

NOTE

Grazing of two euplotid ciliates on the heterotrophic dinoflagellates *Pfiesteria piscicida* and *Cryptoperidiniopsis* sp.

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ABSTRACT: *Pfiesteria piscicida* and *Cryptoperidiniopsis* spp. are common co-occurring heterotrophic dinoflagellates in estuaries along the Atlantic coast of the United States. We isolated *P. piscicida*, *Cryptoperidiniopsis* sp., and 2 benthic ciliates (*Euplotes vannus* and *E. woodruffi*) from North Inlet estuary, South Carolina, and examined the growth and grazing properties of the ciliates on cultures of the dinoflagellates maintained with cryptophyte (*Storeatula major*) prey. Ciliate growth and grazing parameters on cryptophyte monocultures and mixed diets of cryptophytes and *P. piscicida* were significantly higher with *E. woodruffi* than *E. vannus*. Also, the net grazing impact of *E. woodruffi* on *P. piscicida* prey was higher than the impact on *Cryptoperidiniopsis* sp., while the *E. vannus* grazing effect did not differ with dinoflagellate prey. The results indicate the potential for effective predatory control by euplotid ciliates on nontoxic *P. piscicida* and *Cryptoperidiniopsis* sp. under defined laboratory conditions.

KEY WORDS: Benthic ciliates · *Cryptoperidiniopsis* · *Euplotes* · Heterotrophic dinoflagellates · Microzooplankton grazing · *Pfiesteria*

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Harmful algal blooms (HABs) attributed to toxic dinoflagellates at times may result in mass mortality of aquatic organisms, including phytoplankton (Ucko et al. 1989), zooplankton (Spero & Moree 1981), invertebrates (Tangen 1977), and shellfish and finfish (CENR 2000). Two species of heterotrophic dinoflagellates, *Pfiesteria piscicida* and *P. shumwayae* (the Toxic *Pfiesteria* Complex, TPC), have been implicated as causative agents in several fish kill or lesion events in North Carolina and Maryland estuaries over the last decade (Burkholder & Glasgow 1997, Glasgow et al. 2001). Their toxins have been linked to human health problems (Schmechel & Koltai 2001), and TPC out-

breaks have been associated with millions of dollars of lost revenue to the fisheries and tourism industries (Burkholder & Glasgow 1997, CENR 2000).

Increased awareness of *Pfiesteria* spp.'s potential impact on environmental and human health has led to several studies on the dinoflagellates' trophic dynamics. Ingestion of *P. piscicida* by copepods, rotifers, or benthic ciliates has been reported (Burkholder & Glasgow 1995, Mallin et al. 1995). More recently, Stoecker et al. (2000) added 5-chloromethylfluorescein diacetate-stained *P. piscicida* cultures (grown nontoxically) to surface water samples from several sites in the Chesapeake Bay, and quantified ingestion and clearance rates by natural populations of several tintinnids and oligotrichous ciliates. The authors concluded that grazing pressure by these groups was often high enough to prevent net population growth of the dinoflagellate, based on comparisons to laboratory estimates of *P. piscicida* growth rates. In a follow-up study using the same staining technique (Burkholder et al. 2001b, Stoecker et al. 2002), natural community microzooplankton grazing on *P. piscicida* was found to be significantly lower when the dinoflagellate was actively toxic (i.e. 'TOX-A', Burkholder 2001a,b) than when temporarily nontoxic ('TOX-B') or non-inducible with respect to toxicity ('NON-IND'). That is, the susceptibility of *P. piscicida* to grazing was lowest in cells that were actively toxic.

The importance of ciliates to predatory control of dinoflagellates is well established, including their role as grazers during toxic or nontoxic dinoflagellate blooms (Stoecker et al. 1981, Hansen 1995, Jeong et al. 1999). In fact, selective grazing by ciliates on dinoflagellates has been shown (Stoecker et al. 1981, 1986, Gifford 1985). Unlike metazoan predators of dinofla-

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gellates (Turner & Anderson 1983, Burkholder & Glasgow 1995, Mallin et al. 1995), ciliates are capable of reproducing rapidly enough to respond to increases in dinoflagellate abundance, and therefore are believed to be capable of suppressing dinoflagellate bloom formation and limiting bloom magnitude (Sherr & Sherr 1994, Strom & Morello 1998, Montagnes & Lessard 1999). Typically, studies of ciliate grazing impacts on dinoflagellates have focused on tintinnids or oligotrichs, but little is known about potential predatory control by benthic ciliates such as euplotids.

This study examined the grazing properties of 2 benthic ciliates (*Euplotes vannus* and *E. woodruffi*) on *Pfiesteria piscicida* and *Cryptoperidiniopsis* sp., another heterotrophic dinoflagellate that morphologically resembles and often co-occurs with *Pfiesteria* spp. *E. vannus* and *E. woodruffi* are hypotrich ciliates commonly found in a number of aquatic environments, including salt marshes, marine surface and benthic habitats, and estuarine planktonic and bottom waters (Capriulo et al. 1988, Dolan & Coats 1990, 1991a,b, Dolan 1991). Along with another predatory ciliate, *Didinium* spp., *E. woodruffi* was found to comprise up to 20 and 25% of total ciliate biomass in Chesapeake Bay bottom and transition waters, respectively (Dolan 1991). Dolan (1991) also considered *E. woodruffi* grazing to be a potentially important regulatory factor in the population dynamics of a microphagous ciliate, *Pleuronema* sp. In our study, *E. vannus*, *E. woodruffi*, *P. piscicida*, and *Cryptoperidiniopsis* sp. were isolated from North Inlet estuary (Georgetown, South Carolina, USA), a shallow, tidally driven estuary characterized by high mixing and tidal scouring, and therefore close associations between planktonic and benthic microbial communities (Lewitus et al. 2002, Wetz et al. 2002). Here, we compare grazing properties under defined laboratory conditions as a first step towards assessing potential predatory control by euplotid ciliates on *Cryptoperidiniopsis* sp. and NON-IND *P. piscicida* zoospores.

Materials and methods. North Inlet estuary, near Georgetown, South Carolina, USA, comprises 32 km² of pristine tidal creeks, salt marsh, and mudflats. Semi-diurnal tides exchange 55% of the Inlet's water with the coastal ocean (Kjerfve et al. 1991). The tidal creeks are vertically well-mixed, salinity is typically high (32 to 35‰), and water temperature varies from 9 to 31°C (Dame et al. 1986). North Inlet is a shallow estuary, with an average channel depth of 3 m and a mean tidal range of 1.4 m (D. White unpubl. data).

Pfiesteria piscicida and *Cryptoperidiniopsis* sp. were isolated in fall 1997 from fish-mortality bioassay aquariums that were inoculated with North Inlet estuarine sediment in June 1997 (Lewitus et al. 2002). Their identity was confirmed by scanning electron micro-

scopic analysis, PCR amplification and fluorescent *in situ* hybridization (FISH) analyses. The ciliated protozoans *Euplotes vannus* and *E. woodruffi* were isolated from North Inlet surface water collected during a 'red tide' bloom in spring 1999 formed by *Kryptoperidinium* sp. (Kempton et al. 2002). The ciliates were identified after quantitative protargol staining. The cryptophyte *Storeatula major* HP9001 was isolated from the Choptank River, a subestuary of Chesapeake Bay, by A. J. Lewitus in 1990. All test species were maintained in f/2-Si media (Guillard 1975) at 30‰, and the dinoflagellates maintained with *S. major* prey. Experiments were conducted at 23°C under a 12:12 h light:dark cycle at 70 μE m⁻² s⁻¹.

Control treatments consisted of replicate cultures of *Euplotes vannus*, *E. woodruffi*, *Pfiesteria piscicida*, or *Cryptoperidiniopsis* sp., each fed *Storeatula major*, and triplicate cultures of *S. major* alone. Test treatments consisted of *P. piscicida* or *Cryptoperidiniopsis* sp. added to triplicate flasks of *E. vannus* or *E. woodruffi*. Cultures were time-course subsampled and fixed with 2% cold glutaraldehyde. Dinoflagellate zoospore or cryptophyte abundance was determined using a 0.5 mm deep hemacytometer. Ciliate counts were performed using 0.25 ml of Lugol's fixed sample in a Palmer-Maloney chamber.

Growth and grazing properties were determined during the period in which predator cells were in exponential growth (Dolan & Coats 1991a, Jacobson & Anderson 1993). All estimates of euplotid grazing parameters were based on the first 48 h interval. Specific growth rate, μ (d⁻¹), was calculated following Heinbokel (1978). Ingestion rate of dinoflagellates on cryptophyte prey was determined as:

$$I = (g \times P) \times D^{-1}$$

where g (specific grazing rate) = $\mu_n - \mu_w$, the difference between net prey growth rate without grazers (μ_n) and with grazers (μ_w), P (mean prey concentration) = $(P_{t1} - P_{t0}) \times (\ln[P_{t1} \times P_{t0}^{-1}])^{-1}$, and D (mean predator concentration) = $(D_{t1} - D_{t0}) \times (\ln[D_{t1} \times D_{t0}^{-1}])^{-1}$. Clearance rate was calculated as:

$$C = I \times P^{-1}$$

Because ciliates ingested cryptophytes and dinoflagellates, the direct and indirect effects of ciliate grazing on dinoflagellate populations were not differentiated in this study. Therefore, the effect of ciliates on dinoflagellate population growth was calculated based on the equation for ingestion rate above, but the parameter was termed 'net grazing impact' (NGI), which represents the number of dinoflagellates reduced per ciliate per day. Despite the limitations in quantitatively discriminating between dinoflagellate and cryptophyte uptake, qualitative observations from light and epiflu-

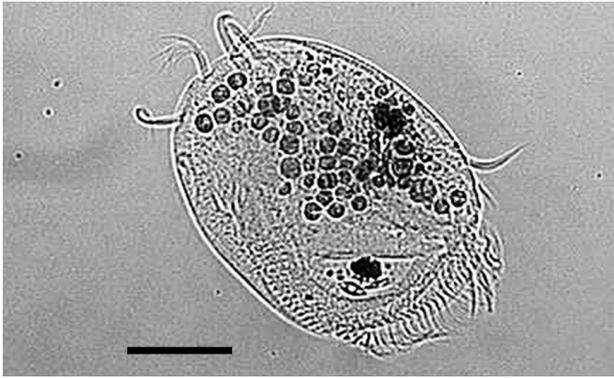


Fig. 1. *Euplotes woodruffi*. Light micrograph of the ciliate with several ingested cells of heterotrophic dinoflagellate *Pfiesteria piscicida*. Scale bar = 25 μm

orescence microscopic inspection of glutaraldehyde-fixed samples indicated that both ciliate species were capable of ingesting large numbers of dinoflagellate prey (e.g. Fig. 1). Statistical significance between means was tested using *t*-tests at the 5% confidence level.

Results. *Pfiesteria piscicida* and *Cryptoperidiniopsis* sp. zoospore abundance increased when fed *Storeatula major*, achieving maximum abundance at 72 and 96 h, respectively, followed by a rapid decrease in abundance (data not shown). The specific growth rate of *P. piscicida* was significantly greater than that of *Cryptoperidiniopsis* sp. (Table 1), while ingestion and clearance rates were not significantly different between the dinoflagellates (Table 1).

When grown with *Storeatula major* as the only prey item, *Euplotes vannus* and *E. woodruffi* abundance increased from the onset of the experiment (Fig. 2), but *E. woodruffi* had a greater specific growth rate than *E. vannus* (Table 1). *E. woodruffi*'s mean ingestion rate was ca. 5-fold higher, and clearance rate >17-fold higher, than that of *E. vannus* feeding on *S. major* (Table 1).

The mean specific growth rate of *Euplotes vannus* or *E. woodruffi* did not differ significantly with prey type

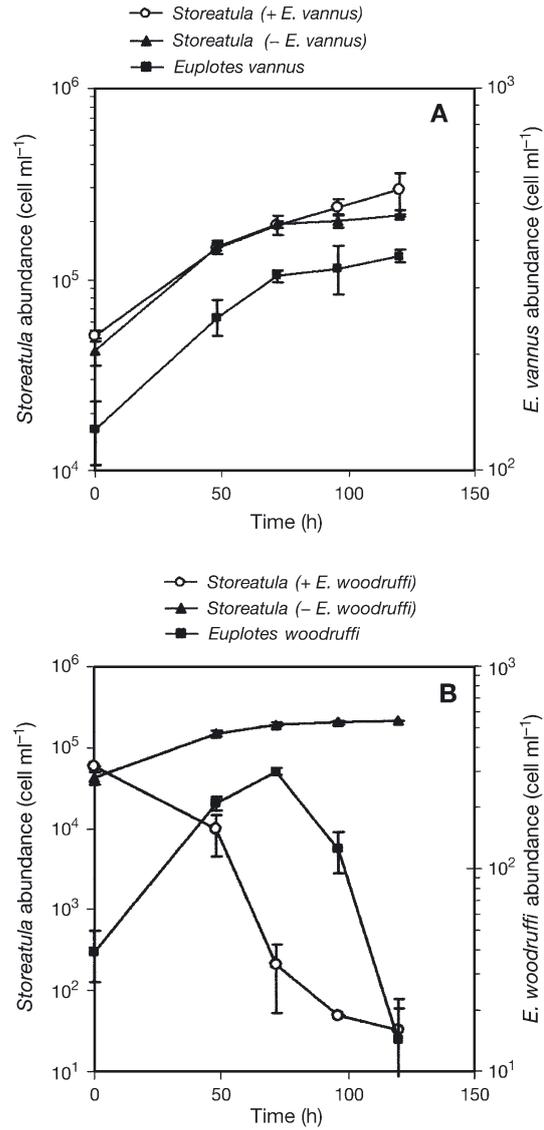


Fig. 2. Growth curves of (A) *Euplotes vannus* alone, and *Storeatula major* in the presence (+*E. vannus*) or absence (-*E. vannus*) of the ciliate, and (B) *E. woodruffi* alone, and *S. major* in the presence (+*E. woodruffi*) or absence (-*E. woodruffi*) of the ciliate

Table 1. Mean (\pm SD) specific growth rate, μ (d^{-1}), ingestion rates, *I* (prey predator⁻¹ h⁻¹), clearance rates, *C* ($\mu\text{l h}^{-1}$), or net grazing impact, NGI (dinoflagellates ciliate⁻¹ h⁻¹), of predators with different prey items. *I*, *C*, and NGI were calculated based on the interval from 0 to 48 h. Identical letters indicate significant differences. na = not applicable

Predator	Prey	μ	<i>I</i>	<i>C</i>	NGI
<i>Pfiesteria piscicida</i>	<i>Storeatula major</i>	0.78 ^a \pm 0.02	0.10 \pm 0.02	0.0024 \pm 0.0002	na
<i>Cryptoperidiniopsis</i> sp.	<i>Storeatula major</i>	0.22 ^a \pm 0.11	0.22 \pm 0.07	0.0029 \pm 0.0009	na
<i>Euplotes vannus</i>	<i>Storeatula major</i>	0.31 ^b \pm 0.06	3.5 ^d \pm 1.5	0.039 ^e \pm 0.017	na
<i>Euplotes vannus</i>	<i>Pfiesteria piscicida</i> + <i>Storeatula major</i>	0.3 ^c \pm 0.03	na	na	1.04 ^f \pm 0.31
<i>Euplotes vannus</i>	<i>Cryptoperidiniopsis</i> sp. + <i>Storeatula major</i>	0.67 \pm 0.14	na	na	0.82 \pm 0.32
<i>Euplotes woodruffi</i>	<i>Storeatula major</i>	0.86 ^b \pm 0.20	17.1 ^d \pm 0.20	0.65 ^e \pm 0.10	na
<i>Euplotes woodruffi</i>	<i>Pfiesteria piscicida</i> + <i>Storeatula major</i>	0.59 ^c \pm 0.08	na	na	3.23 ^{f,g} \pm 0.04
<i>Euplotes woodruffi</i>	<i>Cryptoperidiniopsis</i> sp. + <i>Storeatula major</i>	0.66 \pm 0.16	na	na	0.9 ^g \pm 0.11

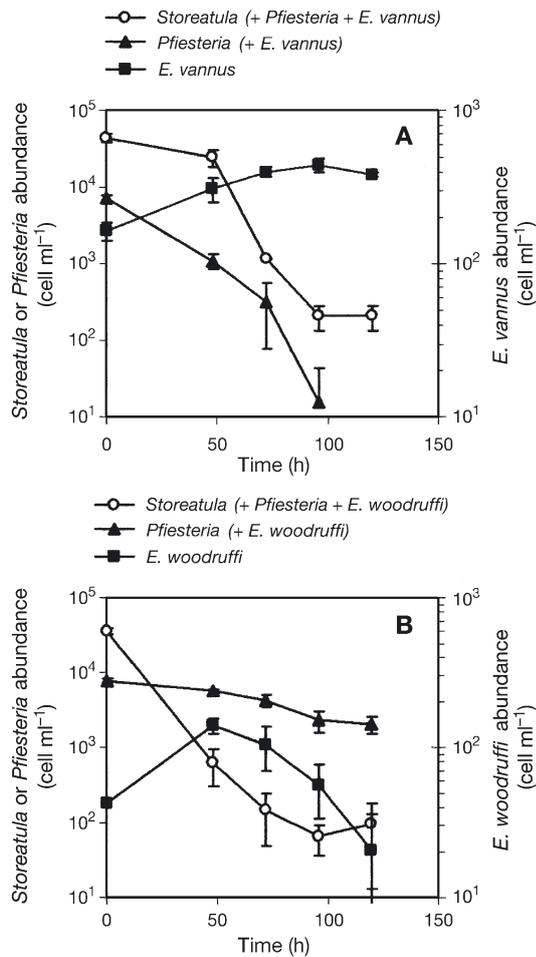


Fig. 3. Growth curves of (A) *Euplotes vannus* alone, *Pfiesteria piscicida* and *E. vannus*, and *Storeatula major*, *P. piscicida* and *E. vannus*, and (B) *E. woodruffi* alone, *P. piscicida* and *E. woodruffi*, and *S. major*, *P. piscicida* and *E. woodruffi*

(Figs. 3 & 4, Table 1). However, *E. woodruffi*'s growth rate was significantly greater than that of *E. vannus* when grown with a mixture of *Pfiesteria piscicida* and *Storeatula major* (Table 1). The NGI of *E. woodruffi* on *P. piscicida* prey was significantly greater than that of *E. vannus* (Table 1), but the NGI on *Cryptoperidiniopsis* sp. did not vary with ciliate species. The NGI did not differ with dinoflagellate prey type in *E. vannus*, but in *E. woodruffi* it was >3-fold higher with *P. piscicida* as prey (Table 1).

Discussion. Ciliates typically have maximal growth rates greater than heterotrophic dinoflagellates under optimal conditions, and therefore ciliate populations can respond rapidly to increases in dinoflagellate biomass (Hansen 1995, Strom & Morello 1998). Under our experimental conditions, the euplotids achieved maximal specific growth rates equivalent to (*Pfiesteria piscicida*) or greater than (*Cryptoperidiniopsis* sp.) those

of the dinoflagellates. Whether these comparisons reflect trophic relationships under complex natural conditions is questionable, but at least the potential for predatory control of these dinoflagellate species is suggested by not only the ciliates' capability for relatively rapid growth, but their effect in reducing dinoflagellate population abundances relative to dinoflagellate/cryptophyte control treatments.

Euplotes vannus and *E. woodruffi* exhibited some similarities and contrasts in potential predatory control and selective grazing on *Storeatula major*, *Pfiesteria piscicida*, and *Cryptoperidiniopsis* sp. prey. In the presence of *S. major* as sole protist prey, both ciliates were capable of active grazing and reproduction. However, *E. woodruffi* exhibited much greater specific growth, ingestion, and clearance rates with the cryptophyte

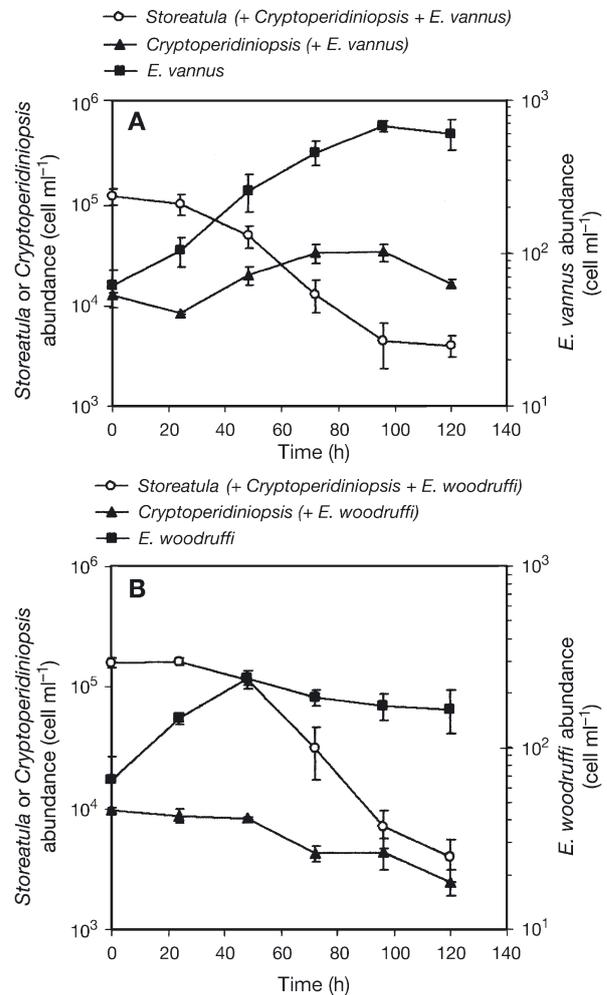


Fig. 4. Growth curves of (A) *Euplotes vannus* alone, *Cryptoperidiniopsis* sp. and *E. vannus*, and *Storeatula major*, *Cryptoperidiniopsis* sp. and *E. vannus*, and (B) *E. woodruffi* alone, *Cryptoperidiniopsis* sp. and *E. woodruffi*, and *S. major*, *Cryptoperidiniopsis* sp. and *E. woodruffi*

prey than *E. vannus*. A comparatively greater potential for predatory control by *E. woodruffi* was also evident in its effect on *P. piscicida*. The ciliate's specific growth rate and NGI on *P. piscicida* were significantly higher than those of *E. vannus*. In contrast, these parameters did not differ between ciliates when grown with *Cryptoperidiniopsis* sp. prey.

The results from this study suggest that *Euplotes woodruffi* had a greater ability to control *Pfiesteria piscicida* population growth than that of *Cryptoperidiniopsis* sp. It should be noted, however, that these dinoflagellate cultures were maintained for over 1 yr on cryptophyte prey. Burkholder et al. (2001a,b) demonstrated that, when *P. piscicida* cultures are not exposed to fish for extended periods, their ability to regain toxicity is reduced (functional type TOX-B) or lost (functional type NON-IND for 'noninducible') depending on the duration of separation from fish. Furthermore, *P. piscicida*'s grazing ability and susceptibility to predation were much lower in recently toxic cultures (i.e. that had recently killed fish under laboratory conditions, functional type TOX-A) than in TOX-B cultures or NON-IND cultures (Burkholder et al. 2001a, Stoecker et al. 2002), including reduced predation by *E. vannus* and *E. woodruffi* (A. J. Lewitus et al. unpubl. data). Therefore, the relatively higher grazing properties of *E. woodruffi* on *P. piscicida* over *Cryptoperidiniopsis* sp. measured in the present study may reflect prey preference under non-toxic, but not necessarily toxic, natural conditions.

'*Pfiesteria*-like organisms', which include *P. piscicida*, *P. shumwayae*, and *Cryptoperidiniopsis* spp., have been consistently found in low abundance in North Inlet estuary (e.g. mean of 1.4 cell ml⁻¹ in near-surface water samples collected weekly from May to October 1998; A. J. Lewitus unpubl. data), and Lewitus et al. (1999, 2002) proposed that their population growth may be limited by low phytoplankton prey supply in this estuary (i.e. bottom-up control). However, in light of Stoecker et al.'s (2000, 2002) results demonstrating high grazing pressure by ciliates in natural waters, top-down control of the population growth of these dinoflagellates also must be considered. Although microzooplankton grazing has been shown to be an important regulatory factor in limiting phytoplankton population growth during the summer bloom in North Inlet (Lewitus et al. 1998, Dame et al. 2000, Wetz et al. 2002), information on the contribution of euplotid ciliates to microzooplankton composition in this estuary does not exist. It is reasonable to assume that encounters between benthic ciliates and plankton should be frequent in this estuary, given its shallow depths (Lewitus et al. 2002), high tidal flow (ca. 25 cm s⁻¹ at mid-ebb; Dame et al. 1985), and associated sediment resuspension. However, adequate assessment

of the role of euplotid ciliates in predatory control of *Pfiesteria* and *Cryptoperidiniopsis* populations requires knowledge of the distributional associations and trophic interactions of natural communities.

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