined and should prove an interesting topic of research.

Acknowledgements. This research was supported by National Science Foundation (OCE-8515834); Contribution No. 286 of the Chesapeake Bay Institute. We thank L. Reid for illustrations, M. Mallonee for technical assistance, and the Captain and crew of the R. V. "Ridgely Warfield" for ship operations.

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Date of final manuscript acceptance: January 23, 1989.
Communicated by J. Grassle, Woods Hole