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Parasitism of photosynthetic dinoflagellates in a shallow subestuary of Chesapeake Bay, USA

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ABSTRACT: Rhode River (USA) populations of the red-tide dinoflagellates *Gymnodinium sanguineum* Hirasaka, 1922, *Gyrodinium uncatenum* Hulburt, 1957, and *Scrippsiella trochoidea* (Stein) Loeblich III, 1976, were commonly infected by their parasitic relative *Amoebophrya ceratii* Cachon, 1964, during the summer of 1992. Mean infection levels were relatively low, with data for vertically integrated samples averaging 1.0, 1.9, and 6.5% for *G. sanguineum*, *G. uncatenum*, and *S. trochoidea*, respectively. However, epidemic outbreaks of *A. ceratii* (20 to 80% hosts parasitized) occurred in *G. uncatenum* and *S. trochoidea* on several occasions, with peak levels of parasitism associated with decreases in host abundance. Estimates for parasite induced mortality indicate that *A. ceratii* is capable of removing a significant fraction of dinoflagellate biomass, with epidemics in the upper estuary cropping up to 54% of the dominant bloom-forming species, *G. uncatenum*, daily. However, epidemics were usually geographically restricted and of short duration, with daily losses for the 3 host species due to parasitism averaging 1 to 3% over the summer. Thus, *A. ceratii* appears capable of exerting a controlling influence on bloom-forming dinoflagellates of the Rhode River only when conditions are suitable for production of epidemic infections. Interestingly, epidemics failed to occur in multiple dinoflagellate taxa simultaneously, even when alternate host species were present at high densities. This observation, along with laboratory experiments demonstrating that parasites isolated from *G. sanguineum* were unable to infect *G. uncatenum*, *S. trochoidea*, and *Ceratium furca*, suggests that the dinoflagellate taxon *A. ceratii* may represent a cluster of relatively host-specific species.

KEY WORDS: Dinoflagellate · Parasitism · Red tide

INTRODUCTION

Microparasites including viruses, bacteria, fungi, and protozoa have been recorded from marine and freshwater environments for many decades (Chatton 1920, Canter & Lund 1948, Spencer 1955); however, their relative abundance and ecological significance in pelagic food webs have received little attention until recently. Lytic viruses are now thought to play a major role in the mortality of marine bacteria and phytoplankton, with the potential of causing population level changes in host organisms on time scales of hours to days (Bratbak et al. 1993, Nagasaki et al. 1994, Suttle 1994, Suttle & Chan 1995). Similarly, fungal parasites of freshwater diatoms and dinoflagellates have been implicated in mass mortalities of host organisms, suppression or retardation of phytoplankton blooms, and selective effects on species composition leading to successional changes in plankton communities (Canter & Lund 1948, Reynolds 1973, Youngman et al. 1976, Van Donk & Ringelberg 1983, Sommer et al. 1984, Heaney et al. 1988, Kudoh & Takahashi 1990, Bruning et al. 1992). Fewer studies have considered protozoan parasites of planktonic organisms, but at least 1 group of protists, the parasitic dinoflagellates, appears sufficiently common and widespread to be of ecological significance (Drebes 1984, Cachon & Cachon 1987). For example, parasitism by dinoflagellates has been estimated to account for about a third of total mortality in the pelagic copepod *Paracalanus indicus* (Kimmerer & McKinnon 1990) and to crop ciliated protozoa at rates equivalent to grazing pressure from metazoan predators (Coats & Heisler 1989, Coats et al. 1994).

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Dinoflagellates of the genus *Amoebophrya* are frequent parasites of marine protists including radiolaria, ciliates, and other dinoflagellates, with 1 species, *A. rosei*, also infecting chaetognaths and siphonophores. Of the 7 species of *Amoebophrya* recognized by Cachon & Cachon (1987), only *A. ceratii* is known to parasitize its free-living, photosynthetic relatives (Cachon 1964, Cachon & Cachon 1987). This parasite appears to have little host specificity and is broadly distributed in the northern hemisphere, with infections recorded for over 20 species representing 18 genera of dinoflagellates from coastal waters of the Mediterranean Sea, Atlantic and Pacific Oceans, and Chesapeake Bay, USA (Cachon 1964, Taylor 1968, Elbrächter 1973, Nishitani et al. 1985, Fritz & Nass 1992, Coats & Bockstahler 1994). *A. ceratii* has a relatively short generation time (<2 d at 23°C) and a simple life cycle that encompasses an intracellular growth phase followed by an extracellular reproductive phase that culminates in the production of infective dinospores (Coats & Bockstahler 1994). During the intracellular phase, *A. ceratii* consumes the nucleus and cytoplasm of its host, thereby preventing reproduction and eventually killing the infected organism. Infection levels ranging from 2 to 80% have been reported for several host taxa, with epidemic outbreaks believed to exert a controlling influence on the development and dissipation of red tides (Cachon 1964, Nishitani et al. 1985). As a result, some authors have suggested that this parasite might serve as a biological control for toxic dinoflagellate blooms (Taylor & Pollingher 1988).

Early studies of *Amoebophrya ceratii* provided little information about factors that regulate the spread of infections, but generally implied that host abundance and parasite prevalence were positively correlated (Cachon 1964, Taylor 1968). By contrast, Nishitani et al. (1985) argued that high host densities were not a prerequisite for development of epidemics in *Alexandrium* (= *Gonyaulax*) *catenella* and suggested that low nutrient concentrations may contribute to the success of the parasite. Similarly, a negative correlation between parasite prevalence and host abundance was recently reported for *Gymnodinium sanguineum* populations of Chesapeake Bay (Coats & Bockstahler 1994). In that system, maximum levels of parasitism were typically associated with low concentrations of *G. sanguineum* near the pycnocline, several meters below dense surface accumulations of lightly infected host assemblages. Additionally, late infections (i.e. just prior to the extracellular reproductive phase of the parasite) were over-represented in host populations at depth, suggesting that parasitized cells either sank out of the surface community or failed to return to the surface following downward migration at night. Thus, interactive effects of organism behavior and stability of the water column during summer appear to vertically segregate infective stages of *A. ceratii* from high concentrations of uninfected hosts and may thereby limit parasite prevalence in the deep central channel of Chesapeake Bay.

If proximity of late infections to uninfected hosts is critical to the success of *Amoebophrya ceratii*, then this parasite should have a greater influence on host population dynamics in shallow and/or more turbulent environments that maintain greater contact between infected and uninfected individuals. To explore that hypothesis, we examined temporal and spatial aspects in parasitism of 3 host species, *Gymnodinium sanguineum*, *Gyrodinium uncatenum*, and *Scrippsiella trochoidea*, in the shallow Rhode River subestuary of Chesapeake Bay. We also used species-specific distributional patterns and infection levels, along with experimental data, to consider host preference and/or specificity of *A. ceratii*.

MATERIALS AND METHODS

Study site. The Rhode River is a shallow oligo- to mesohaline embayment of the Chesapeake Bay located on the western shore of Maryland, USA (38° 52' N, 76° 32' W; Fig. 1). It is contiguous with Muddy Creek, the primary source of freshwater for the subestuary, and joins the West River to form a common mouth on the mainstem of Chesapeake Bay. The subestuary has an area of 550 ha and a mean depth of 2 m, with salinity ranging from 0‰ in Muddy Creek during spring to <20‰ at the mouth of the Rhode and West Rivers during fall. Dissolved nutrients are maintained at relatively high background concentrations (Jordan et al. 1991), with periodic increases reflecting runoff from the local watershed and/or remote inputs from the Susquehanna River at the head of Chesapeake Bay (Gallegos et al. 1992). Increased nitrate loading associated with local summer storms stimulates the development of dense dinoflagellate blooms (10^3 to 10^5 cells ml^{-1}) in the upper estuary that are generally dominated by large species, including *Gymnodinium* spp., *Gyrodinium uncatenum*, and *Scrippsiella trochoidea* (Gallegos 1992).

Collection and analysis of field samples. Vertically integrated samples for documenting temporal and spatial occurrence of *Amoebophrya ceratii* infections in Rhode River populations of *Gymnodinium sanguineum*, *Gyrodinium uncatenum*, and *Scrippsiella trochoidea* were obtained at weekly intervals from spring to early fall 1992, with less frequent sampling (biweekly to monthly) in late fall and winter. On each date, samples were collected at 6 stations along a transect from 1.4 km downstream to 5.2 km upstream of

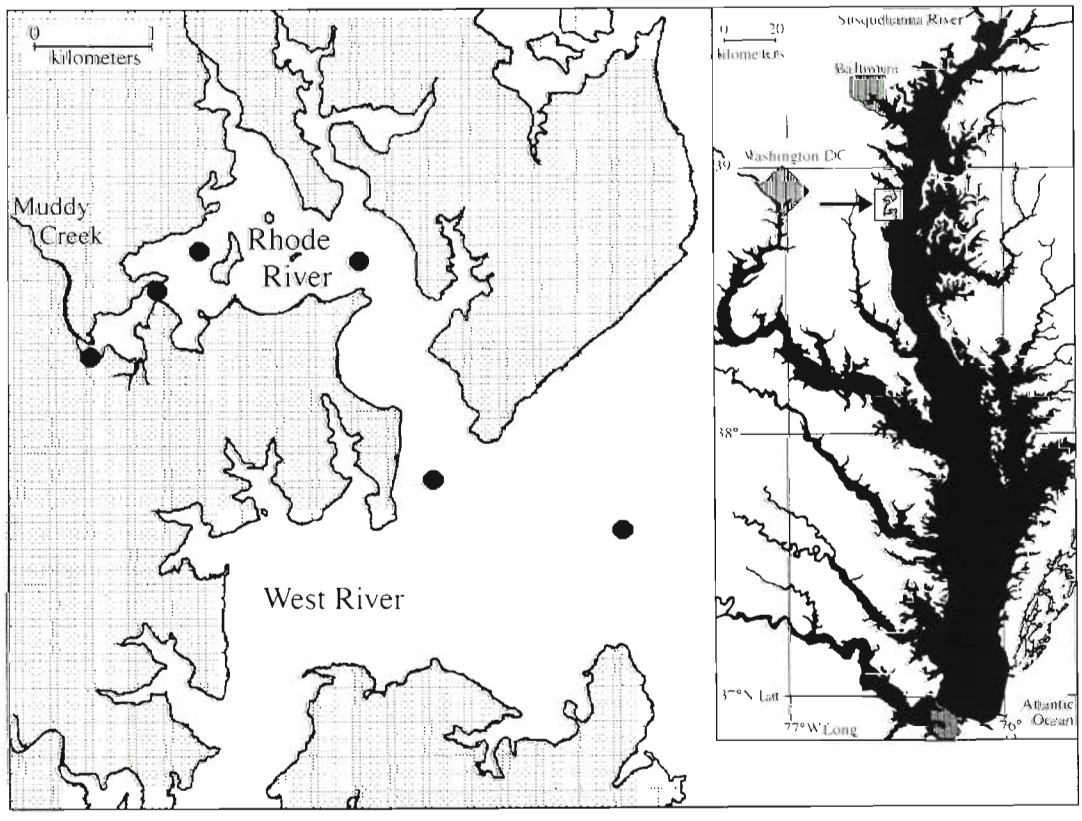

Fig. 1 Routine stations (●) in the Rhode River, USA, with inset showing location of the subestuary on the western shore of Chesapeake Bay

the mouth of the Rhode River (Fig 1); the union of the subestuary with the West River is considered the mouth of the Rhode River Integrated water-column samples were obtained by steadily lowering a 2 l Labline Teflon sampler to just above the sediment-water interface and then gradually returning the device to the surface before the sample reservoir was completely filled. Subsamples for identification and enumeration of free-living dinoflagellates were preserved using 1% acid Lugol's solution and later examined by inverted microscopy following procedures of Gallegos (1992). For determining parasite prevalence, subsamples were fixed in a modified Bouin's solution (Coats & Heinbokel 1982), and 10 to 50 ml aliquots were subsequently stained by the quantitative protargol staining (QPS) technique of Montagnes & Lynn (1993). Parasite prevalence was determined as previously reported (Coats & Bockstahler 1994), with at least 100 individuals examined for each host species present at ≥0.5 cells ml^{-1}

Integrated Rhode River values for host abundance and parasite prevalence were calculated as volume-weighted averages using station data and water volumes for discrete portions of the subestuary (segments 1 to 5) as given by Jordan et al. (1991). Parasite induced mortality of host species was estimated as: proportion of host population killed d^{-1} = (parasite prevalence)(infection time)$^{-1}$ Infection time, 1.65 d at 23°C (Coats & Bockstahler 1994), was assumed to be the same for all host species and was corrected for ambient temperature using a Q_{10} of 2.

Laboratory cultures and experiments. *Ceratium furca*, *Gymnodinium sanguineum*, and *Gyrodinium uncatenum*, isolated from Chesapeake Bay by D.W.C., and *Scrippsiella trochoidea*, UTEX strain LB 1017, were cultured in f/2-Si medium (Guillard & Ryther 1962) formulated using 15‰ Bay water supplemented with 5% (v/v) soilwater [GR+] (Starr & Zeikus 1993). Stock cultures were maintained at 23°C on a 14:10 h light:dark cycle, with cool-white fluorescent bulbs providing ~100 µE m^{-2} s^{-1}. *Amoebophrya ceratii* was established in culture by adding a single cell of *G. sanguineum* in late-stage infection to an exponentially growing culture of the same host species. Stock cultures of the parasite were subsequently maintained by transferring aliquots of infected host culture to uninfected *G. sanguineum* stocks at ~3 d intervals.

Transmission of infections in *Gymnodinium sanguineum* and the ability of *Amoebophrya ceratii* (ex *G. sanguineum*) to infect *Ceratium furca*, *Gyrodinium un-*

catenum, and *Scrippsiella trochoidea* were experimentally examined by exposing uninfected cultures to recently formed dinospores, the infective dispersal stage of the parasite. Dinospores (2.5×10^4 ml^{-1}) were separated from hosts by size-fractionation of 2 d old infected *G. sanguineum* culture using a 12 µm Nucleopore filter. Aliquots of dinospores and uninfected, exponentially growing dinoflagellate cultures were added to 20 ml scintillation vials to yield replicate 10 ml volumes for each of 10 treatments represented by: (1) *G. sanguineum* at 1×10^3 cells ml^{-1}, with dinospore density adjusted over a range from 10^2 to 10^4 ml^{-1} (6 treatments); (2) *C. furca*, *G. uncatenum*, and *S. trochoidea* separately, at 1×10^3 cells ml^{-1}, with 5×10^3 dinospores ml^{-1}; and (3) a mixture of the 4 'host' species at 2.5×10^2 ml^{-1} each, with *A. ceratii* dinospores at 5×10^2 ml^{-1}. All vials were lightly capped, incubated for 24 h under conditions described above, and then preserved with Bouin's solution. Fixed samples were processed by QPS and the percentage of 'hosts' infected by *A. ceratii* determined by examining the first 100 cells encountered on each filter.

Table 1. *Amoebophrya ceratii* infections in Rhode River populations of *Gyrodinium uncatenum*, *Scrippsiella trochoidea* and *Gymnodinium sanguineum* from May to October 1992. Data listed as mean ± standard error (range)

Host species	Host abundance (cells ml^{-1})	Parasite prevalence (%)	Percent host population removed d^{-1}
Vertically integrated samples[a]			
G. uncatenum (n = 135)	1800 ± 360 (13–34000)	1.9 ± 0.9 (0–81)	1.1 ± 0.5 (0–54)
S. trochoidea (n = 74)	200 ± 42 (13–2700)	6.5 ± 0.8 (0–33)	4.0 ± 0.5 (0–18)
G. sanguineum (n = 81)	11.6 ± 1.7 (0.5–61)	1.0 ± 0.2 (0–14)	0.7 ± 0.2 (0–13)
Cumulative (n = 153)	1700 ± 320 (1.3–35000)	2.4 ± 0.7 (0–81)	1.4 ± 0.4 (0–44)
Volume-weighted averages for the estuary[b]			
G. uncatenum (n = 26)	370 ± 87 (43–2000)	1.7 ± 0.8 (0–18)	1.0 ± 0.5 (0–12)
S. trochoidea (n = 23)	32 ± 5.9 (0–120)	5.1 ± 0.8 (0–20)	3.2 ± 0.6 (0–13)
G. sanguineum (n = 18)	12 ± 2.7 (0–38)	1.0 ± 0.2 (0–3)	0.6 ± 0.2 (0–2)
Cumulative (n = 26)	410 ± 90 (56–2100)	1.7 ± 0.5 (0–12)	1.0 ± 0.2 (0–5)

[a] For samples where host abundance was ≥0.5 ml^{-1}
[b] For dates when abundance of 1 or more host species was ≥0.5 ml^{-1} for at least 1 station

RESULTS

Host and parasite distributions

Gymnodinium sanguineum, *Gyrodinium uncatenum*, and *Scrippsiella trochoidea* represented a progressively larger fraction of total dinoflagellate abundance and accounted for more than 70% of dinoflagellate biomass along the axis of the Rhode River from late spring through fall of 1992 (Fig. 2). Collectively, these species averaged about 400 cells ml^{-1} throughout the estuary from May to October, with peak volume-weighted abundance for the Rhode River system reaching 2100 cells ml^{-1} (Fig. 3A, Table 1). *G. uncatenum* was the most prominent of these species and occasionally exceeded 30000 cells ml^{-1} in the upper estuary (Fig. 4A). *S. trochoidea* was also more prevalent in the mid- to upper Rhode River, where its maximum densities approached 3000 cells ml^{-1} (Fig. 4B, Table 1), while *G. sanguineum* was primarily restricted to the mid- to lower portion of the estuary and never exceeded 100 cells ml^{-1} (Fig. 4C). The 3 species also showed temporal differences in peak abundance, with *G. uncatenum* producing multiple blooms between late spring and fall, *S. trochoidea* forming maxima in early to mid summer, and *G. sanguineum* reaching peak concentrations in late summer and fall (Figs. 3B–D & 4).

Combined infection levels for *Gymnodinium sanguineum*, *Gyrodinium uncatenum*, and *Scrippsiella trochoidea* varied widely during the summer with daily averages for the estuary ranging from 0 to 12% (Fig. 3A,

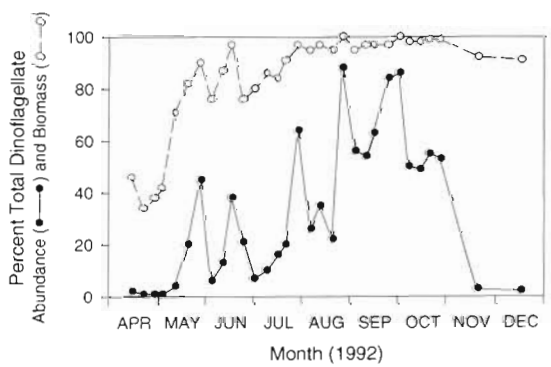

Fig. 2. Proportion of total dinoflagellate abundance (●) and biomass (○) in the Rhode River represented by *Gyrodinium uncatenum*, *Scrippsiella trochoidea*, and *Gymnodinium sanguineum* during 1992. Data represent integrated Rhode River values calculated as volume-weighted averages using station data and water volumes for discrete portions of the subestuary

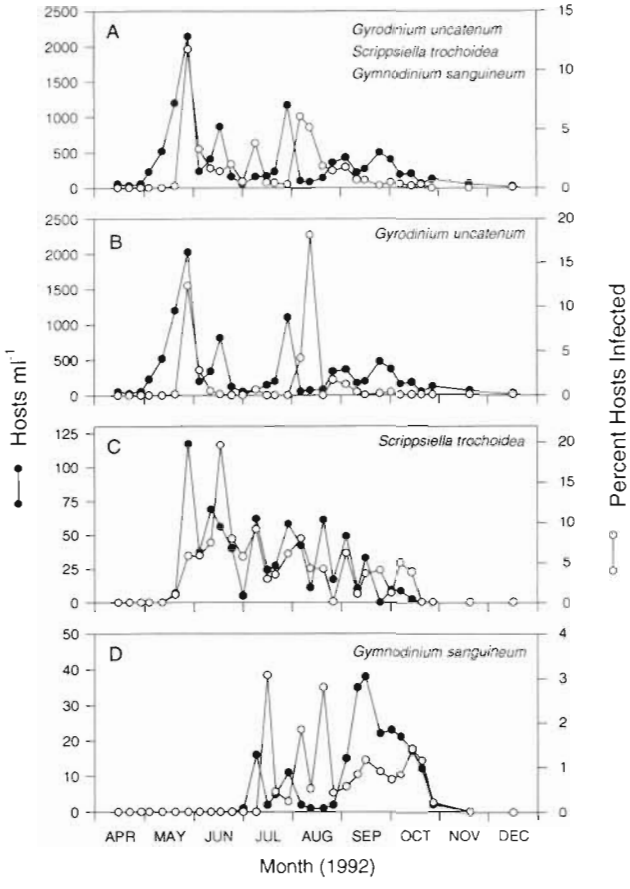

Fig. 3. Integrated Rhode River values for host abundance (●) and parasite prevalence (○) during 1992 calculated as volume-weighted averages using station data and water volumes for discrete portions of the subestuary. (A) Combined data for 3 of the most predominant species. (B) *Gyrodinium uncatenum*. (C) *Scrippsiella trochoidea*. (D) *Gymnodinium sanguineum*

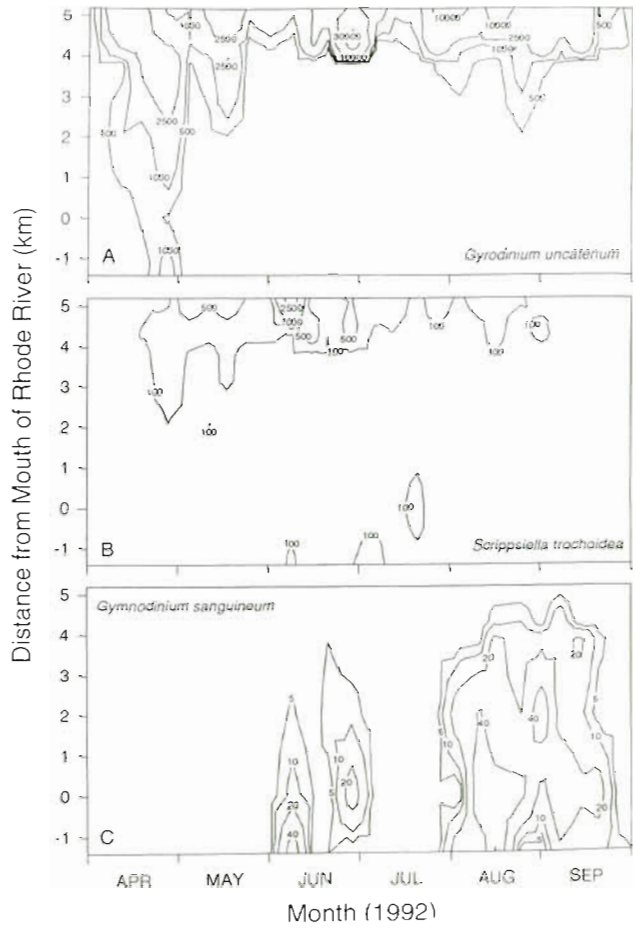

Fig. 4. Distributional contours for abundance (cells ml^{-1}) of (A) *Gyrodinium uncatenum*, (B) *Scrippsiella trochoidea*, and (C) *Gymnodinium sanguineum* in the Rhode River during 1992. *y*-axis represents sample distance upstream (positive values) or downstream (negative values) from the confluence of the Rhode and West Rivers

Table 1). Parasitism of individual species showed similar fluctuations, with maximum infection levels coinciding with or following temporal peaks in host abundance (Fig. 3B–D). While average parasite prevalence in the estuary never exceeded 20% for any of the species, localized epidemics occurred on several occasions, with infection levels of 40 to 80% persisting for short periods (Fig. 5A–C). Peak infection levels in *G. uncatenum* (60 to 80%) were of relatively short duration, and were either followed by a localized decline in host abundance (e.g. in the lower estuary during early May) or were associated with locally depressed host densities between bloom events (e.g. in the upper estuary during mid July). Highest infection levels in *S. trochoidea* (30 to 40%) were also associated with reduced host abundance between bloom events (e.g. in the upper estuary during late May), while less pronounced epidemics (~20%) in the lower estuary occurred at low host densities and were not clearly linked to changes in host populations.

Assuming that generation time of *Amoebophrya ceratii* is independent of host species, then parasitism of *Gymnodinium sanguineum*, *Gyrodinium uncatenum*, and *Scrippsiella trochoidea* removed about 1% of cumulative host standing stock d^{-1} throughout the estuary in summer (Table 1). *G. sanguineum* appeared to be least affected by *A. ceratii*, with ≤2% of its volume-weighted abundance removed d^{-1}, while comparable values for *G. uncatenum* and *S. trochoidea* reached 12 to 13%. Localized epidemics appeared to have a more pronounced impact on host populations, with parasite induced mortality removing as much as 54, 18 and 13% of host stock d^{-1} for the 3 species, respectively (Table 1).

In most cases, epidemic outbreaks corresponded geographically with high host abundance, but rarely occurred in more that 1 host species simultaneously (cf. Figs. 4 & 5). For example, high infection levels

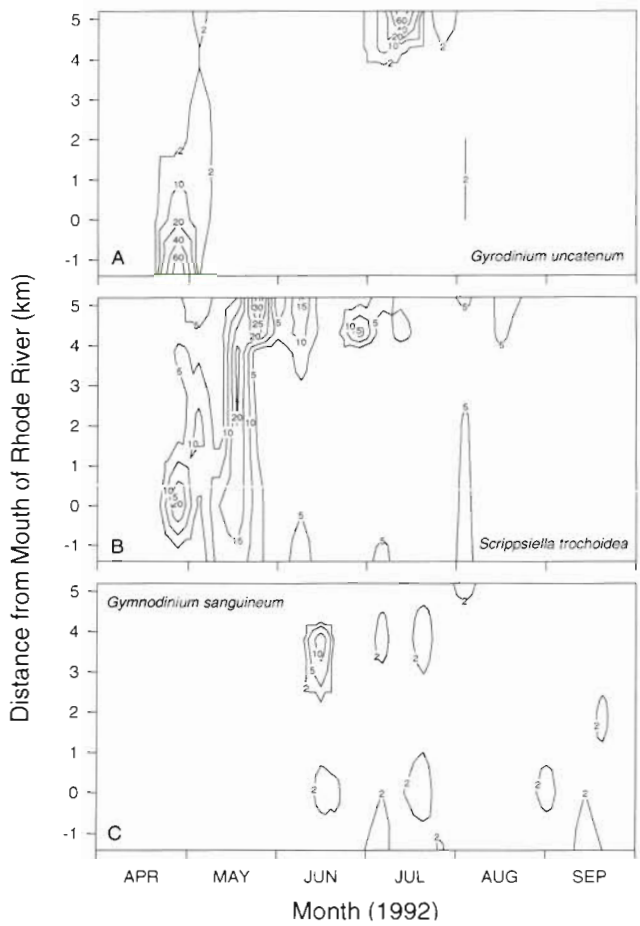

Fig. 5. Distributional contours for parasite prevalence (percent hosts infected) in Rhode River populations of (A) *Gyrodinium uncatenum*, (B) *Scrippsiella trochoidea*, and (C) *Gymnodinium sanguineum* in 1992. *y*-axis as in Fig. 4

(15 to 30%) were present in *Scrippsiella trochoidea* throughout much of the Rhode River in May, while *Gyrodinium uncatenum*, which was also present at high concentrations (500 to 2500 cells ml^{-1}), was relatively unaffected (infection level < 2%). Similarly, an epidemic in *G. uncatenum* in the upper estuary during July was not accompanied by increased parasitism in other host species. Only on 1 occasion were epidemic outbreaks temporally coincident in multiple dinoflagellate taxa (viz *G. uncatenum* and *S. trochoidea* during late April; Fig. 5A, B), and, in that instance, centers of maximum infection for the 2 host species were spatially separated.

Host specificity

In laboratory studies, dinospores of *Amoebophrya ceratii* readily infected hosts of the same species, with infection levels in *G. sanguineum* increasing hyperbolically as a function of dinospore abundance (Fig. 6A). At low dinospore densities ($\leq 1 \times 10^3$ ml^{-1}), each infected host contained only 1 parasite; however, parasite load [i.e. parasites (infected host)$^{-1}$] increased linearly at higher dinospore abundances (Fig. 6B), with as many as 8 parasites observed in individual host cells. Thus, while the mean number of hosts infected dinospore^{-1} decreased from 0.200 to 0.092 over the range of 10^2 to 10^4 dinospores ml^{-1} (data not plotted), the percentage of dinospores that successfully invaded host cells remained relatively constant (Fig. 6; mean for all treatments: 19.4 ± 1.1 SE, n = 6).

Amoebophrya ceratii failed to infect *Ceratium furca*, *Gyrodinium uncatenum*, and *Scrippsiella trochoidea* when incubated singly at dinospore densities sufficient to promote high infection levels in *G. sanguineum* (Table 2). Infections also failed to develop in *C. furca*, *G. uncatenum*, and *S. trochoidea* when incubated in mixed species assemblages in which *G. sanguineum* became moderately infected (Table 2). Interestingly, the percentage of available dinospores that invaded host (*G. sanguineum*) cells in the mixed species treatment (18.8 ± 3.2 SE, n = 2) was the same as that observed in single species incubations reported above.

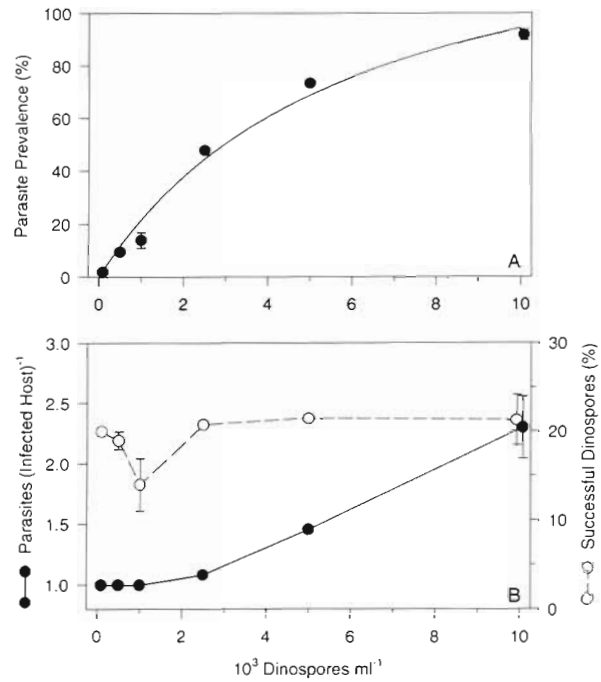

Fig. 6. Infection of *Gymnodinium sanguineum* by *Amoebophrya ceratii* in culture. (A) Percent hosts parasitized as a function of dinospore density. (B) Mean number of parasites present inside infected host cells (●) and percent of dinospores that successfully invaded host organisms (○). Error bars represent standard error of means where n = 2

Table 2. Infection of dinoflagellate species following 24 h exposure to dinospores of *Amoebophrya ceratii* (ex *Gymnodinium sanguineum*); mean ± standard error (n = 2)

Host species	Hosts ml^{-1}	Dinospores ml^{-1}	% hosts infected	Parasite load	% successful dinospores
Gymnodinium sanguineum	1×10^3	5×10^3	73.5 ± 0.5	1.5 ± 0.03	21.5 ± 0.3
Ceratium furca	1×10^3	5×10^3	0	0	0
Gyrodinium uncatenum	1×10^3	5×10^3	0	0	0
Scrippsiella trochoidea	1×10^3	5×10^3	0	0	0
Mixed species assemblage					
G. sanguineum	2.5×10^2	5×10^2	34 ± 5.0	1.1 ± 0.03	18.8 ± 3.2
C. furca	2.5×10^2		0	0	
G. uncatenum	2.5×10^2		0	0	
S. trochoidea	2.5×10^2		0	0	

Thus, the presence of other potential host species did not affect the success of *A. ceratii* in parasitizing *G. sanguineum*.

DISCUSSION

Spatial and temporal patterns in the abundance of bloom-forming dinoflagellates of the Rhode River and associated prevalence of the intracellular parasite *Amoebophrya ceratii* were consistent with earlier reports suggesting periodic regulation of red-tide species through parasitism (Cachon 1964, Nishitani et al. 1985). Infection levels were most pronounced in *Gyrodinium uncatenum* and *Scrippsiella trochoidea*, with epidemic outbreaks of *A. ceratii* (20 to 80% of hosts parasitized) associated with short-lived blooms (1 to 2 wk duration) on several occasions. Estimates for parasite induced mortality indicate that *A. ceratii* is capable of removing a significant fraction of host biomass, with epidemics in the upper estuary cropping up to 54% of the dominant bloom-forming species, *G. uncatenum*, daily. Since infected hosts do not undergo cell division (Coats & Bockstahler 1994), peak levels of parasitism would offset host reproduction equivalent to about 1 division d^{-1}, near the maximal growth rate for most dinoflagellate species (Banse 1982). Under nutrient replete conditions, *G. uncatenum* exhibits temperature dependent growth ranging from 0.1 to 0.7 divisions d^{-1} between 12 and 30°C (Anderson et al. 1985). Thus, *A. ceratii* appears capable of exerting a controlling influence on dinoflagellates in the Rhode River, with the potential of causing rapid declines in host abundance when conditions become suboptimal for growth (e.g. with reduced nutrient input from terrestrial runoff or nutrient depletion following bloom formation). However, epidemics were usually localized to relatively small portions of the estuary, with parasitism by *A. ceratii* having less effect on host populations at the system level. During epidemic outbreaks, 12 to 13% of *G. uncatenum* and *S. trochoidea* were removed d^{-1} throughout the estuary, but the impact of parasitism averaged over the summer only represented a daily loss of 1 to 3% for these species.

Coats & Bockstahler (1994) suggested that parasitism of *Gymnodinium sanguineum* by *Amoebophrya ceratii* in the mainstem of Chesapeake Bay was limited by the vertical separation of infected and uninfected hosts at a critical period in the parasite's life cycle. If true, then infection levels might be expected to increase in systems that prevent physical separation of infected and uninfected hosts. Mean water-column prevalence of *A. ceratii* in Rhode River populations of *G. sanguineum* (mean ± SE: 1.0 ± 0.2%, n = 81) was slightly less than that reported for the mainstem of Chesapeake Bay (2.7 ± 0.3%, n = 60; Coats & Bockstahler 1994), with maximum values for the 2 areas being comparable, 13 and 11%, respectively. Thus, infection levels in *G. sanguineum* do not appear to be substantially influenced by increased proximity of infected and uninfected cells resulting from the shallower environment of the Rhode River. However, *G. sanguineum* abundance in the Rhode River during 1992 (<100 cells ml^{-1}) was substantially less than that previously observed in the mainstem of Chesapeake Bay (bloom concentrations over 10^3 cells ml^{-1}; Coats & Bockstahler 1994) and, thus, data on infection levels may not provide a good test for our hypothesis. For example, *A. ceratii* may require threshold concentrations of host organisms to generate heavy infections, with the failure of epidemic outbreaks to develop in Rhode River populations of *G. sanguineum* reflecting the relatively low densities of that species present during 1992. That epidemics did occur in *Gyrodinium uncatenum* and *Scrippsiella trochoidea* circumstantially supports our expectation that parasitism among dinoflagellates should be enhanced in shallower regions of Chesapeake Bay; however, the high population densities attained by these species in the Rhode

River may be of equal or greater importance than physical constraints in facilitating the spread of infections. Unfortunately, such consideration must remain largely speculative, as data on parasitism of *G. uncatenum* and *S. trochoidea* in the mainstem of Chesapeake Bay are not currently available.

The absence of concurrent epidemics in multiple host species may reflect the sequential spread of *Amoebophrya ceratii* in different host taxa, perhaps due to limitations imposed by changes in host availability or host preference/selectivity. However, the presence of heavy infections in *Scrippsiella trochoidea* (15 to 30%) throughout the Rhode River in May, when dense populations of *Gyrodinium uncatenum* (500 to 2500 cells ml^{-1}) were relatively unaffected (parasite prevalence < 2%), argues against this interpretation. Alternatively, earlier reports that free-living photosynthetic dinoflagellates are only parasitized by a single species of *Amoebophrya* may be incorrect. In the latter case, temporal and spatial patterns in epidemic infections of Rhode River dinoflagellates may reflect the spread of different parasite species as particular host taxa become more abundant. Interestingly, the description of *A. ceratii* given by Cachon (1964) included some morphological variations that could be interpreted as species distinctions. For example, infections develop in the nucleus of some host taxa, including *Gymnodinium sanguineum* (Coats & Bockstahler 1994) and *S. trochoidea* (authors' pers. obs.), but occur intracytoplasmically in other species (e.g. *G. uncatenum*; authors' pers. obs.). While not conclusive, developmental differences among parasites suggest that dinoflagellates of the Rhode River are parasitized by more than 1 species of *Amoebophrya*. Further support for this contention is provided by cross-infection experiments that demonstrate the inability of parasites isolated from *G. sanguineum* to infect *G. uncatenum*, *S. trochoidea*, and *Ceratium furca* under conditions used here. Thus, our estimates for parasite induced mortality for *G. uncatenum* and *S. trochoidea* may be biased, as calculations were based on parasite development time in *G. sanguineum*, with the possibility of significant differences in timing of developmental events existing for other host species.

When making preliminary observations on parasitism in the toxin-producing dinoflagellate *Alexandrium* (= *Gonyaulax*) *catenella*, Taylor (1968) first suggested that *Amoebophrya ceratii* might serve as an effective biological control for red tides. Nishitani et al. (1985) later dismissed that possibility, arguing that the lack of host specificity made *A. ceratii* an undesirable, if not impossible, means of altering *A. catenella* abundance. If, however, multiple *Amoebophrya* spp., each exhibiting some degree of host specificity, have indeed been incorrectly classified as *A. ceratii*, then parasitic interactions in red-tide organisms would be far more complicated than previously recognized. In that situation, Taylor's suggestion would seem to warrant reexamination.

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