

Trophic accumulation of PSP toxins in zooplankton during *Alexandrium fundyense* blooms in Casco Bay, Gulf of Maine, April–June 1998. II.

Zooplankton abundance and size-fractionated community composition

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Abstract

During spring blooms of the toxic dinoflagellate *Alexandrium fundyense* in Casco Bay, Maine in 1998, we investigated vectorial intoxication of various zooplankton size fractions with PSP toxins, including zooplankton community composition from quantitative zooplankton samples ($>102\ \mu\text{m}$), as well as zooplankton composition in relation to toxin levels in various size fractions (20–64, 64–100, 100–200, 200–500, $>500\ \mu\text{m}$).

Zooplankton abundance in 102 μm mesh samples was low (most values $<10,000$ animals m^{-3}) from early April through early May, but increased to maxima in mid-June (cruise mean = 121,500 animals m^{-3}). Quantitative zooplankton samples ($>102\ \mu\text{m}$) were dominated by copepod nauplii, and *Oithona similis* copepodites and adults at most locations except for those furthest inshore. At these inshore locations, *Acartia hudsonica* copepodites and adults were usually dominant. Larger copepods such as *Calanus finmarchicus*, *Centropages typicus*, and *Pseudocalanus* spp. were found primarily offshore, and at much lower abundances than *O. similis*. Rotifers, mainly present from late April to late May, were most abundant inshore. The marine cladoceran *Evadne nordmani* was sporadically abundant, particularly in mid-June.

Microplankton in 20–64 μm size fractions was generally dominated by *A. fundyense*, non-toxic dinoflagellates, and tintinnids. Microplankton in 64–100 μm size fractions was generally dominated by larger non-toxic dinoflagellates,

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tintinnids, aloricate ciliates, and copepod nauplii, and in early May, rotifers. Some samples (23%) in the 64–100 μm size fractions contained abundant cells of *A. fundyense*, presumably due to sieve clogging, but most did not contain *A. fundyense* cells. This suggests that PSP toxin levels in those samples were due to vectorial intoxication of microzooplankters such as heterotrophic dinoflagellates, tintinnids, aloricate ciliates, rotifers, and copepod nauplii via feeding on *A. fundyense* cells.

Dominant taxa in zooplankton fractions varied in size. Samples in the 100–200 μm size fraction were overwhelmingly dominated in most cases by copepod nauplii and small copepodites of *O. similis*, and during late May, rotifers. Samples in the 200–500 μm size fraction contained fewer copepod nauplii, but progressively more copepodites and adults of *O. similis*, particularly at offshore locations. At the most inshore stations, copepodites and adults of *A. hudsonica* were usual dominants. There were few copepod nauplii or *O. similis* in the $>500 \mu\text{m}$ size fraction, which was usually dominated by copepodites and adults of *C. finmarchicus*, *C. typicus*, and *Pseudocalanus* spp. at offshore locations, and *A. hudsonica* inshore.

Most of the higher PSP toxin concentrations were found in the larger zooplankton size fractions that were dominated by larger copepods such as *C. finmarchicus* and *C. typicus*. In contrast to our earlier findings, elevated toxin levels were also measured in numerous samples from smaller zooplankton size fractions, dominated by heterotrophic dinoflagellates, tintinnids and aloricate ciliates, rotifers, copepod nauplii, and smaller copepods such as *O. similis* and, at the most inshore locations, *A. hudsonica*. Thus, our data suggest that ingested PSP toxins are widespread throughout the zooplankton grazing community, and that potential vectors for intoxication of zooplankton assemblages include heterotrophic dinoflagellates, rotifers, protozoans, copepod nauplii, and small copepods.

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1. Introduction

As part of the Gulf of Maine regional study of the ECOHAB (Ecology and Oceanography of Harmful Algal Blooms) Program, we determined abundance of the toxic dinoflagellate *Alexandrium fundyense*¹, toxin levels in various microplankton and zooplankton size fractions, and zooplankton community composition in those size fractions during the course of the spring *A. fundyense* bloom of 1998 in Casco Bay, Maine. Doucette et al. (2005) have presented distributions of *A. fundyense*

cells, as well as levels of toxins in particulate and various zooplankton size fractions (20–64, 64–100, 100–200, 200–500, $>500 \mu\text{m}$). Here we present results on zooplankton community composition in these size fractions, and in quantitative zooplankton samples ($>102 \mu\text{m}$). These are among the first zooplankton data from the Gulf of Maine (except for extreme southern locations such as Massachusetts Bay, Cape Cod Bay and Georges Bank) collected with net meshes that quantitatively sample the numerically dominant smaller zooplankton such as copepod nauplii, rotifers and small copepods such as *Oithona similis*. We also present information on zooplankton composition in relation to toxin levels in various size fractions, and discuss the implications of these patterns for trophic transport of toxins through pelagic food webs.

2. Methods

Sampling locations and schedules, as well as descriptions of plankton collection and toxin analysis methods are presented in Doucette et al. (2005); however, brief summaries, particularly as they apply to zooplankton analyses, are presented below.

¹Both *A. tamarensis* and *A. fundyense* occur in the Gulf of Maine (Anderson et al., 1994). We consider these to be varieties of the same species (Anderson et al., 1994; Scholin et al., 1995). Neither antibody nor oligonucleotide probes can distinguish between them, and only detailed analysis of the thecal plates on individual cells can provide this resolution. This is not practical for large numbers of field samples. Accordingly, for the purpose of this study, the name *A. fundyense* is used to refer to both forms. Likewise, during this study, an antibody probe was used that was unexpectedly found unable to distinguish between *A. fundyense* and *A. ostenfeldii* during subsequent field seasons. For reasons that are discussed in detail in the companion paper by Doucette et al. (2005) the effect this antibody cross-reaction on the PSP toxin trophic transfer data presented is likely to be minimal. Accordingly, the name *A. fundyense* will be used throughout when referring to *Alexandrium* cells enumerated using the antibody probe or light microscopy.

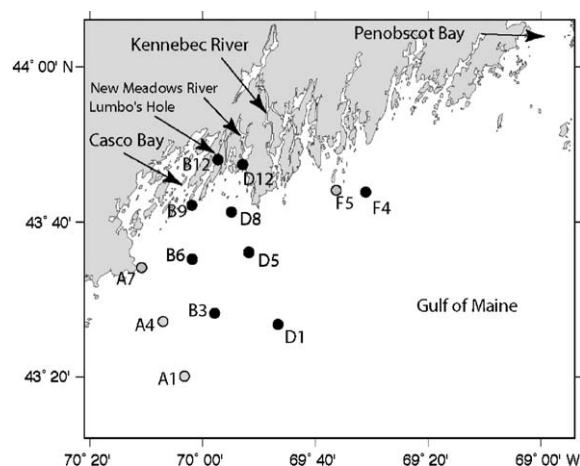


Fig. 1. Station locations for zooplankton sampling in Casco Bay, Gulf of Maine, in spring of 1998. Stations A1, A4, A7, and F5 were sampled only during Cruise 98CB01, but all other stations were sampled during Cruises 98CB01 (6–9 April), 98CB02 (21–23 April), 98CB04 (4–7 May), 98CB06 (18–20 May), 98CB08 (2–4 June), and 98CB10 (17–18 June). North latitude and west longitude are shown on the left and bottom margins, respectively.

Sampling was along four transects in Casco Bay, Gulf of Maine (Fig. 1), during six cruises from early April through mid-June, 1998 (Table 1 of Doucette et al., 2005). Quantitative timed tows were made using a 0.5 m diameter, 102 μ m mesh net equipped with a flowmeter (General Oceanics Model 2030) and all zooplankton were preserved immediately in 5–10% formalin:seawater solutions for quantitative taxonomic analyses. Care was taken to ensure that flowmeters were still turning upon retrieval, indicating that there was no net clogging. If clogging occurred, the tow was repeated for shorter time periods until there was no clogging. Generally, the quantitative tows lasted <2 min. Zooplankton from quantitative tows were transferred to 70% ethanol solutions and split with a Folsom plankton splitter to obtain aliquots of approximately 300–500 animals each. Animals in these aliquots were counted and identified to the lowest possible taxonomic level with a dissecting microscope. Abundances were calculated as animals m^{-3} .

Microplankton samples were collected by pumping surface water through a 20 μ m net, and

then separating the catch into 20–64 μ m and 64–100 μ m size fractions by sieving for both toxin and community composition analyses (details given in Doucette et al., 2005). The material for determination of community composition consisted of a 0.5 mL subsample that was added to 100 mL jars and preserved in Utermöhl's solution (Guillard, 1973) after bringing the total volume to approximately 100 mL with filtered seawater. Although not strictly quantitative, these samples were entirely adequate for obtaining relative percent composition data. This material was examined by compound microscopy, and all dinoflagellates, ciliates, and micrometazoans were counted and expressed as percentages of total cells or animals counted in 1 mL Sedgwick-Rafter counting chamber aliquots. Diatoms were not enumerated in these aliquots, since they would not be expected to contain PSP toxins.

Samples for zooplankton community composition in size fractions were collected in long, unflowmetered (non-quantitative) tows with the aim of collecting sufficient zooplankton biomass for robust measurements of PSP toxins. After sieving into multiple size fractions (100–200, 200–500, >500 μ m), samples were backwashed off sieves and split into separate aliquots for toxin and community composition analyses (details in Doucette et al., 2005). The samples for community composition were preserved in 5–10% formalin: seawater solutions, transferred to 70% ethanol for counting, split with a Folsom plankton splitter, and individual organisms counted with a dissecting microscope in the same way as the quantitative samples. Data were expressed as relative percentages.

3. Results

3.1. Zooplankton abundance in quantitative zooplankton (>102 μ m) samples

Zooplankton abundance (Fig. 2) was generally similar and low early in the season. Cruise means for the B and D transects, and Station F4 or F5 were 9450, 13,200, and 19,000 animals m^{-3} for Cruises 98CB01, 98CB02, and 98CB04,

respectively, from early April through early May, with most values $< 10,000$ animals m^{-3} (Fig. 2). Abundance values for the A transect on Cruise 98CB01 ranged from 2800 to 6120 animals m^{-3} with no discernable inshore:offshore trend. These data are not plotted in Fig. 2 since the A transect was not repeated after the first cruise.

Zooplankton abundance generally increased from mid-May (Cruise 98CB06) through early June (Cruise 98CB08) and mid-June (Cruise 98CB10) (cruise means = 35,800, 53,300, and 121,000 animals m^{-3} , respectively) particularly at the inshore location D12 (Fig. 2). There were no consistent gradients in abundance on the B transect moving inshore from the more offshore stations. Similarly, there were no consistent

patterns along the D transect, except for the dramatic seasonal increase in abundance at Station D12 for the last two cruises (98CB08 and 98CB10) in early and mid-June, respectively.

3.2. Zooplankton community composition

Selected data for percent composition for dominant taxa in quantitative tows (labeled as “Quant.Tow”), as well as data for samples from zooplankton size fractions from either pumped samples (20–64, 64–100 μm fractions) and qualitative tows (100–200, 200–500, $> 500 \mu m$ fractions) are presented as stacked histograms for selected stations shown in Figs. 3–8. These figures are numbered chronologically by cruise, and within a

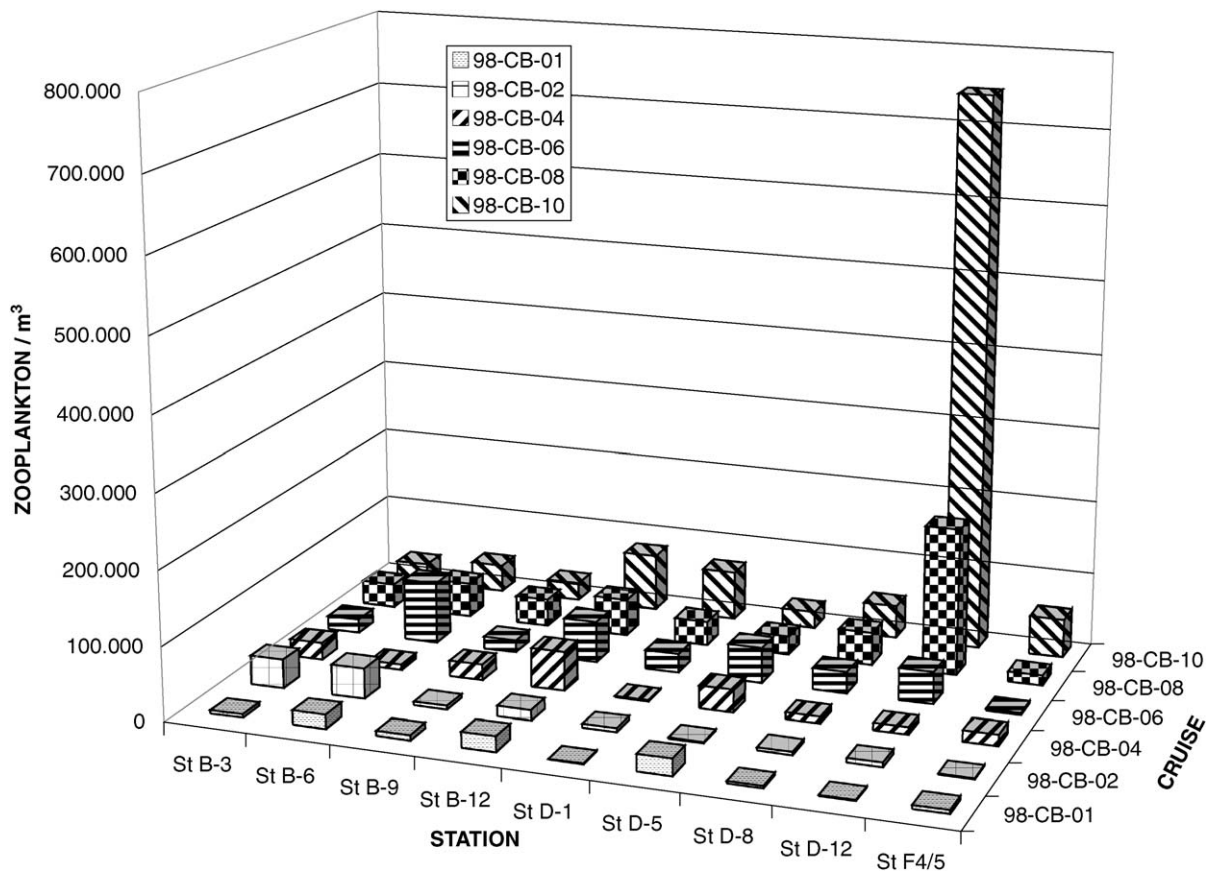


Fig. 2. Abundance of total zooplankton (animals m^{-3}) for all zooplankton sampling stations on the B and D transects, and at Station F4 or F5 during Cruises 98CB01 (6–9 April), 98CB02 (21–23 April), 98CB04 (4–7 May), 98CB06 (18–20 May), 98CB08 (2–4 June), and 98CB10 (17–18 June). Abundances for stations on the A transect during Cruise 98CB01 are not shown.

figure are presented alphabetically by transect, and numerically by station; therefore, figures are not referenced sequentially in the text.

Taxonomic categories shown as different patterns in stacked histograms are as follows: “copepod nauplii” (all taxa combined), “*Acartia*” (copepodites + adults of *Acartia hudsonica*), “*Calanus*” (copepodites + adults of *Calanus finmarchicus*), “*Centropages*” (copepodites + adults of *Centropages typicus* + *C. hamatus*), “*Oithona*” (copepodites + adults of *Oithona similis*), “*Pseudocalanus*” (copepodites + adults of *Pseudocalanus newmani* + *P. moultoni*), “*Temora*” (copepodites + adults of *Temora longicornis*), “other copepods”

(combined copepodites + adults of all other copepod taxa not listed above), “barnacle nauplii” (not further differentiated taxonomically), “*Evadne*” (all stages of *Evadne nordmani*), “*Oikopleura*” (all stages of *Oikopleura dioica*), “*Podon*” (all stages of *Podon polyphemoides*), “polychaete larvae” (not further differentiated taxonomically), “rotifers” (not further differentiated taxonomically, but all appeared to be *Synchaeta* spp.), “*Alexandrium*” (*Alexandrium fundyense*, see footnote ¹), “non-toxic dinos” (all dinoflagellates other than *A. fundyense*), “tintinnids” (not differentiated further taxonomically), “ciliates” (all aloricate ciliates that were not tintinnids), and “other”

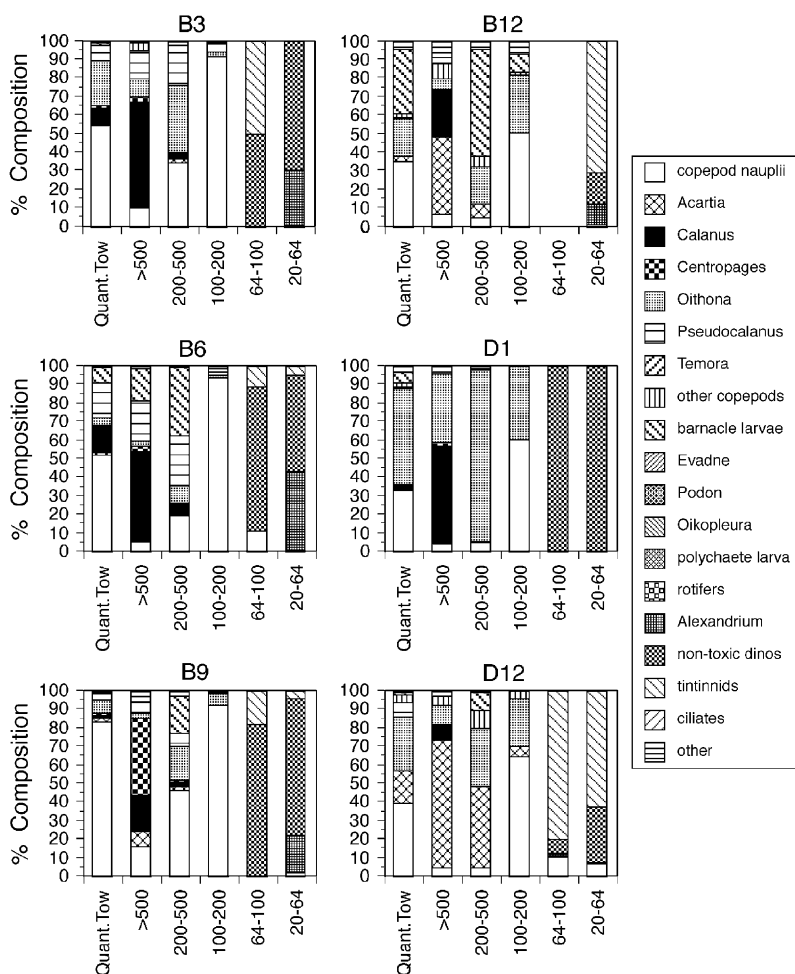


Fig. 3. Percent composition of dominant taxa in quantitative tows and in zooplankton size fractions from qualitative tows (100–200, 200–500, > 500 µm) and pumped samples (20–64, 64–100 µm) from Cruise 98CB01 (6–9 April)—Stations B3, B6, B9, B12, D1, D12.

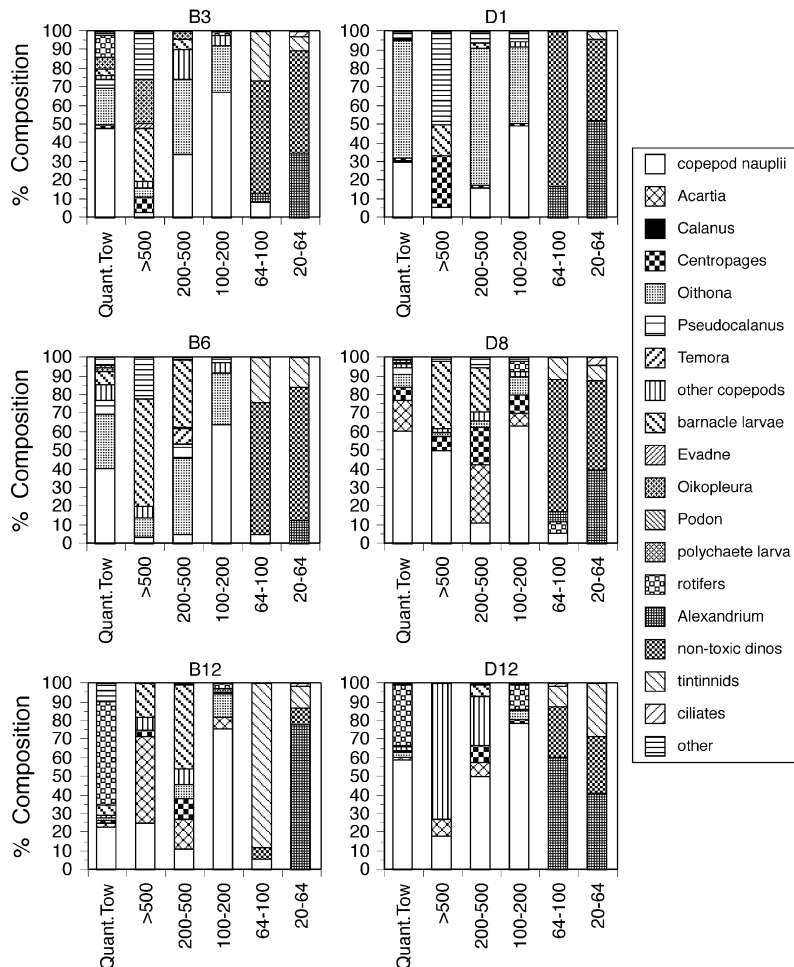


Fig. 4. Percent composition of dominant taxa in quantitative tows and in zooplankton size fractions from qualitative tows (100–200, 200–500, >500 μm) and pumped samples (20–64, 64–100 μm) from Cruise 98CB02 (21–23 April)—Stations B3, B6, B12, D1, D8, D12.

(any zooplankters not included in the categories listed above).

3.3. Zooplankton community composition in quantitative (>102 μm) samples

Samples collected with 102 μm mesh nets, assemblages were usually dominated by smaller zooplankters such as copepod nauplii, *Oithona similis*, and sporadically by other groups (e.g., rotifers). While there were no major temporal or spatial differences in overall abundance throughout most of the sampling period until the June increases, there were appreciable differences in the

dominant organisms at inshore versus offshore stations.

Copepod nauplii and *O. similis* dominated numerically at offshore stations such as B3 (Figs. 3 and 5), B6 (Fig. 4), and D1 (Figs. 3 and 8). Larger copepods such as *Calanus finmarchicus*, *Centropages typicus*, *Temora longicornis*, and *Pseudocalanus* spp. were also most abundant offshore. Conversely, *A. hudsonica*, barnacle nauplii (*Semibalanus* sp.), and rotifers (probably *Synchaeta* sp.) dominated collections at inshore locations such as Station B9 (Fig. 7), B12 (Figs. 3–5, 7, and 8), D8 (Figs. 4, 7, and 8) and Station D12 (Figs. 3, 4, 7, and 8). Rotifers were

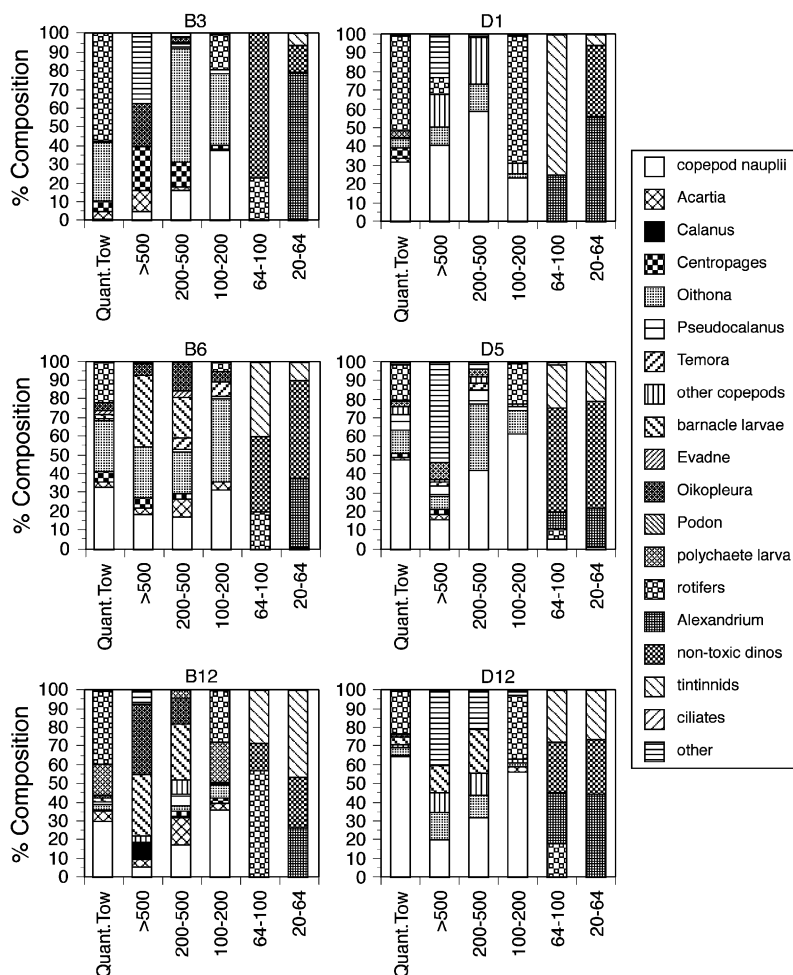


Fig. 5. Percent composition of dominant taxa in quantitative tows and in zooplankton size fractions from qualitative tows (100–200, 200–500, > 500 μm) and pumped samples (20–64, 64–100 μm) from Cruise 98CB04 (4–7 May)—Stations B3, B6, B12, D1, D5, D12.

particularly abundant during Cruises 98CB04 and 98CB06 in May, comprising 31–67% of animals recorded. A combination of *A. hudsonica* copepodites + adults and copepod nauplii (most of which were *Acartia* nauplii) accounted for the extremely high total abundance of 744,000 animals m^{-3} recorded for innermost Station D12 (Fig. 2) on Cruise 98CB10 in mid-June. The marine cladoceran *Evadne nordmani* was sporadically abundant in early and mid-June, comprising up to 31–50% of abundance during Cruise 98CB08 at Stations D5 (Fig. 7) and D8 (Fig. 7), and 92% at Station F4 (Fig. 8) during Cruise 98CB10.

3.4. Microplankton community composition (20–64 μm and 64–100 μm size fractions)

Most samples from the 20–64 μm size fraction had varying, but mainly low, proportions of *A. fundyense*, although this dinoflagellate largely accounted for the elevated PSP toxin concentrations in this size fraction (as high as 450 nmol STX equiv. g wet wt.⁻¹; Doucette et al., 2005). This fraction also contained other non-toxic dinoflagellates of the genus *Ceratium* (*C. furca*, *C. longipes*, and *C. tripos*), *Heterocapsa triquetra*, *Prorocentrum micans*, *Protoperidinium depressum*,

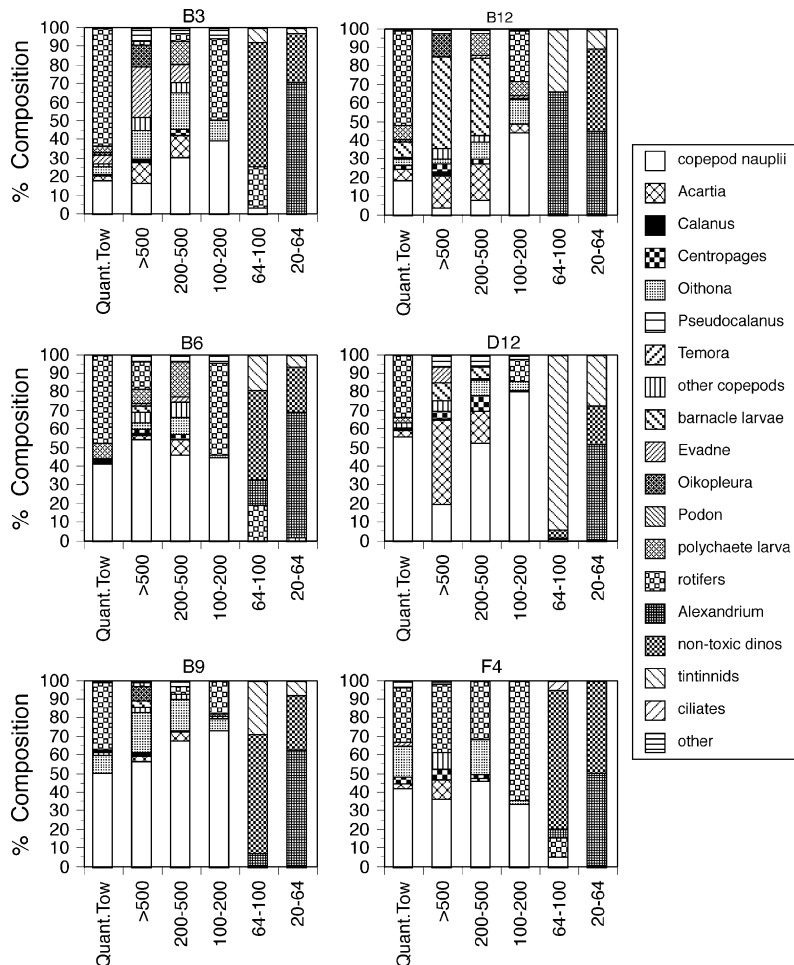


Fig. 6. Percent composition of dominant taxa in quantitative tows and in zooplankton size fractions from qualitative tows (100–200, 200–500, > 500 µm) and pumped samples (20–64, 64–100 µm) from Cruise 98CB06 (18–20 May)—Stations B3, B6, B9, B12, D12, F4.

P. pellucidum, *P. brevipes*, *P. depressum*, *Dinophysis norvegica*, and *Scrippsiella trochoideum*. There was a general tendency for the proportions of *A. fundyense* to increase from offshore to inshore locations. Conversely, proportions of non-toxic dinoflagellates generally decreased from offshore to inshore. Tintinnids such as *Helicostomella sublata* and *Tintinnopsis* spp. were frequently abundant at the most inshore stations B12 (Fig. 3) and D12 (Figs. 3 and 4). Samples from the 64–100 µm size fractions from all locations were dominated by non-toxic dinoflagellates, mainly the larger species of the genus *Ceratium*,

with variable combinations of tintinnids, aloricate ciliates, and copepod nauplii. There were a few rotifers in the 64–100 µm size fractions from cruises prior to and after Cruises 98CB04 and 98CB06 in May, but during these cruises, rotifers were often an abundant component of many samples, comprising up to 57% at Station B12 during Cruise 98CB04 (Fig. 5).

Most samples from the 64–100 µm size fractions generally contained few *A. fundyense* cells. However, 13 samples in the 64–100 µm size fractions (D1, D12 on Cruise 98CB02; D1, D5, D12 on Cruise 98CB04; B6, B9, B12, F4 on Cruise

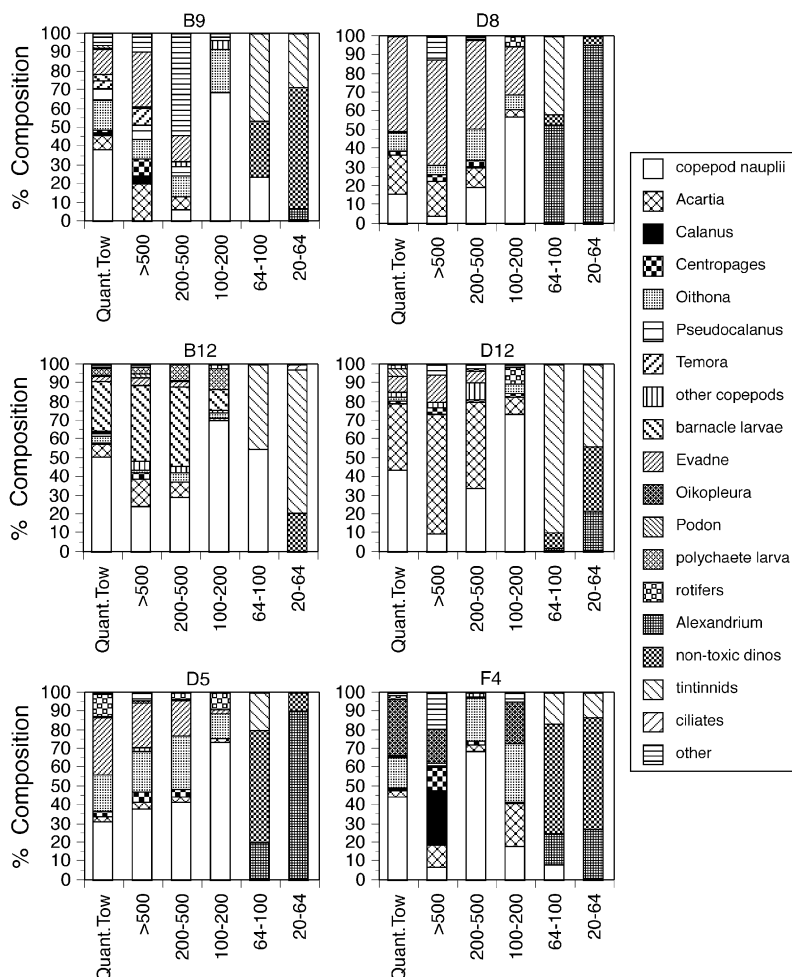


Fig. 7. Percent composition of dominant taxa in quantitative tows and in zooplankton size fractions from qualitative tows (100–200, 200–500, >500 μm) and pumped samples (20–64, 64–100 μm) from Cruise 98CB08 (2–4 June)—Stations B9, B12, D5, D8, D12, F4.

98CB06; D5, D8, F4 on Cruise 98CB08; and B12 on Cruise 98CB10) contained abundant *A. fundyense* cells, presumably due to clogging (Figs. 4–8). Although *A. fundyense* cells (diameter approximately 50 μm) should have passed through the 64 μm mesh, clogging of sieves with other larger plankton likely caused retention of these high proportions of *A. fundyense*. Nonetheless, the majority (44 of 57) of the samples in the 64–100 μm size fractions did not contain *A. fundyense* cells, suggesting that any PSP toxin detected in those samples would represent vectorial intoxication of microzooplankters such as heterotrophic dinoflagellates, tintinnids, aloricate ciliates, rotifers, and

copepod nauplii from feeding on *A. fundyense*. This contention was supported by direct microscopic observations of several cells of the tintinnids *H. sublata* and *Tintinnopsis* spp. containing from 1 to 3 *A. fundyense* cells.

3.5. Zooplankton community composition in size fractions (100–200 μm , 200–500 μm , and >500 μm)

Samples in the 100–200 μm size fraction were overwhelmingly dominated in most cases by copepod nauplii and small copepodites of *O. similis*. Most nauplii were those of *O. similis*

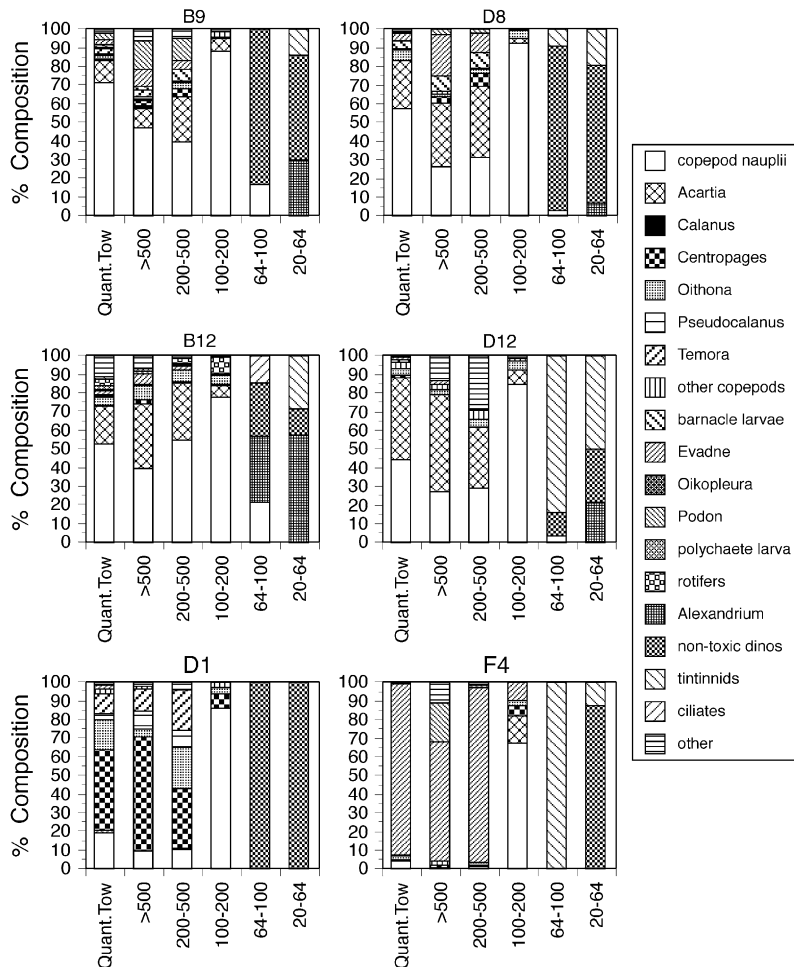


Fig. 8. Percent composition of dominant taxa in quantitative tows and in zooplankton size fractions from qualitative tows (100–200, 200–500, > 500 μm) and pumped samples (20–64, 64–100 μm) from Cruise 98CB10 (17–18 June)—Stations B9, B12, D1, D8, D12, F4.

except at the most inshore stations. There was generally a progressive decline in the relative proportions of *O. similis* copepodites moving from offshore to inshore. Rotifers were a major component of this size fraction during Cruise 98CB06.

Samples in the 200–500 μm size fraction contained fewer copepod nauplii, but progressively more copepodites and adults of *O. similis*, particularly at offshore locations. *C. typicus* and *Pseudocalanus* spp. copepodites were also abundant in the samples from offshore stations (Fig. 8). At the most inshore stations, such as B12 and D12, copepodites and adults of *A. hudsonica* usually

predominated (Figs. 3, 4, and 8). Also, during periods when barnacle nauplii and planktonic polychaete larvae were present in this size fraction (Fig. 6), they were most abundant inshore. The marine cladoceran *Evadne nordmani* was sporadically abundant, mainly offshore, comprising up to 93% of animals recorded for some samples (Fig. 8).

There were usually few copepod nauplii in the > 500 μm size fraction, except at a few inshore locations, where most nauplii were those of *A. hudsonica* (Figs. 4, 6, and 8). There were also few *O. similis* in these samples, except sporadically at offshore locations (Fig. 4). The > 500 μm size

fraction was usually dominated by copepodites and adults of *C. finmarchicus*, *C. typicus*, and *Pseudocalanus* spp. at offshore locations (Figs. 3 and 8), and by *A. hudsonica* inshore (Figs. 3 and 8). Also occasionally present in this size fraction were *O. dioica* (Fig. 7), *E. nordmani* (Figs. 6 and 8), barnacle nauplii (Figs. 6 and 7), and copepodites + adults of *T. longicornis*, the latter particularly in June during Cruise 98CB10 (Fig. 8).

4. Discussion

Zooplankton assemblages in size fractions that contained PSP toxins included a wide variety of microplankton (20–64 and 64–100 μm) and meso-zooplankton (100–200, 200–500, and > 500 μm) animals. Most previous zooplankton studies in the Gulf of Maine (reviewed by Davis, 1987) have used net meshes of 300–333 μm , which would severely underestimate the abundance of small zooplankters that are quantitatively sampled by the 102- μm mesh nets employed herein. Although a few studies in southern areas of the Gulf of Maine such as Georges Bank (Durbin et al., 2000, and references therein) and Massachusetts and Cape Cod Bays (Turner, 1994) have employed finer meshes of 35–150 μm , only the recent investigations of Durbin et al. (2002, 2003) have sampled non-estuarine areas of the central and northern offshore Gulf of Maine with similarly fine-mesh nets. The size-fractionation approach employed in our study highlights the extremely high springtime abundance of small zooplankters (e.g., copepod nauplii, *O. similis*, and rotifers) relative to larger but less abundant copepods that have dominated most previous collections. Also, our sampling regime revealed pronounced inshore to offshore gradients in zooplankton community composition for Casco Bay and its adjacent offshore waters.

The widespread presence of PSP toxins in all zooplankton size fractions (see Doucette et al., 2005) was surprising. Some of the zooplankters dominating samples containing PSP toxins are known to ingest toxic dinoflagellates, but certain other taxa representing heterotrophic and mixotrophic dinoflagellates, tintinnids and aloricate

ciliates, rotifers, and copepod nauplii are not. These findings suggest the existence of potential pathways of PSP toxin trophic transfer into zooplankton assemblages that are considered below.

Approximately half of the known species of dinoflagellates do not contain chlorophyll *a* and appear to feed heterotrophically (Hansen and Calado, 1999; Jacobson, 1999; Jeong, 1999). Several heterotrophic dinoflagellates have been shown to feed upon toxic algae (Jeong et al., 2003a, b), and such predation may influence development and/or termination of toxic algal blooms (Nakamura et al., 1992, 1995a,b; Matsuyama et al., 1999).

In Casco Bay, many of the non-toxic dinoflagellates recorded for the microplankton size fractions (20–64 and 64–100 μm) belong to genera known to contain heterotrophic species. It is therefore possible that these dinoflagellates consumed *A. fundyense* cells, and the toxin levels recorded for some of these size fractions may reflect trophic accumulation of PSP toxins due to predation by non-toxic dinoflagellates on toxic species.

Non-PSP toxin producing dinoflagellates frequently observed in Casco Bay include potentially heterotrophic genera such as *Protoberidinium* and *Dinophysis*. Members of the genus *Protoberidinium*, including several of the species recorded here, such as *P. brevipes*, *P. depressum*, and *P. pellucidum*, are known to feed on diatoms and other dinoflagellates using an extracellular pallium or feeding veil (Jacobsen and Anderson, 1986). Other species of *Protoberidinium* are known to feed on red-tide dinoflagellates (Jeong, 1994a; Jeong and Latz, 1994), including *Alexandrium* spp. (Jacobson and Anderson, 1986), as well as on copepod eggs and nauplii (Jeong, 1994b). Many species of *Dinophysis* do not contain chlorophyll *a* (Lessard and Swift, 1986), and some, including two that were often observed in our samples (i.e. *D. acuminata* and *D. norvegica*), are mixotrophic, in that they contain chlorophyll *a*; but they also have food vacuoles apparently containing other dinoflagellates (Jacobson and Anderson, 1994).

Some confirmed autotrophic dinoflagellates are also capable of mixotrophy (Granéli and Carlsson,

1998; Hansen, 1998; Stoecker, 1999), exhibiting photosynthetic traits as well as ingestion of other dinoflagellates (e.g., *Alexandrium* spp.). Several photosynthetic dinoflagellates such as *S. trochoidea*, *C. longipes*, and *P. micans*, which were abundant in our samples, have been observed to contain food vacuoles with ingested ciliates and other dinoflagellates (Jacobson and Anderson, 1996). The chlorophyll-bearing dinoflagellate, *C. furca*, which was often numerous in our samples, is mixotrophic and thus capable of ingesting ciliates, dinoflagellates, and other phytoplankton (Smalley and Coats, 2002; Smalley et al., 1999).

Several heterotrophic and mixotrophic dinoflagellates have been shown to ingest other dinoflagellates with confirmed toxicity (Jeong et al., 2001a,b; 2003b), but only the studies of Jeong et al. (2001a, 2003a) show that heterotrophic dinoflagellates can retain dinoflagellate toxins, making them potential vectors for these compounds. Interestingly, Jeong et al. (2001a) found that copepods ingested fewer cells of a heterotrophic dinoflagellate that itself had been feeding on a toxic dinoflagellate, compared to diets of the same heterotrophic dinoflagellate that had been feeding on a non-toxic dinoflagellate. Nevertheless, some of the toxicity recorded for 20–64 μm size fractions that contained few *A. fundyense*, but abundant non-toxic and potentially heterotrophic dinoflagellate could reflect vectorial intoxication of the non-toxic dinoflagellate via ingestion of *A. fundyense*.

Tintinnids and aloricate ciliates are abundant and important components of planktonic marine food webs (Pierce and Turner, 1992; and references therein). Several species of tintinnids (Stoecker et al., 1981; Maneiro et al., 2000; Kamiyama and Arima, 2001) and aloricate ciliates (Jeong et al., 1999, 2002; Gransden and Lewitus, 2003) are known to ingest toxic dinoflagellates or other harmful phytoplankton, and may be important in controlling blooms (Watras et al., 1985; Montagnes and Lessard, 1999). However, others have reported that ingestion of toxic dinoflagellates or other harmful phytoplankton can have deleterious effects on ciliates such as changes in swimming behavior (Hansen, 1989; Jakobsen

et al., 2001), an inability to support growth (Hansen, 1989, 1995; Buskey and Hyatt, 1995) or even causing ciliate mortality (Kamiyama and Arima, 1997).

In what is apparently the only indication of phytoplankton toxin accumulation in tintinnids (since the early work of White, 1979), Maneiro et al. (2000) found that concentrations of okadaic acid in smaller zooplankton size fractions (100–200, 200–300 μm) showed good correlation with abundance of the tintinnid, *Favella serrata*, indicating that the tintinnid had accumulated this toxin from feeding on blooms of the dinoflagellate *D. acuminata*. Thus, we suspect that PSP toxins occurring in the smallest zooplankton size fraction (64–100 μm) from Casco Bay, during periods when tintinnids but not *Alexandrium* were abundant in that size fraction, may reflect vectorial intoxication of these ciliates from consuming toxic dinoflagellate cells.

Rotifers are abundant components of the spring zooplankton in various temperate coastal waters (Johansson, 1983; Hernroth, 1983; Heinbokel et al., 1988; Dolan and Gallegos, 1992). A combination of requirements for low-salinity, high concentrations of phytoplankton prey, and shallow water to accommodate the benthic resting egg portion of their life cycle limit the distribution of marine rotifers to estuarine or coastal waters; however, such constraints, together with parthenogenetic reproduction, allow for explosive population growth, high biomass, and high grazing impact on phytoplankton where these conditions are met (Hernroth, 1983; Heinbokel et al., 1988; Park and Marshall, 2000). Thus, the presence of abundant *Synchaeta* spp. in Casco Bay during Cruise 98CB04 in May, particularly under conditions of a strong runoff event, is consistent with the conditions supporting high rotifer abundance.

Marine rotifers feed upon a variety of autotrophic and heterotrophic flagellate prey. The rotifer *Synchaeta cecilia* ingests autotrophic microflagellates and numerous dinoflagellate taxa (e.g., *A. fundyense* identified as *Gonyaulax tamarensis* var. *excavata*), although several of these dinoflagellates, including *A. fundyense*, failed to sustain rotifer growth when offered as unialgal diets (Egloff, 1988). The rotifer *Brachionus plicatilis*

fed upon the toxic dinoflagellate *Pfiesteria piscicida* with no apparent adverse effects in terms of reduced fecundity or increased mortality (Mallin et al., 1995), but the same rotifer species failed to exhibit sustained growth on a diet of the Texas brown tide alga (Buskey and Hyatt, 1995). Rotifers also prey upon bacterivorous microflagellates (Dolan and Gallegos, 1991) and are themselves consumed by omnivorous marine copepods (Stoecker and Egloff, 1987; Egloff, 1988; Dolan and Gallegos, 1992), thereby linking the microbial and mesozooplankton food webs. There is no available information indicating that marine rotifers can concentrate and retain PSP toxins from toxic dinoflagellates, but our finding of toxins in the microplankton size fractions dominated by rotifers suggests that this is a plausible scenario.

Various copepods and other mesozooplankters (>200 µm in length) have been shown to feed upon toxic phytoplankton (Turner and Tester, 1997; Turner et al., 1998a,b and references therein; Dutz, 1998; Teegarden, 1999; Frangópulos et al., 2000; Maneiro et al., 2000, 2002; da Costa and Fernández, 2002) and to accumulate phytoplankton toxins (White, 1981; Turriff et al., 1995; Tester et al., 2000, 2001; Lincoln et al., 2001; Bargu et al., 2002; Hamasaki et al., 2003; Teegarden et al., 2003). Also, zooplankton size fractions dominated by such larger taxa have been shown to contain PSP toxins or other algal toxins (White, 1979; Hayashi et al., 1982; Maneiro et al., 2000; Turner et al., 2000). Zooplankton that have accumulated these toxins have been implicated in field intoxication or mortality of fish (White, 1977, 1980; Lefebvre et al., 2002), sea birds (Nisbet, 1983; Work et al., 1993), and marine mammals (Geraci et al., 1989; Scholin et al., 2000; Durbin et al., 2002). However, the recent studies of Guisande et al. (2002) and Teegarden et al. (2003) suggested that copepods may be inefficient in retaining ingested PSP toxins, and that such grazers may metabolize and/or disperse considerable proportions of ingested PSP toxins into the environment where they are less likely to serve as vectors for the intoxication of higher trophic levels. Nonetheless, Teegarden et al. (2003) concluded that even if copepods do not retain much of the large amounts

of toxins calculated to have been consumed, the body burdens of PSP toxins in copepods in the Gulf of Maine might still be sufficient to transfer toxins to higher trophic levels. This conclusion is supported by the findings of Durbin et al. (2002), who measured body burdens of PSP toxins exceeding 1 ng STX eq. per animal in zooplankton assemblages dominated by the primary North Atlantic right whale prey species, *Calanus finmarchicus*. Moreover, Doucette et al. (in press) recently detected PSP toxins in fecal samples of north Atlantic right whales, although the effect of these algal toxins on this highly endangered marine mammal remains uncertain.

5. Conclusions

Similar to our earlier findings in the southern portion of the Gulf of Maine (Turner et al., 2000), the highest PSP toxin concentrations generally occurred in the larger zooplankton size fractions dominated by larger copepods such as *C. finmarchicus* and *C. typicus*. In contrast, the current study also revealed elevated toxin levels in many samples from smaller zooplankton size fractions in Casco Bay, dominated by heterotrophic dinoflagellates, tintinnids and aloricate ciliates, rotifers, copepod nauplii, and smaller copepods such as *O. similis* and, at inshore locations, *A. hudsonica*. Thus, during spring blooms of *A. fundyense* in Casco Bay, PSP toxins can be more widespread throughout the zooplankton grazing community than previously realized. Finally, our observations suggest numerous avenues for investigation of previously unstudied routes of toxin transfer into higher trophic levels, involving such potential vectors as heterotrophic dinoflagellates, rotifers, protozoans, copepod nauplii, and small copepods.

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