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Zooplankton Grazing during Dinoflagellate Blooms in a Cape Cod Embayment, with Observations of Predation upon Tintinnids by Copepods

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With 14 figures and 1 table

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Abstract. The patterns and rates of feeding by the copepod *Acartia hudsonica* and larvae of the polychaete *Polydora* sp. were investigated during the spring in an estuarine embayment. These dominant macrozooplankters fed upon the natural particulate assemblages (predominantly dinoflagellates) spiked with the toxic dinoflagellate *Gonyaulax tamarensis*. *G. tamarensis* was ingested by both zooplankters, as was *Heterocapsa triquetra,* the most abundant alternative food item. Ingestion rates generally increased as dinoflagellate concentrations increased, resulting in a relatively constant (and low) filtration rate for each grazer. *Dinophysis acuminata,* another dominant dinoflagellate, was essentially ungrazed. Thus, the zooplankters did not ingest one dinoflagellate and consumed others in proportion to their availability but at low rates. Based on these low rates and the small number of *A. hudsonica* observed during the spring, we infer minimal grazing impact on a 1980 *G. tamarensis* bloom. In contrast, the impact of polychaete larvae may have been substantial, since their extreme numerical abundance more than compensated for low filtration rates.

In one instance, the tintinnid *Eutintinnus pectinis* was accidentally included in a grazing experiment. Our ingestion data demonstrate that *A. hudsonica,* when presented with a combination of tintinnids and several species of phytoplankton (*G. tamarensis* and *D. acuminata*) ingested the tintinnids at high rates, in proportion to their high abundance. Since the nanoflagellate *Chroomonas amphioxea* was found within the loricae of many of the surviving tintinnids, this also provided a qualitative demonstration of the often-hypothesized nanoplankton to tintinnid to copepod link in a marine food chain.

Problem

The toxic dinoflagellate *Gonyaulax tamarensis* LEBOUR blooms regularly in coastal waters of New England and eastern Canada, often causing paralytic

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shellfish poisoning (PRAKASH, 1967; HARTWELL, 1975; HURST & YENTSCH, 1981; WHITE & MARANDA, 1978). Although blooms are widespread in the Gulf of Maine region, relatively localized *G. tamarensis* populations occur in isolated embayments on Cape Cod, Long Island, and in Connecticut (ANDERSON & WALL, 1978; ANDERSON & MOREL, 1979; ANDERSON *et al.*, 1982).

It is evident from other studies that grazing can be a significant factor affecting phytoplankton bloom development (*e. g.*, CUSHING, 1958), yet the possible effects of zooplankton grazing on *G. tamarensis* blooms have remained largely uninvestigated. Studies documenting the ingestion of *G. tamarensis* by zooplankton are limited, and thus far have been obtained only with algal cultures as food sources. DAGG (1977) found that three species of copepods survived longer with *G. tamarensis* as food than animals kept under constant starvation. WHITE (1977, 1979, 1980) presented field evidence which suggested that toxic *Gonyaulax* were ingested by cladocerans, pteropods and copepods. Further, WHITE (1981) confirmed that the copepod *Acartia clausi* (= *A. hudsonica*) and barnacle nauplii (*Balanus* sp.) fed upon unialgal *G. tamarensis* cultures. STOECKER *et al.* (1981) also found that *G. tamarensis* was ingested by the tintinnid *Favella ehrenbergii*.

While these studies clearly show that a variety of zooplankton is capable of feeding upon *G. tamarensis* cultures, the results are difficult to apply to field situations, since no information is available on the abundance of potential grazers during *G. tamarensis* blooms. More importantly, nothing is known of the grazing behaviour of these zooplankters in a mixed phytoplankton population. *G. tamarensis* rarely blooms in nature in the absence of other phytoplankton species, and in many instances, is not the dominant species.

The objective of this study was to examine the grazing behaviour of dominant zooplankters during the spring bloom season in an embayment subject to recurrent outbreaks of paralytic shellfish poisoning. Since the concentration of *G. tamarensis* was very low throughout the study, cultures of this species were added to the natural phytoplankton assemblage (predominantly dinoflagellates). The study area chosen was Perch Pond, a shallow embayment typical of the lagoons and salt ponds in which this organism blooms at the southern limit of its geographic distribution in the New England region (ANDERSON *et al.*, 1982).

Material and Methods

1. Zooplankton collection

All samples were collected in Perch Pond (Falmouth, Massachusetts). Duplicate samples were collected on each date of sampling in spring with a 73 µm mesh net (30 cm mouth diameter) equipped with a flowmeter. Tows were made near the surface behind a skiff which was vigorously rowed as nearly as possible at constant velocity for 60–75 sec. This resulted in filtration volumes of 0.6–2.2 m^3. Samples were fixed with formalin and reduced for counting with a FOLSOM plankton splitter. Aliquots of 222–2726 ($\bar{x}$ = 989) animals were counted.

2. Feeding experiments

Integrated samples to be used for feeding experiments were collected over the entire water column (ca. 2 m depth). Replicate and control aliquots from these natural samples were spiked with cultures of *G. tamarensis* since natural concentrations in 1981 were too low for acceptable grazing statistics. Cultures were of *G. tamarensis* clone GTPP previously isolated from Perch Pond by ANDERSON. The

culture additions gave initial concentrations of 7–47 cells · ml^{-1}, well within the range of natural *G. tamarensis* population densities recorded for Perch Pond (ANDERSON & MOREL, 1979; ANDERSON *et al.*, in press). Initial abundance levels of other taxa were determined by inverted microscope counts of field water samples. Thus, each feeding experiment included initials, a spiked control (natural phytoplankton plus cultured *G. tamarensis*), a natural control (natural phytoplankton without cultured *G. tamarensis*), two spiked experimental (natural phytoplankton plus cultured *G. tamarensis* plus added zooplankters), and two natural experimental (natural phytoplankton without cultured *G. tamarensis* but with added zooplankters) containers.

Prior to each feeding experiment, the integrated water samples were screened through 64 µm-mesh netting and divided into 400 ml subsamples in 500 ml jars. *G. tamarensis* cultures were added to spiked containers followed by either 50–100 polychaete larvae or 12–20 *A. hudsonica* mixed adults (males + females). Males were used only in cases where there were not enough females available to perform an experiment. Thus, although copepod sex ratios in grazing experiments were not always comparable from one date to another, they were generally representative of those for the Perch Pond population of *A. hudsonica.* Feeding experiments typically lasted 24 hours, and were performed in the dark in a temperature controlled incubator. Temperatures for the experiments were maintained within the range recorded over the course of the spring bloom in Perch Pond (6–20 °C). Since natural concentrations of nitrate plus ammonium in Perch Pond water used in these experiments were 6.1–13.4 µM (ANDERSON *et al.*, in press), it was not necessary to add nitrogen to grazing containers to prevent stimulation of phytoplankton growth by nitrogen excreted by grazers (see ROMAN & RUBLEE, 1980). Experimental and control containers were placed on a tilted rotating wheel (4 rpm) to prevent algal sedimentation. Viability of the grazing population was checked by examination of the swimming behaviour of the animals at the beginning and end of each experiment and by the presence of fecal pellets. Experiments were terminated by the addition of UTERMOHL's preservative, and samples were subsequently concentrated by a factor of 10 using sedimentation. Phytoplankton counts were made at 100 × in a SEDGWICK-RAFTER cell with raw counts of at least 200 cells, and usually > 400 cells of the phytoplankton species of interest. This results in accuracy of ± 10 % (GUILLARD, 1973). Ingestion and filtration rates were determined with the equations of FROST (1972), thus including growth of the phytoplankton during the experiment.

Results

1. Dominant phytoplankton and zooplankton

Dominant zooplankton in Perch Pond during the spring *G. tamarensis* bloom season were typically polychaete larvae (*Polydora* sp.), adults and copepodites of the copepod *Acartia hudsonica,* and undifferentiated copepod nauplii, predominantly of *A. hudsonica.* Population data for 1980 is presented in Fig. 1 and those of 1981 elsewhere (ANDERSON *et al.*, in press). Of the grazers sufficiently large to ingest *G. tamarensis,* the polychaete larvae were by far the most numerous.

Throughout the 1981 grazing experiments, the *G. tamarensis* population in Perch Pond remained at low concentrations (< 1000 · l^{-1}). Other phytoplankton species were numerous, however, with dominance of *Heterocapsa triquetra* from 1–27 April, and on other dates by either a combination of *Skeletonema costatum* and other diatoms, the dinoflagellate *Dinophysis acuminata,* and the nanoflagellate *Chroomonas amphioxea* (see Table 1).

2. Feeding experiments

Fecal pellets (as indicators of feeding activity) were observed in aliquots from all experimental containers except for the two unspiked samples for 4 May. No

ingestion was detected in these samples with *S. costatum* and *C. amphioxea* in low concentrations and polychaete larvae as the only grazers.

The added *G. tamarensis* were ingested by *A. hudsonica* on all dates except 15 April (when the calculated ingestion rate of one replicate was negative and the other was positive). On all other dates and with a variety of competing food sources, ingestion of *G. tamarensis* was positive but low (< 9 cells · animal^{-1} · h^{-1} (Table 1). *G. tamarensis* was also consumed by polychaete larvae on each of the three dates tested but rates of ingestion were < 4 cells · animal^{-1} · h^{-1} (Table 1).

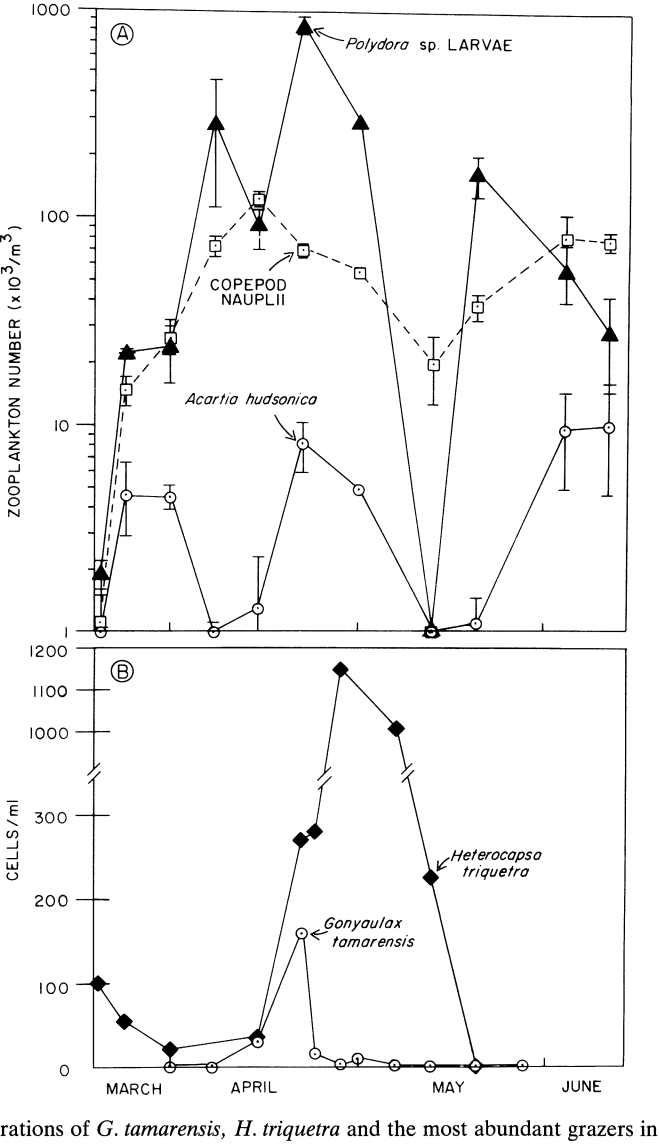


Fig. 1. Concentrations of *G. tamarensis*, *H. triquetra* and the most abundant grazers in Perch Pond during the 1980 spring bloom season. A: Zooplankton. Data points are means of two replicates and vertical bars are ranges. B: Phytoplankton.

Table 1. Rates of ingestion and filtration by *A. hudsonica* and *Polydora* sp. larvae feeding upon *G. tamarensis*, *H. triquetra*, *D. acuminata* and *E. pectinis* in either natural water samples or the same samples spiked with *G. tamarensis* cultures. Samples: SE = spiked experimental; NE = natural (unspiked) experimental; I = ingestion rate (cells · grazer^{-1} · h^{-1}); F = filtration rate (ml · grazer^{-1} · h^{-1}). Grazers: Ah = *A. hudsonica; Poly* = *Polydora* sp. larvae; temp = experimental temperature (°C); neg. = negative I or F.

Date	Sample	temp	Grazers	*G. tamarensis* I	*G. tamarensis* F	*H. triquetra* I	*H. triquetra* F	*D. acuminata* I	*D. acuminata* F	*E. pectinis* I	*E. pectinis* F	Dominant phytoplankters in field samples (cells · ml^{-1})	*G. tamarensis* added to SE containers (cells · ml^{-1})
4/01	SE	9.0	20 Ah	2.6	0.09	190.3	0.13	–	–	–	–	*Heterocapsa triquetra* (1340)	26.6
4/01	SE	9.0	20 Ah	4.6	0.16	321.3	0.23	–	–	–	–	*Chaetoceros* sp. (58)	26.6
4/01	NE	9.0	12 Ah	–	–	398.7	0.28	–	–	–	–	*Calycomonas gracilis* (17)	–
4/01	NE	9.0	14 Ah	–	–	592.4	0.45	–	–	–	–		–
4/15	SE	17.0	20 Ah	1.9	0.08	196.1	0.07	–	–	–	–	*Heterocapsa triquetra* (2521)	19.8
4/15	SE	17.0	20 Ah	neg.	neg.	183.2	0.06	–	–	–	–	*Skeletonema costatum* (4)	19.8
4/15	NE	17.0	20 Ah	–	–	292.7	0.10	–	–	–	–		–
4/15	NE	17.0	20 Ah	–	–	780.9	0.32	–	–	–	–		–
4/21	SE	8.0	20 Ah	4.6	0.09	126.8	0.16	–	–	–	–	*Heterocapsa triquetra* (777)	46.5
4/21	SE	8.0	20 Ah	8.5	0.18	99.0	0.12	–	–	–	–	*Chroomonas amphioxea* (38)	46.5
4/21	NE	8.0	20 Ah	–	–	149.9	0.19	–	–	–	–	*Elbria tripartita* (4.5)	–
4/21	NE	8.0	20 Ah	–	–	131.4	0.16	–	–	–	–		–
4/27	SE	8.0	50 Poly	2.3	0.07	17.5	0.04	–	–	–	–	*Heterocapsa triquetra* (402)	31.5
4/27	SE	8.0	50 Poly	2.1	0.06	16.8	0.04	–	–	–	–	*Chroomonas amphioxea* (116)	31.5
4/27	NE	8.0	50 Poly	–	–	29.9	0.06	–	–	–	–	*Katodinium rotundatum* (16)	–
4/27	NE	8.0	50 Poly	–	–	35.6	0.08	–	–	–	–		–
5/04	SE	9.5	80 Poly	1.8	0.05	–	–	–	–	–	–	*Chroomonas amphioxea* (84)	37.1
5/04	SE	9.5	80 Poly	3.9	0.12	–	–	–	–	–	–	*Skeletonema costatum* (8)	37.1
5/04	NE	9.5	100 Poly	–	–	–	–	–	–	–	–		–
5/04	NE	9.5	100 Poly	–	–	–	–	–	–	–	–		–
5/18	SE	20.0	50 Poly	0.8	0.09	–	–	1.2	0.01	–	–	*Thalassiosira nana* (1910)	7.2
5/18	SE	20.0	50 Poly	0.3	0.03	–	–	neg.	neg.	–	–	*Skeletonema costatum* (500)	7.2
5/18	NE	20.0	50 Poly	–	–	–	–	neg.	neg.	–	–	*Dinophysis acuminata* (120)	–
5/18	NE	20.0	50 Poly	–	–	–	–	2.7	0.02	–	–	*Chroomonas amphioxea* (180)	–
5/26	SE	20.0	20 Ah	1.2	0.12	–	–	4.2	0.04	12.4	0.19	*Chroomonas amphioxea* (606)	8.4
5/26	SE	20.0	20 Ah	0.8	0.08	–	–	neg.	neg.	15.6	0.23	*Dinophysis acuminata* (99)	8.4
5/26	NE	20.0	20 Ah	–	–	–	–	neg.	neg.	19.6	0.23	*Skeletonema costatum* (8)	–
5/26	NE	20.0	20 Ah	–	–	–	–	neg.	neg.	21.6	0.38	*Gyrodinium estuariale* (14) *(Eutintinnus pectinis* [66–83])	–

Even though the grazer density was relatively high in each experimental container, the differences between control and grazed *G. tamarensis* concentrations were typically small. Approximately 400 cells were counted in nearly every case, giving a ± 10 % counting error (GUILLARD, 1973). Although there were sometimes overlapping error bars between control and grazed cell concentrations, there were significantly fewer *G. tamarensis* and *H. triquetra* cells remaining in experimental containers than in controls (t-test for paired data, $p < 0.05$). Thus, ingestion rates were positive but low.

For both *A. hudsonica* and *Polydora* sp., the rate of ingestion of *G. tamarensis* increased as the number of available *G. tamarensis* increased (Fig. 2). Further, ingestion of *G. tamarensis* by *A. hudsonica* was slightly higher than that by *Polydora* sp. As ingestion rates increased with increasing food concentration, filtration rates (Fig. 3) remained relatively constant.

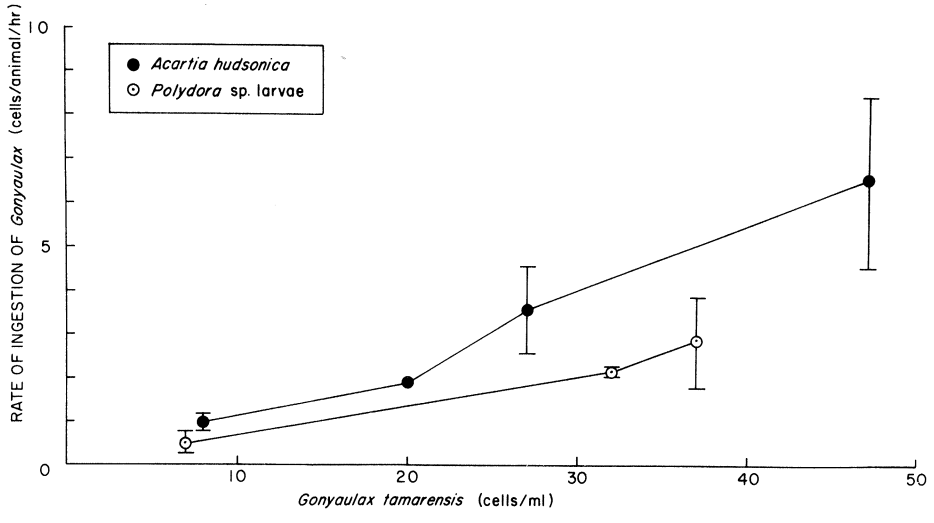


Fig. 2. Rates of ingestion of *Gonyaulax tamarensis* by *Acartia hudsonica* and *Polydora* sp. larvae vs. available concentration of *G. tamarensis*. Data points are means of two replicates, and vertical bars are ranges.

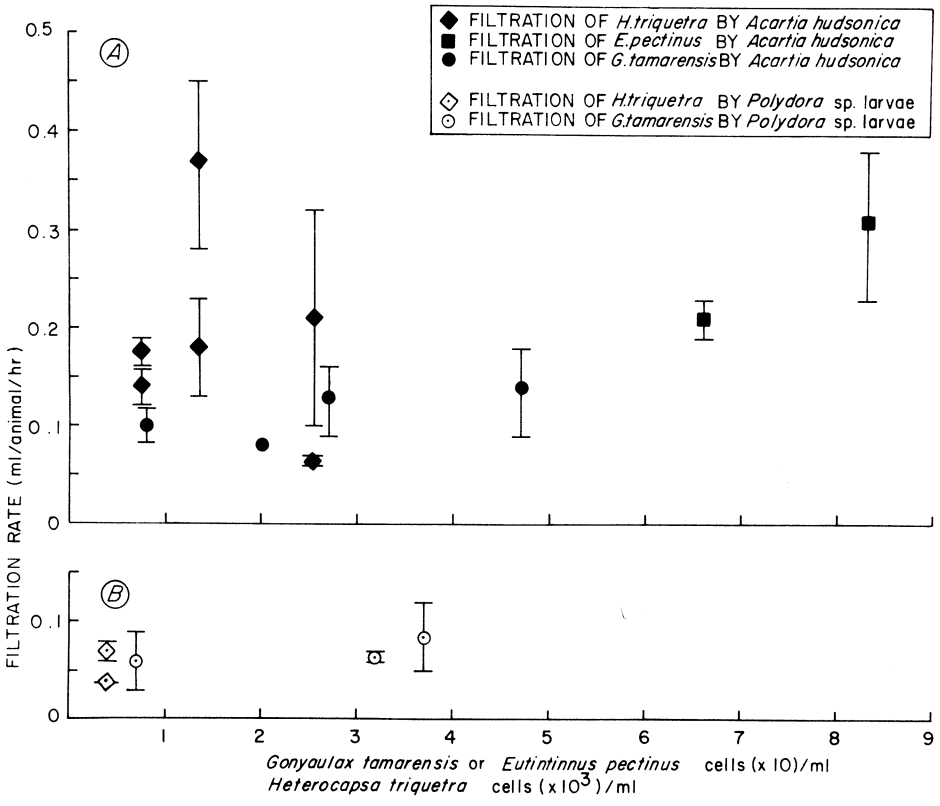


Fig. 3. Filtration rates. A: *A. hudsonica* feeding on *G. tamarensis, H. triquetra,* and *E. pectinis.* B: *Polydora* sp. larvae feeding on *G. tamarensis* and *H. triquetra.*

From 1–27 April, the natural phytoplankton was almost exclusively dominated by *H. triquetra,* with densities between 400 and 2600 · ml^{-1}. *G. tamarensis* concentrations were <1 cell · ml^{-1}. Grazing experiments with *A. hudsonica* on these dates reveal two generalities. First, fewer *H. triquetra* were consumed in containers spiked with *G. tamarensis* than in unspiked containers (Fig. 4, Table 1). Second, rates of ingestion of *H. triquetra* generally increased as the available concentration of that species increased (Fig. 4), consistent with the relatively constant filtration rate calculated from the disappearance of this species (Fig. 3). Grazing by *Polydora* sp. on *H. triquetra* was only tested once (27 April). Here again the ingestion rate decreased by a factor of two with the addition of *G. tamarensis,* while the filtration rate was approximately the same as those calculated for *Polydora* grazing on various *G. tamarensis* concentrations (Fig. 4).

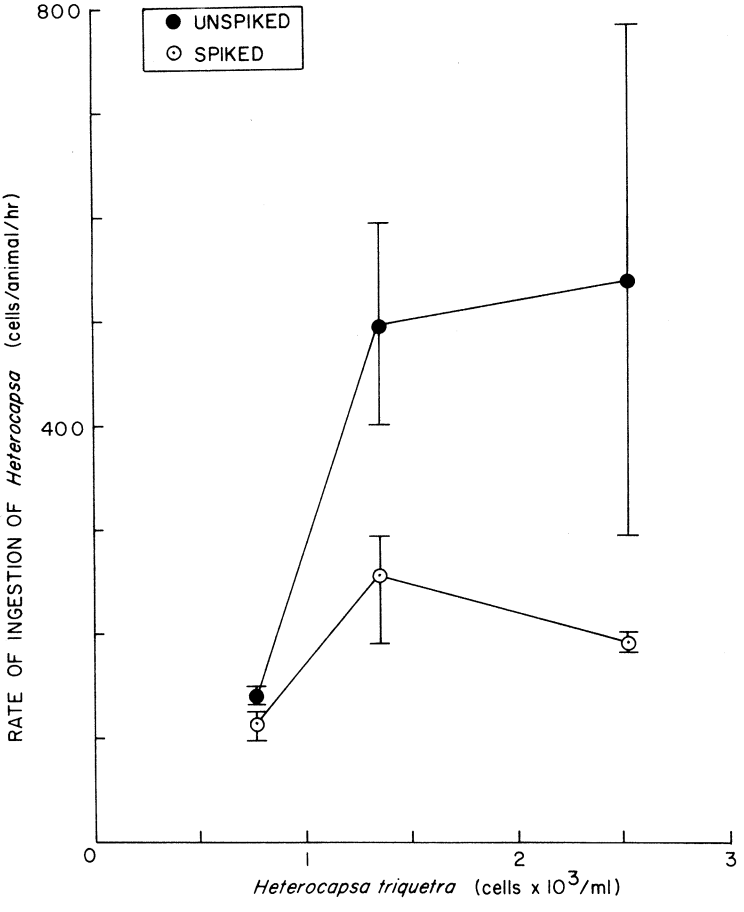
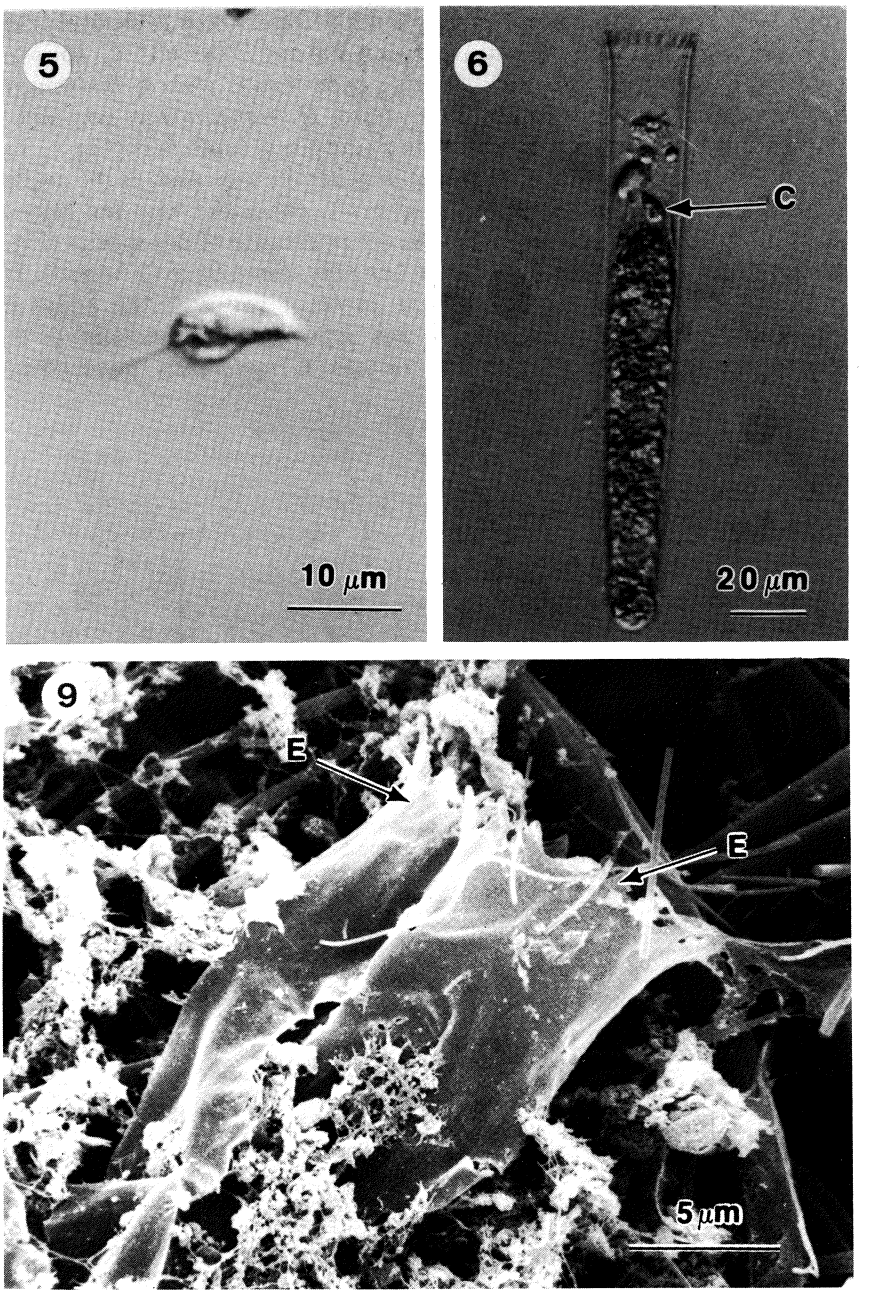
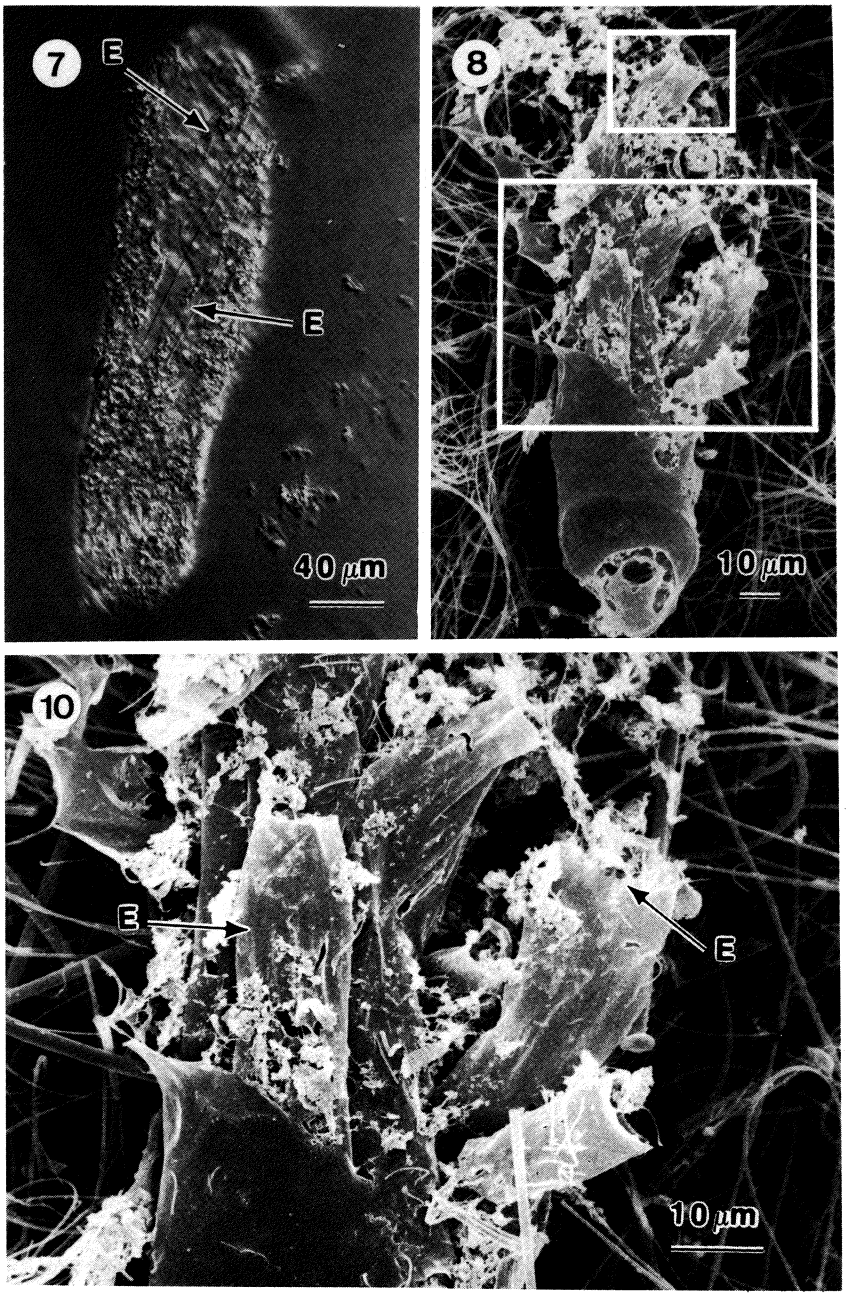


Fig. 4. Rates of ingestion of *Heterocapsa triquetra* by *Acartia hudsonica* vs. available concentration of *H. triquetra* in containers either spiked or not spiked with *G. tamarensis*. Data points are means of two replicates, and vertical bars are ranges.



Figs. 5–10. 26 May, 1981 samples. Fig. 5. *Chroomonas amphioxea* cell. Fig. 6. *Eutintinnus pectinis* with *C. amphioxea* cell (C) inside. Fig. 7. Light micrograph of *Acartia hudsonica* fecal pellet with *E. pectinis* loricae (E) inside. Fig. 8. Scanning electron micrograph of *A. hudsonica* fecal pellet



(background is glass fiber filter). Fig. 9. High magnification of area in upper box in Fig. 8, note *E. pectinis* loricae (E.). Fig. 10. High magnification of area in lower box in Fig. 8, note *E. pectinis* loricae (E.).

3. Copepod predation upon tintinnids

Although the major competing food items in these experiments were typically dinoflagellates, on one occasion (26 May), large numbers of a small tintinnid were accidentally included despite the screening of experimental water samples through 64 μm mesh netting. The tintinnid was *Eutintinnus pectinis* (KOFOID & CAMPBELL, 1939), an abundant species in the Woods Hole area (GOLD & MORALES, 1976). Since *E. pectinis* was present in both experimental and control samples (81–101 animals · ml^{-1}), we have no quantitative data on the grazing activity of the tintinnid. However, observations made during counting revealed that *Chroomonas amphioxea* (Fig. 5) was present in most *E. pectinis* loricae (Fig. 6). Thus, there is qualitative evidence that *E. pectinis* fed upon the small nanoplankter. For this reason, as well as the observation that most of the *G. tamarensis* cells added to the spiked containers had cell diameters (35 μm) larger than the lorica diameter of *E. pectinis* (20 μm), the feeding activities of tintinnid did not affect the estimates of grazing of *G. tamarensis* by *A. hudsonica.*

In this experiment, ingestion and filtration rates of *A. hudsonica* on *G. tamarensis* were very low. Likewise, *Dinophysis acuminata* was essentially ungrazed, although it was present in natural bloom concentration of 100 cells · ml^{-1}. There was no significant difference between the numbers of *D. acuminata* cells in experimental and control containers (t-test for paired data, $p < 0.05$). The major food item for *Acartia* was clearly the tintinnid, which was removed at rates of 12–22 tintinnids · $copepod^{-1} \cdot h^{-1}$ (Table 1). Rates of ingestion were higher in samples without added *G. tamarensis* than in those containing the dinoflagellate (mean values 20.6 versus 14.0 tintinnids · $copepod^{-1} \cdot h^{-1}$, respectively). These high rates of predation of copepods on tintinnids are supported by observation that *every* fecal pellet seen in the aliquots contained, and in most cases was packed with, tintinnid loricae (Figs. 7–10). In general, filtration rates and ingestion rates calculated from the removal of *G. tamarensis* were within the broad trends established in other experiments using *H. triquetra* as the dominant competing food item (Fig. 3). Thus the presence of the tintinnids did not clearly alter the feeding behaviour of *A. hudsonica* towards *G. tamarensis.* Filtration rates of *Acartia* calculated from the disappearance of tintinnids were, however, more than double those calculated from *G. tamarensis* losses.

Discussion

In mixed populations of phytoplankton, *Gonyaulax tamarensis* was ingested by both *Acartia hudsonica* and the larvae of *Polydora* sp., the dominant zooplankters in the study area. The ingestion and filtration rates were very low, however. Our data indicates a general increase in mean ingestion rate by both *A. hudsonica* (0–8.5 cells · $animal^{-1} \cdot h^{-1}$) and *Polydora* sp. larvae (0.3–3.9 cells · $animal^{-1} \cdot h^{-1}$) in the presence of increasing *G. tamarensis* cell concentrations, even with a wide variety of alternative food concentrations and types. Ingestion of the major co-occurring food item, the dinoflagellate *Heterocapsa triquetra*

followed a similar trend. These ingestion rates are in keeping with a relatively constant (and low) filtration rate for each grazer calculated from the disappearance of both *G. tamarensis* and *H. triquetra* (Fig. 3).

Our results suggest that there was no preferential feeding on *G. tamarensis* or *H. triquetra* – that each species was removed in approximate proportion to its availability. The validity of this statement rests on the assumption of a constant filtration rate over a wide range of food types and concentrations. There are instances when selection might be inferred (*e. g.* the decrease in ingestion of *H. triquetra* following addition of *G. tamarensis* on two of the three dates examined [Fig. 3]), but the associated filtration rates still fall within the generally constant range seen in Fig. 3. This was not the case with *Dinophysis acuminata,* which is slightly larger than either *G. tamarensis* or *H. triquetra* (50 µm versus 37 and 29, respectively) but which was essentially ungrazed by both polychaetes and copepods. Thus the grazers did not ingest one dinoflagellate and consumed others at low rates.

We have no explanation for the limited feeding behaviour we observed. Temperature effects can be discounted since the reduced feeding occurred over a 8–20 °C range. Although bottle effects are always worrisome in 24 h experiments, we observed significant increases in dinoflagellate concentrations in control containers over initial counts, equivalent to realistic growth rates of 0.3–0.5 divisions · day^{-1}. This does not mean that the added grazers were unaffected, but combined with our observation of fecal pellets in essentially all of the experimental containers, it does suggest that bottle effects were not severe. Although shorter experiments would seem preferable, the possibility of significant diel variations in grazing behaviour makes extrapolation of 4–6 hour studies difficult. Furthermore, our rates are low in comparison with other grazing studies that also used long incubations (DEASON, 1980; RICHMAN *et al.*, 1977; ANRAKU, 1964). Published data on *A. hudsonica* filtration rates are limited and in some cases, suspect due to the use of electronic particle counters (see HARBISON & MCALISTER, 1980), but the general indication is that this animal is capable of feeding much faster than we observed. For example, when *A. hudsonica* fed upon the diatom *Skeletonema costatum* at the same general temperatures used in our study, filtration rates were between 0.5 and 3.3 ml · animal^{-1} · h^{-1} (DEASON, 1980). Our rates averaged 0.1 ml · animal^{-1} · h^{-1}. Similar calculations for *A. hudsonica* (listed as *A. clausii*) gave maximum rates of 0.4 or 0.8 ml · animal^{-1} · h^{-1} using natural particles in the Chesapeake Bay or cultures of *Thalassiosira pseudonana,* respectively (RICHMAN *et al.*, 1977; ANRAKU, 1964).

A recent study lends support to our findings, however, in that HUNTLEY (1982) demonstrated avoidance of a non-toxic dinoflagellate by the copepod *Calanus pacificus* during a yellow-water bloom off California. Filtration rates calculated from the reduction in dinoflagellate cells were not significantly different from zero, while co-occuring particle assemblages or unialgal diatom cultures were removed at rates as high as 2.3–8.4 ml · animal^{-1} · h^{-1}.

Since our filtration rates were obtained from a wide range of dinoflagellate concentrations (Table 1), we felt justified in using our calculated rates to estimate the impact of grazing during 1980 when *G. tamarensis* bloomed in Perch Pond. Details of the population dynamics are given elsewhere (ANDERSON

et al., in press), but the dinoflagellate and zooplankton densities are presented in Fig. 1.

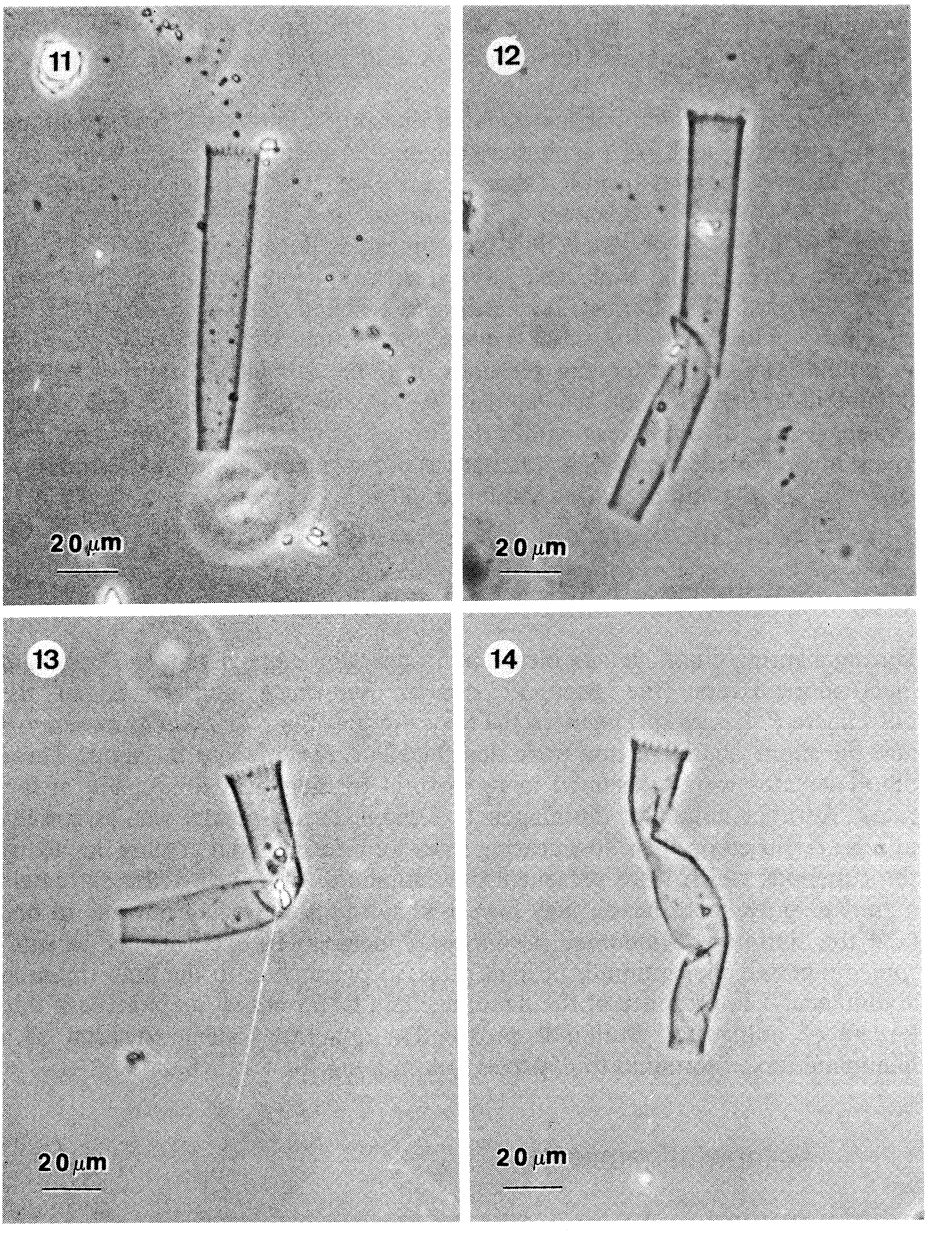
Based on their relative abundance, we would estimate a maximum *G. tamarensis* grazing loss of 1 % day^{-1} by *A. hudsonica.* The copepod's population size and filtration rate were both simply too low for significant impact. This was not the case with polychaete larvae, however. Even though rates of ingestion of *G. tamarensis* by polychaete larvae tended to be even lower than those of *A. hudsonica,* the larvae were much more abundant (Fig. 1). If we apply an average filtration rate of 0.07 $ml \cdot animal^{-1} \cdot h^{-1}$ to the 1980 Perch Pond populations, we can estimate a *G. tamarensis* grazing loss between 3 and 16 % day^{-1} in the early stages of the bloom. At the peak *G. tamarensis* concentration, the polychaete larvae were sufficiently dense ($855 \cdot l^{-1}$) to represent a potential grazing loss of over 100 % of the *G. tamarensis* population in one day. It is thus noteworthy that the *G. tamarensis* (and polychaete larval) densities dropped sharply after this date.

These grazing impacts are based on abundance of polychaete larvae determined from surface net tows. Vertical migration of the larvae could result in significant over or underestimates of grazing impact depending on the timing of migration relative to our sampling. It is also possible that spatial separation of vertically migrating dinoflagellates and polychaete larvae may reduce the estimated grazing loss. Despite these drawbacks there is a strong suggestion that investigations of zooplankton grazing pressure in estuarine waters may, at certain times of the year, have to account for the potentially substantial impact of planktonic polychaete larvae, even when filtration rates are expected to be low. These larvae have been shown to ingest several types of phytoplankton in field and culture studies (DARO & POLK, 1973; BLAKE & WOODWICK, 1975). Examination of zooplankton assemblages in other estuaries of the north-eastern United States (DEEVEY, 1948; HULSIZER, 1976; BARLOW, 1955; SAGE & HERMAN, 1972; TURNER, 1982) reveals no other instance in which spring zooplankton assemblages were as overwhelmingly dominated by polychaete larvae as in Perch Pond. However, DARO & POLK (1973) recorded *Polydora ciliata* larvae in concentrations of approximately $600 \cdot l^{-1}$ in surface waters along the Belgian coast. This is close to our maximum value for surface waters of Perch Pond ($855 \cdot l^{-1}$).

The largest surprise in our results was the intense predation of *A. hudsonica* on tintinnids. We present this information here for two reasons. First, the feeding behaviour of *Acartia* towards *G. tamarensis* was not affected in any obvious way by the presence of large numbers of tintinnids as competing food items. The low ingestion and filtration rates both fell into the general trends established in other experiments. Second, to our knowledge, this is the first data to show that copepods presented with a combination of tintinnids and several species of phytoplankton (*G. tamarensis* and *D. acuminata*) ingested the tintinnids at high rates. This argument is supported by the filtration rates calculated from the disappearance of tintinnids – rates over twice as fast as those calculated from *G. tamarensis* losses in the same container or in other experiments (Fig. 3). Although these ingestion rates were approximately ten times higher than those for co-occuring *G. tamarensis,* tintinnid abundance was also higher ($75 \cdot ml^{-1}$ versus $8.4 \cdot ml^{-1}$). The net result was that *A. hudsonica* removed 17 % of the

available *G. tamarensis* and 20 % of available tintinnid cells. Thus, as with other food items, tintinnids were ingested in proportion to their availability.

Ingestion of the tintinnids is evidenced by both the feeding data (Table 1) and by fecal pellet contents. Examination of Figs. 7–10 reveals that ingested loricae were, in most cases, intact. Thus, *A. hudsonica* can ingest entire tintinnid cells.



Figs. 11–14. 26 May, 1981 samples. Fig. 11. Intact empty *Eutintinnus pectinis* lorica from control sample. Figs. 12–14. Crumpled empty *E. pectinis* loricae from experimental samples.

There is a suggestion, however, of yet another mechanism of copepod predation on tintinnids. In the control samples, 18 % of the tintinnid loricae counted in the aliquots were empty and all were undamaged (Fig. 11). In the experimental containers, however, an average of 33 % of the loricae were empty, and most of these were crumpled (Figs. 12–14). This suggests that in addition to ingesting entire tintinnids, *A. hudsonica* may capture some, remove the contents, and discard the empty (damaged) loricae. Alternatively, the disturbance of being captured by a copepod may cause some *E. pectinis* to abandon their loricae. Thus, some empty crumpled loricae may be evidence of unsuccessful attempts at predation.

Although it has often been speculated that predation by macrozooplankters upon tintinnids which graze nanoplankton may be a major link in certain marine food chains (examples include BEERS & STEWART, 1967; HEINBOKEL & BEERS, 1979; POMEROY, 1974; PARSONS & TAKAHASHI, 1973), little evidence for this hypothesis has been obtained thus far. Tintinnids have been found in the gut contents of copepods, tunicates, larval fishes, and euphausiids (ZEITZSCHEL, 1967; SOROKIN, 1981; PONOMAREVA *et al.*, 1962 – cited in HARGRAVES, 1981), but conclusive evidence for the entire sequence is lacking. Although we were unable to obtain data on the feeding activities of *E. pectinis* in our experiment, the documented ingestion of this animal by *Acartia* and the presence of the nanoflagellate *C. amphioxea* within the loricae of the surviving tintinnids provides further evidence (albeit qualitative) for a nanoplankton to tintinnid to copepod grazing and predation sequence.

Summary

During a spring dinoflagellate bloom in a Cape Cod embayment, the dominant macrozooplankters (the copepod *Acartia hudsonica* and larvae of the polychaete *Polydora* sp.) ingested the toxic dinoflagellate *Gonyaulax tamarensis* and the more abundant non-toxic dinoflagellate *Heterocapsa triquetra.* These dinoflagellates were consumed in proportion to their availability, but at low rates. Another abundant dinoflagellate *Dinophysis acuminata* was essentially ungrazed. Based on these low grazing rates we infer minimal grazing impact by the copepods which were present in low numbers. Conversely, the extremely abundant polychaete larvae may have had substantial grazing impact. In one case the tintinnid *Eutintinnus pectinis* was included in experiments. *A. hudsonica* ingested the tintinnids at high rates, in proportion to the high tintinnid abundance. The presence of the nanoflagellate *Chroomonas amphioxea* within loricae of uningested tintinnids provided a qualitative demonstration of a nanoplankton to tintinnid to copepod link in a marine food chain.

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