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TROPHIC INTERACTIONS WITHIN THE PLANKTONIC FOOD WEB IN MANGROVE CHANNELS OF TWIN CAYS, BELIZE, CENTRAL AMERICA

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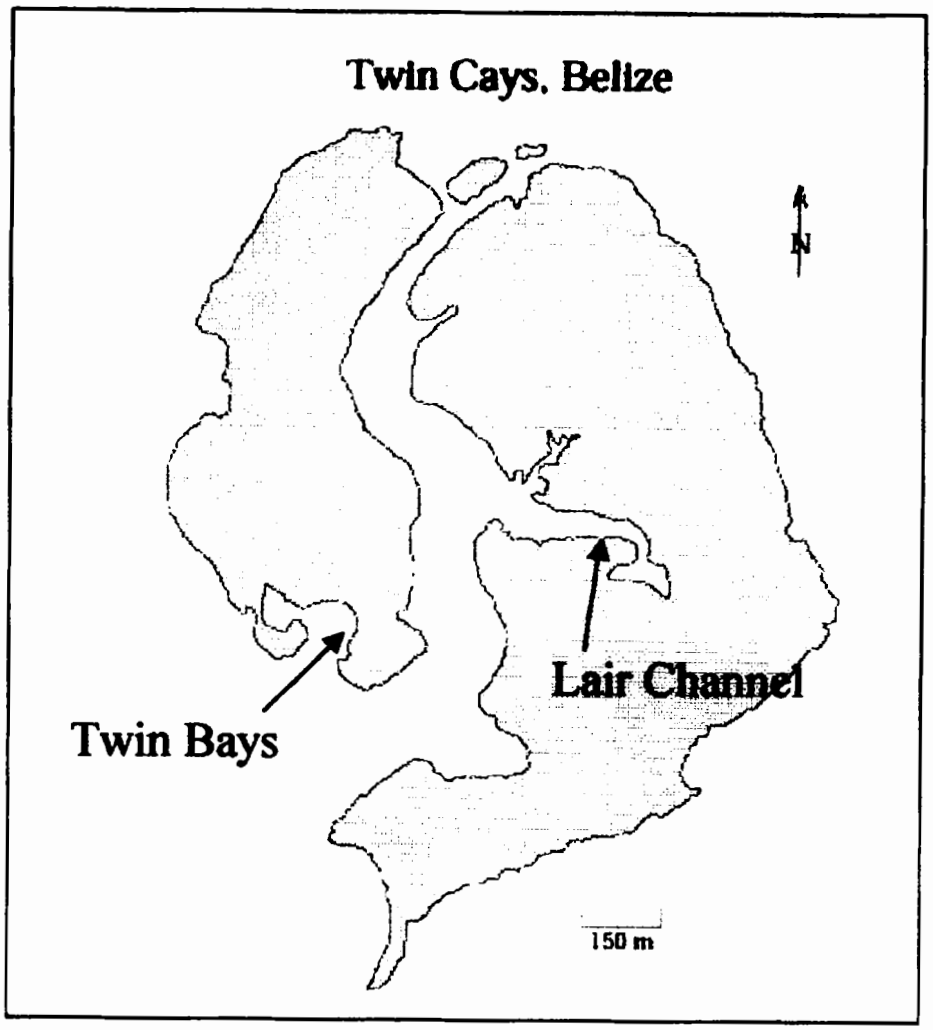

Figure 1. Index map showing study sites, Twin Cays, Belize

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ABSTRACT

The tidal channels of mangrove islands such as Twin Cays, Belize support a productive and diverse microplankton assemblage. In turn, this microplankton community supports large populations of copepods that form dense aggregations in the prop-root environment along the margins of these channels. The growth rate of the phytoplankton community and the grazing rate of the heterotrophic microzooplankton community were measured using the seawater dilution method. In separate experiments, the grazing rate of the swarm-forming copepod *Dioithona oculata* on natural microplankton assemblages was measured. Chlorophyll concentrations in the natural plankton assemblages used in these experiments ranged from 1-to-11 μg Chl *a* L^{-1}. Dinoflagellate populations typically ranged from 17-to-50 cells ml^{-1}, with heterotrophic dinoflagellates generally exceeding autotrophic forms in abundance. Ciliates were the second most abundant form of heterotrophic microzooplankton with populations ranging from 1-15 cells ml^{-1}. Results of the dilution experiments indicate that, during the study period, microzooplankton grazed between ca. 60-90% of potential phytoplankton production and phytoplankton growth exceeded microzooplankton grazing in all experiments. Grazing studies with *D. oculata* indicated that copepod ingestion rates were highest on ciliates and autotrophic dinoflagellates and that copepod populations are capable of grazing about 10% of the protozoan population each day.

INTRODUCTION

Microzooplankton populations, composed mainly of heterotrophic protozoa and small larval metazoa, such as copepod nauplii, form an important trophic link between phytoplankton and larger zooplankton, such as copepods (Sherr et al., 1986; Stoecker and Capuzzo, 1990). Heterotrophic protists feed efficiently on pico- and nanoplankton size classes that are too small for many copepods, and they repackage this organic matter into sizes that are more easily consumed by copepods (Sherr and Sherr, 1992). Copepods in turn may play an important role in structuring the planktonic community; by grazing on microplankton-sized particles such as ciliates and dinoflagellates they may indirectly

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enhance the growth of small-sized phytoplankton that are grazed by protozoa (Sherr and Sherr, 1994; Buskey et al., 2003). This study examines the trophic interactions between phytoplankton, heterotrophic microplankton and copepods within the mangrove channels of Twin Cays, Belize.

The dominant copepod species found in the mangrove channels is *Dioithona oculata* (Ferrari et al., 2003). Adult and late copepodites of this species form dense swarms in light shafts penetrating the mangrove canopy during the day. These swarms disperse at dusk and reform at dawn (Ambler et al., 1991). Copepod densities average 30 copepods ml^{-1} in swarms (Buskey et al., 1996) but are reduced to only a few copepods L^{-1} when the copepods are dispersed at night (Ferrari et al., 2003). These extraordinary densities within swarms suggest that competition for food must be intense. Gut pigment analysis demonstrated that swarming copepods had less chlorophyll in their guts compared with dispersed copepods at night (Buskey et al., 1996), but this difference could also be due to a diel pattern of feeding behavior which has been demonstrated in other copepod species (e.g. Mackas and Bohrer, 1976).

In addition, copepods are well known to be omnivorous and gut-pigment analysis reveals nothing about feeding on heterotrophic organisms that do not contain chlorophyll. The adaptive value of this swarming behavior is thought to include protection from predation, reduced dispersion and enhanced mating opportunities (Hamner and Carlton, 1979). These benefits are thought to compensate for the energetic costs of swarming behavior in terms of reduced feeding within swarms (due to intense competition) and high metabolic costs of increased swimming speeds to maintain swarms within light shafts in spite of tidal currents (Buskey et al., 1996; Buskey, 1998). These currents may also renew the food supply to a swarm, reducing food competition. *D. oculata* also have strong diel patterns in their reproductive behavior and physiology. Females carry their eggs externally in two clusters and these eggs usually hatch at night between midnight and 6 AM (Ambler et al., 1999) while the copepods are dispersed from their swarms. If adult *D. oculata* fed on their own nauplii they would be exposed to high predation pressure if eggs hatched within swarms during the day.

In this study we measured phytoplankton growth and microzooplankton grazing using the seawater dilution method (Landry and Hassett, 1982) and we measured the feeding rates of adult *Dioithona oculata* on natural microplankton assemblages using 24-hour incubations similar to the method used by Gifford and Dagg (1988). A second set of experiments using 12-hour day-or-night incubations was performed to determine if there was a natural diel pattern in the feeding rate of *D. oculata*. Finally, in order to determine if *D. oculata* prey on their own young, we ran feeding experiments with adult *D. oculata* and newly released nauplii.

METHODS

Field experiments were carried out at Twin Cays, a pair of mangrove-covered islands ca. 2 km NW of the Smithsonian Institution's field station on Carrie Bow Cay in Belize, Central America. Microzooplankton-grazing experiments were carried out during April, 2002. Seawater for microzooplankton grazing studies was collected in the Lair Channel of Twin Cays (Fig. 1) by gently submerging a 20 L carboy with a-200 μm mesh screen over the opening to exclude larger zooplankton. The dilution method (Landry and Hassett, 1982; Landry et al., 1995) was used to assess the growth of phytoplankton populations and the grazing impact of microzooplankton. This method uses serial dilution of natural microplankton assemblages to decouple growth of phytoplankton and grazing of microplankton. The method is based on the assumption that microzooplankton grazing declines linearly with increased dilution of natural microplankton assemblages with filtered seawater (decreasing grazers' encounter rate with food) but that phytoplankton growth is unaffected by this dilution.

Filtered seawater for dilution experiments was produced by gravity filtering seawater from the Lair Channel successively through 3.0 and 0.2 μm porosity Gelman capsule filters. Mixtures of filtered seawater and whole seawater containing the natural microplankton community were then prepared consisting of 100%, 50%, 25% or 10% whole seawater. Triplicate 500 ml polycarbonate bottles were filled with each mixture. Small amounts of phytoplankton nutrients (equivalent to F/200, Guillard and Ryther, 1962) were added to each bottle to compensate for a possible reduction in regenerated nutrients caused by the dilution of grazers. Three additional bottles containing whole seawater were incubated without added nutrients to assess the effects of nutrient addition. Initial samples (in triplicate) for enumeration of microzooplankton and for chlorophyll *a* analysis were collected from each dilution mixture. The bottles were incubated under ambient temperature and light conditions by hanging them in a mesh bag suspended in partial shade beneath the pier on Carrie Bow Cay. The alternate periods of shade and sunlight along the edge of the pier simulate the light environment within the mangrove channels and the gentle rocking motion of the waves beneath the pier served to help keep the bottles mixed. At the end of the incubation period, final samples were taken from each bottle for microzooplankton enumeration and chlorophyll analysis.

The apparent growth rate of phytoplankton in individual bottles (based on changes in chl *a*) was calculated using the exponential growth model (Landry and Hassett, 1982):

$$P_t = P_0 \exp[k-g]t$$

where P_0 and P_t are chl *a* concentrations at the beginning and end of the experiment, respectively; k and g are instantaneous coefficients of phytoplankton growth and grazing mortality, respectively; t is time (d). Coefficients k and g were determined from linear regression of apparent growth rate of phytoplankton ($1/t \ln[p_t/p_0]$) on the fraction of diluted seawater. The negative slope of the line is the daily grazing coefficient (g) and the

y-intercept is the phytoplankton growth rate (k) with added nutrients. Phytoplankton growth in control bottles with no added nutrients was calculated as $(1/t \ln [p_t/p_0] + g)$.

Copepods for grazing experiments were collected during early morning or late afternoon from swarms at one of two locations along the shoreline of Twin Cays: either from Twin Bays or the Lair Channel (Fig. 1). Swarms of *Dioithona oculata* typically form in shafts of sunlight within the shade along the fringes of red-mangrove shorelines (Ambler et al., 1991). Copepods were collected with a 153-μm mesh sieve attached to a small transparent plastic bag. While snorkeling, the sieve was gently pulled through the swarm to capture copepods and then the top of the plastic bag was sealed and returned to a nearby small boat. The copepods were gently rinsed into a large plastic bucket containing seawater. A plastic carboy of whole seawater, excluding mesozooplankton, was collected at the same site by placing a piece of 200 μm mesh over the opening to the carboy and gently submerging it.

At the beginning of a grazing experiment, the carboys of whole seawater were gently mixed and poured into five 500-ml polycarbonate bottles. The polycarbonate bottles were gently mixed again, a sample of 100 ml was removed from each bottle for chlorophyll analysis, and a 60 ml sample was removed for microzooplankton enumeration. A target number of approximately 25 copepods was added to each of three experimental bottles for each experiment. The actual number of copepods was counted at the end of experiments. Two bottles did not receive copepods and were used as controls. All bottles were then topped with whole seawater and sealed with parafilm before tightening the screw caps. The bottles were then placed in a mesh bag and hung in partial shade along the edge of the pier at Carrie Bow Cay to incubate. An initial set of four experiments was run with 24-hour incubations during April 2000 to determine the feeding rates of *Dioithona oculata* on various groups of microplankton. A second series of experiments were performed during March 2001 with 12-hour incubations during daylight (6AM - 6PM) or nighttime hours (6PM - 6AM) to determine if there were diel variations in feeding behavior. Following the period of incubation, the bottles were gently inverted several times to ensure that the contents were well-mixed, and then 100 ml samples were removed for chlorophyll analysis and 60 ml samples were removed for preservation with Lugol's Iodine and later microzooplankton enumeration.

Initial examination of microzooplankton samples was performed on Carrie Bow Cay to learn which species of dinoflagellate were heterotrophic and which were autotrophic because formaldehyde or glutaraldehyde-preserved samples (which would retain chlorophyll autofluorescence) could not be transported easily back to Texas for analysis. Samples from the whole seawater (20 ml) were fixed with three drops of 37% formalin and gently filtered onto a 0.4-μm polycarbonate filter with a 0.4 μm-Metricel filter as a backing to ensure a more even distribution of cells on the sample filter. These samples were examined using a Zeiss epifluorescent microscope with a blue excitation filter to determine the composition of autotrophic and heterotrophic dinoflagellates in our samples. Sketches and measurements were made of the predominant autotrophic and

heterotrophic dinoflagellates for later reference in counting the Lugol's Iodine-preserved samples.

Samples for total chlorophyll *a* analysis were filtered through 0.4 μm porosity polycarbonate membrane filters; size-fractionated chlorophyll *a* samples were first filtered through a 10 μm-porosity polycarbonate membrane filter and then again through a 0.4 μm-porosity filter. Filters were placed in 10 ml of 95% acetone in a glass scintillation vial, refrigerated in the dark (bottles covered with aluminum foil), and chlorophyll was allowed to extract for 12 hours. Chlorophyll concentration was measured using a Turner Designs TD-700 fluorometer using the nonacidification method of Welschmeyer (1994). Field calibration of the fluorometer was confirmed using a solid fluorescence standard (Turner Designs 7000-994). During the dilution experiments performed in April 2002, a Turner Designs Aquafluor portable fluorometer was used for chlorophyll *a* measurements.

Samples for microzooplankton analysis were preserved in 5% (v/v) Lugol's Iodine. Dinoflagellates were typically more numerous than ciliates in our samples so samples of 10 ml were settled to enumerate dinoflagellates and 40 ml samples were settled in an Utermohl chamber to enumerate ciliates. Notes on the sizes and shapes of autotrophic and heterotrophic species examined in the field were used to differentiate autotrophic and heterotrophic species in the Lugol's Iodine-preserved samples. The dimensions of each cell were measured under the microscope at (300X) magnification for later estimation of cell biovolumes using the equations recommended by Hillebrand et al. (1999). These biovolumes were converted to carbon estimates using the conversion factor for ciliates of Putt and Stoecker (1989) and that of Menden-Deuer and Lessard (2000) for heterotrophic dinoflagellates. Filtration and ingestion rates of the copepods were calculated based on the equations of Frost (1972).

A second set of experiments was run to determine if *Dioithona oculata* would prey on their own nauplii. Adults collected from swarms in the late afternoon were placed in a small 20 L aquarium overnight. The next morning water from this aquarium was gently passed through a nested pair of sieves. The top sieve (153 μm mesh) retained the adult *D. oculata* while allowing the newly hatched nauplii to pass through and be retained on the second sieve (20 μm mesh). The nauplii captured on the second sieve were gently rinsed into a plastic petri dish. These were then used in the predation experiments. Known numbers of nauplii were counted out and added to each of four 70 ml-clear-plastic tissue culture flasks. Six adult copepods were added to three of the four flasks while a fourth flask served as a control without added copepods. These flasks were then incubated for ca. 24 hours on a shaded table in a small water bath with ambient-temperature seawater flowing through (28 - 29 °C). After incubation, Lugol's Iodine was added to the contents of the tissue culture flask to kill and stain the copepods and the number of nauplii and copepods counted.

RESULTS

The microplankton assemblage near Twin Cays during the first set of experiments in April 2000 was characterized by moderately high chlorophyll *a* concentrations (6.4 - 11 μg L^{-1}), abundant dinoflagellates (ca. 5-18 x 10^3 L^{-1} for autotrophs, 7-34 x 10^3 L^{-1} for heterotrophs), numerous aloricate ciliates (ca. 1-3 x 10^3 L^{-1}) and a small number of tintinnids (<1 L^{-1}) (Fig. 2). During the second set of experiments in March 2001, the microplankton assemblages at the same locations were characterized by lower chlorophyll *a* concentrations (3.4 - 6.5 μg L^{-1}), lower dinoflagellate concentrations (ca. 2-4 x 10^3 L^{-1} for autotrophs, 5-10 x 10^3 L^{-1} for heterotrophs), fewer ciliates (0.2 - 1.6 x 10^3 L^{-1}) and a similar concentration of tintinnids (<1 L^{-1}). Although we did not examine the distribution of chlorophyll *a* into different size fractions during the first set of experiments in April 2000, during the second set of experiments in 2001 chlorophyll *a* was fairly evenly distributed between the <10-μm size fraction (1-3 μg L^{-1}) and the >10-μm size fraction (2-3.5 μg L^{-1}). During the microzooplankton grazing experiments in April 2002, the waters of Lair Channel were characterized by lower chlorophyll *a* concentrations (1.1–2.3 μg L^{-1}), abundant dinoflagellates (ca. 4-17 x 10^3 L^{-1} for autotrophs, 6-34 x 10^3 L^{-1} for heterotrophs), numerous aloricate ciliates (ca. 2-14 x 10^3 L^{-1}) and a small number of tintinnids (<1 L^{-1}).

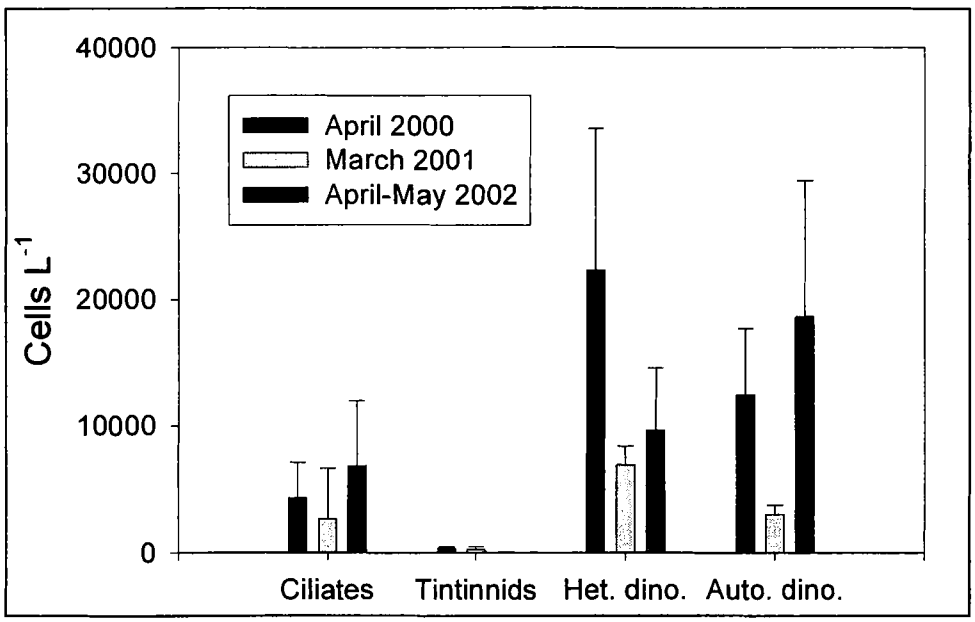

Figure 2. Mean abundances (±1 SD) of broad categories of microplankton in the mangrove channels of Twin Cays during each of the three years of this study, including ciliates, tintinnids, heterotrophic dinoflagellates (het. dino.) and autotrophic dinoflagellates (aut. dino.). Means from four experiments in April 2000, eight experiments in March 2001 and four experiments in April-May 2002.

The microplankton assemblage in the water column of the mangrove channels near Twin Cays was dominated by a fairly small number of genera. The autotrophic dinoflagellates belonged mainly to species of *Peridinium*, *Gymnodinium* or *Prorocentrum* in samples taken in all three years (2000-2002). Other common phytoflagellates in samples from both years included cryptomonads and euglenoids. Among the heterotrophic dinoflagellates, the dominant genera included *Protoperidinium*, *Gyrodinium*, *Gymnodinium* and *Cochlodinium* during both sampling years. Ciliate populations were strongly dominated by *Mesodinium* with smaller numbers of *Laboea* in both years. During 2001 and 2002, *Strombidium* were also abundant. Although generally rare compared with the aloricate ciliates, the most abundant tintinnids were species of *Eutintinnus* and *Tintinnopsis*. The size-frequency distributions for broad taxonomic categories of microplankton indicate that most ciliates had cell volumes comparable to equivalent spherical diameters (ESD) between 10-20 μm (Fig. 3). Autotrophic dinoflagellates were present in a wide range of sizes from ca. 6-40 μm ESD, whereas a large proportion of heterotrophic dinoflagellates were <20 μm ESD.

The results of the four dilution experiments are revealed through plots of apparent phytoplankton growth as a function of dilution factor (Fig. 4). The slope of the regression line represents the grazing coefficient (g) and the y-intercept of the regression line represents the growth rate of the phytoplankton with added nutrients when released from grazing (k). The grazing coefficients measured in these experiments ranged from 0.32-0.95 (d^{-1}) and phytoplankton growth coefficients ranged from 0.94-1.55 (d^{-1}) with added nutrients and from 0.66-1.27 (d^{-1}) in control bottles without added nutrients (Table 1). The enhanced growth of the 100% seawater dilution with f/200 nutrient additions compared with similar incubations without nutrient addition indicates that the phytoplankton populations in the mangrove channels were nutrient-limited. The phytoplankton growth coefficients for control bottles without added nutrients correspond to a range of 0.95-1.83 doublings per day, indicating very rapid phytoplankton growth (Table 1). Growth of broad categories of microplankton within the control bottles was lower with specific growth rates (mean $\pm$ SD) of ciliates, autotrophic dinoflagellates and heterotrophic dinoflagellates calculated at 0.22 ± 0.31, 0.35 ± 0.25 and 0.15 ± 0.11 d^{-1}, respectively. The calculated estimates of potential phytoplankton production, actual phytoplankton production and grazing indicate that microzooplankton grazing removed between 57-91% of potential phytoplankton production per day (Table 1).

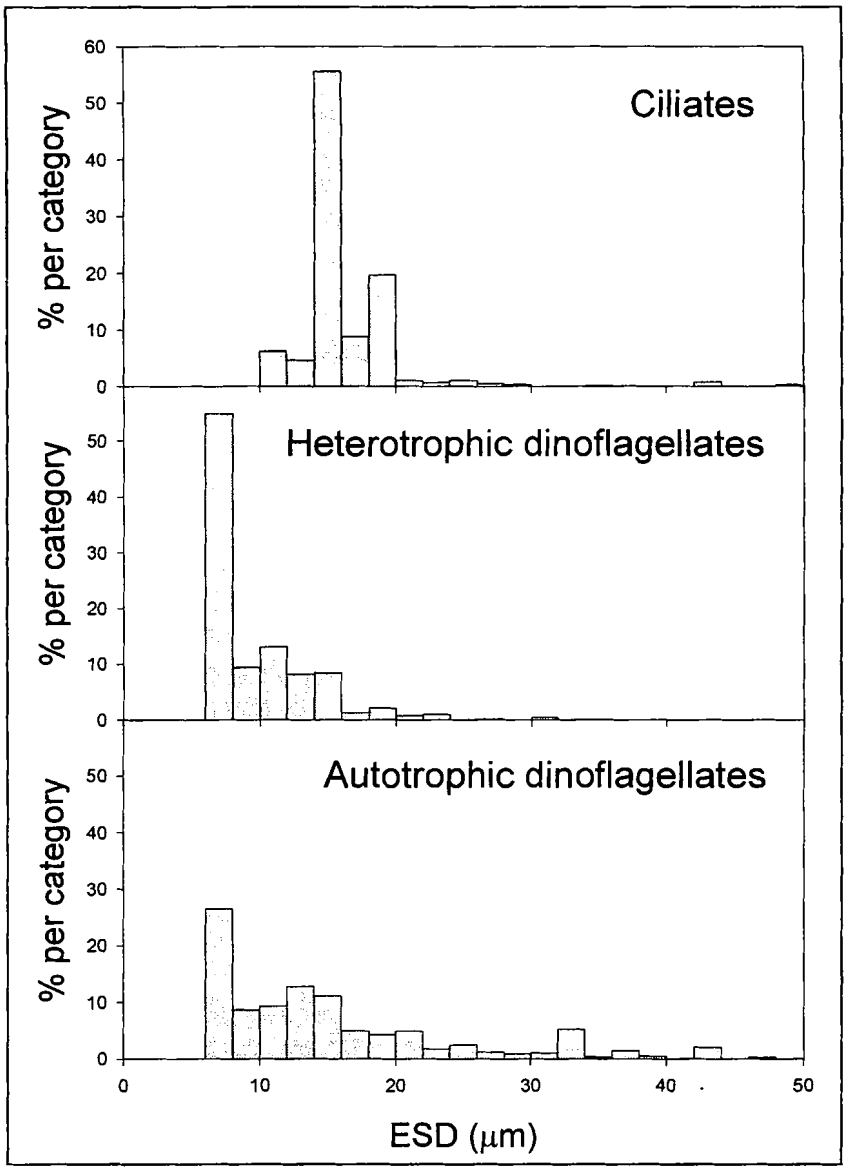

Figure 3. Size-frequency distribution of ciliates, heterotrophic dinoflagellates and autotrophic dinoflagellates based on pooled data from control samples of grazing experiments performed during April 2000. Cell volumes were calculated and then converted to equivalent spherical diameters (ESD).

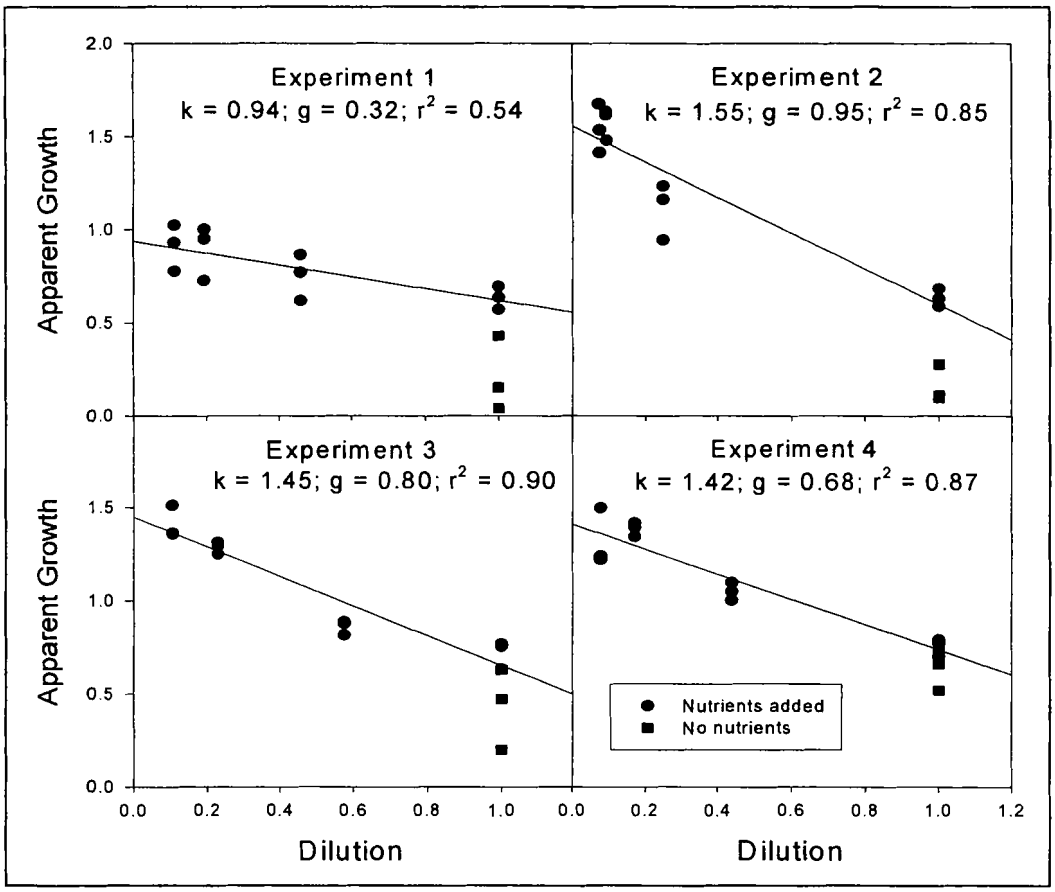

Figure 4. Results of dilution experiments. Apparent growth is plotted against the actual dilution factor based on chlorophyll *a* measurements. The phytoplankton growth coefficient (k) is the y-intercept of the regression line and the grazing coefficient (g) is the negative slope of the regression line. Squares represent the apparent growth of undiluted seawater without added nutrients. All experiments performed with samples collected from Lair Channel.

Table 1. Grazing by microzooplankton on phytoplankton based on dilution experiments. k: phytoplankton growth in bottles with nutrients added; μ: phytoplankton growth in control bottles without nutrients added; phytoplankton doublings = μ /ln2; g = grazing coefficient; potential phytoplankton production = $(P_0e^{\mu}) - P_0$; actual phytoplankton production = $(P_0e^{(\mu-g)}) - P_0$; % potential production removed = (potential production – actual production)/potential production.

Date (2002)	k (d^{-1})	μ (d^{-1})	Phyto doublings(d^{-1})	g (d^{-1})	% potential phyto prod. removed (d^{-1})
25 April	0.94	0.66	0.95	0.32	57
28 April	1.55	1.11	1.60	0.95	91
30 April	1.45	1.25	1.80	0.80	77
5 May	1.42	1.27	1.83	0.68	69

Clearance rates of *Dioithona oculata* estimated from 24-hr incubation experiments indicated generally higher clearance rates on ciliates compared with those for dinoflagellates (autotrophs or heterotrophs) or total phytoplankton, estimated with bulk chlorophyll *a* measurements (Fig. 5).

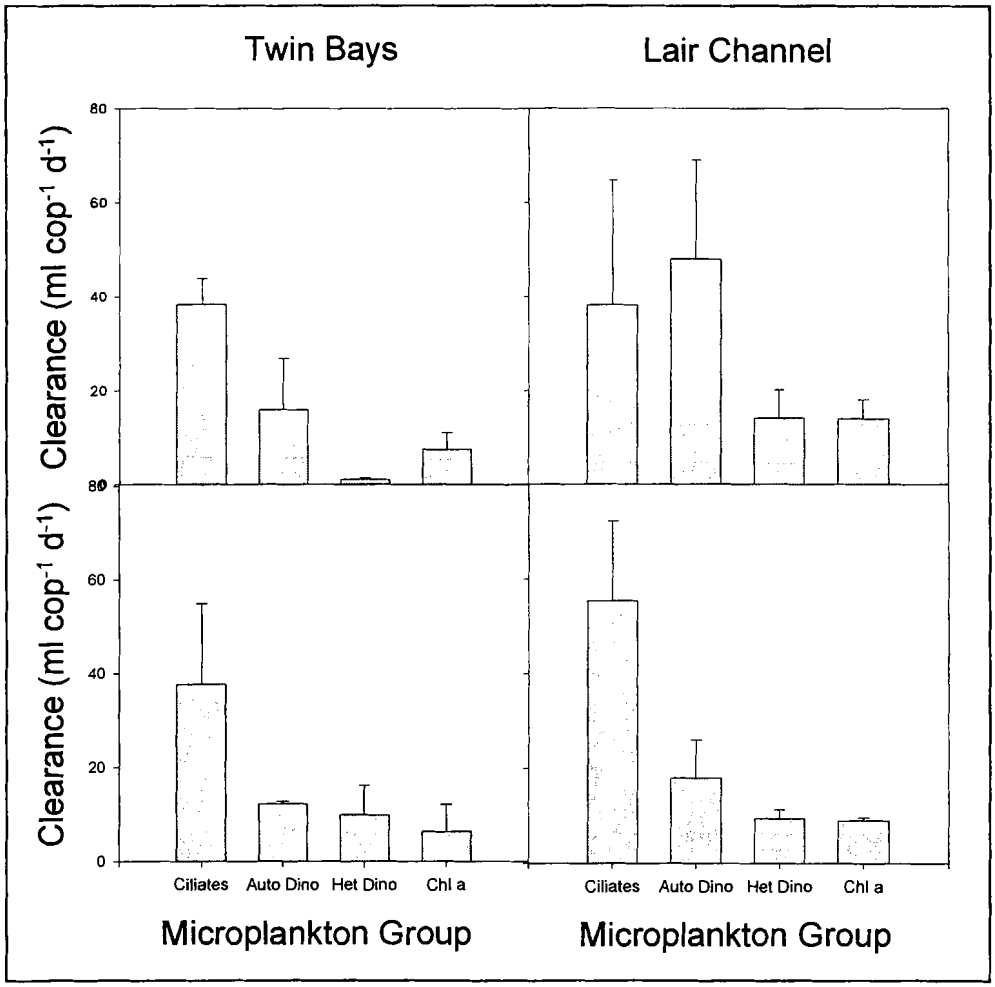

Figure 5. Daily clearance rates of *Dioithona oculata* on ciliates, autotrophic dinoflagellates (Auto Dino), heterotrophic dinoflagellates (Het Dino) and total phytoplankton measured as chlorophyll *a* (Chl a) during 24-hour incubation experiments carried out during two days with samples collected in Twin Bays and during two days with samples collected in Lair Channel during April 2000.

Mean clearance rates on ciliates ranged from about 38-55 ml copepod^{-1} d^{-1} with clearance rates on autotrophic and heterotrophic dinoflagellates ranging from 12-48 and from 1-14 ml copepod^{-1} d^{-1}, respectively. Clearance rates from 12-hour incubations were performed to determine if there were diel patterns of grazing in *D. oculata* independent of any effects caused by swarming behavior. These 12-hour clearance rates were

doubled to produce daily clearance rates comparable with the 24-hour incubation experiments. There was no consistent pattern of clearance rates being higher during day or night (Fig. 6) suggesting that there is no innate pattern of diel variations in feeding. Clearance rates calculated in these 12-hour incubations were somewhat higher than those found in the 24-hour incubations.

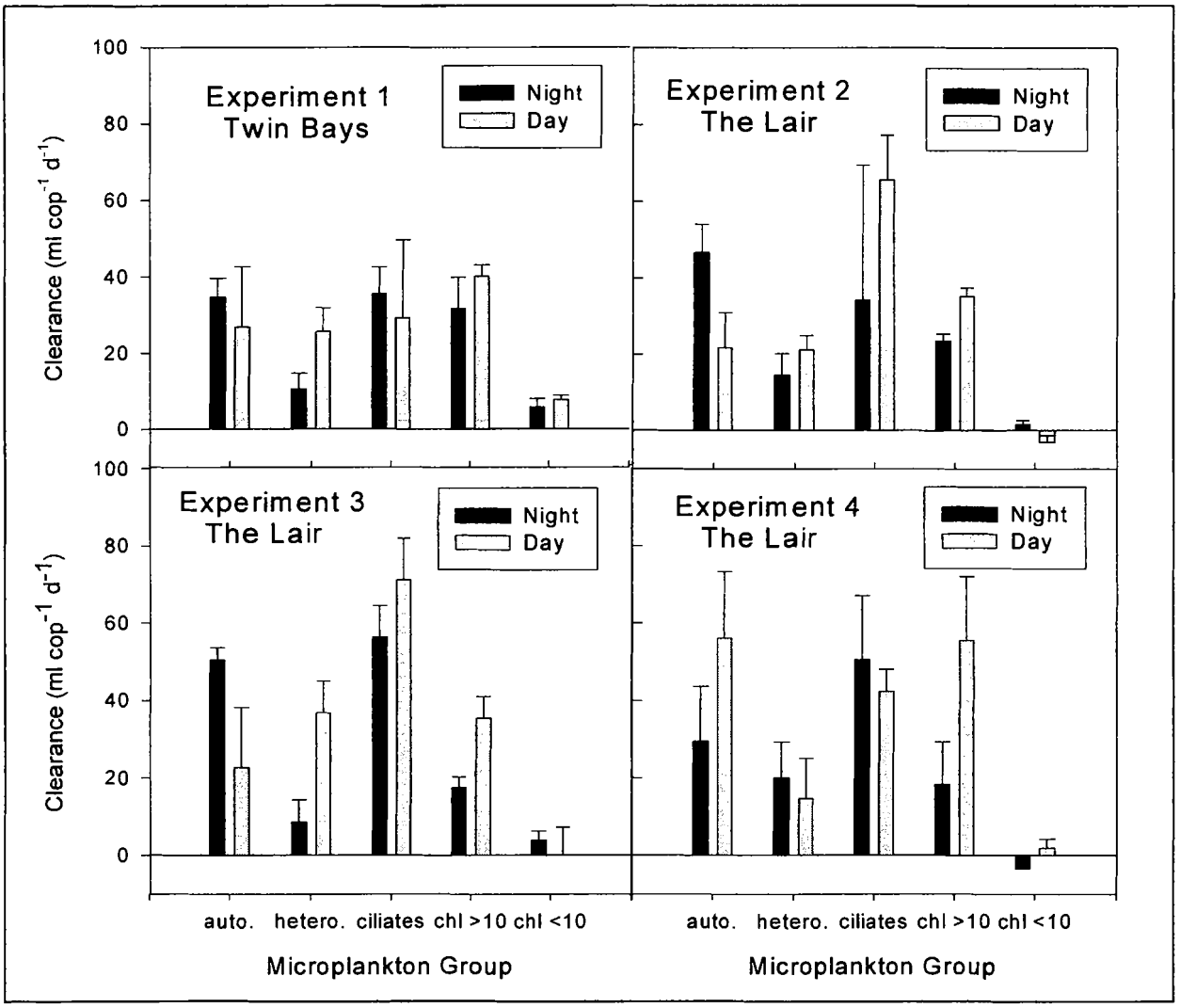

Figure 6. Clearance rates of *Dioithona oculata* on autotrophic dinoflagellates (auto.), heterotrophic dinoflagellates (hetero.) and size-fractionated total phytoplankton measured as chlorophyll *a* greater than 10 μm (chl >10) and as chlorophyll *a* less than 10 μm (chl < 10) during 12-hour incubation experiments carried out during either daylight or nighttime conditions in April 2001.

This may be due, in part, to the generally lower abundances of protozoan populations during the 12-hour incubations in 2001 (Fig. 2). When clearance rates for ciliates, autotrophic dinoflagellates and heterotrophic dinoflagellates are plotted as a function of

their initial abundance in samples, there is a general trend of lower clearance rates at higher cell abundances (Fig. 7). Clearance rates for ciliates during the 12-hour incubations ranged from 30-71 ml copepod^{-1} d^{-1}, and clearance rates on autotrophic and heterotrophic dinoflagellates ranged from 22-56 and 10-37 ml copepod^{-1} d^{-1}, respectively. The overall mean clearance rates for both sets of experiments were 47, 32 and 16 ml copepod^{-1} d^{-1} for ciliates, autotrophic dinoflagellates and heterotrophic dinoflagellates, respectively. Growth rates of microplankton within control bottles during both sets of grazing experiments were uniformly low for all broad categories with mean specific growth rates of 0.02, 0.04 and 0.01 d^{-1} for ciliates, autotrophic dinoflagellates and heterotrophic dinoflagellates, respectively.

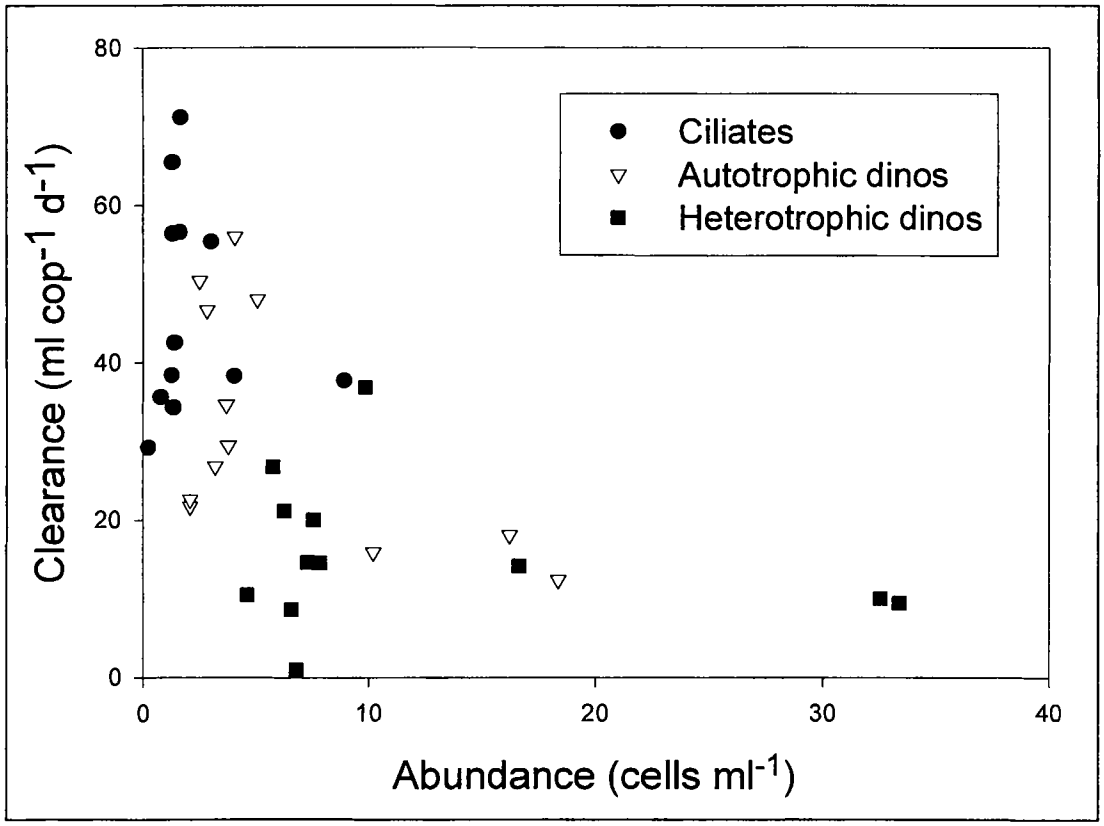

Figure 7. Relationship between clearance rate of *Dioithona oculata* on ciliates, autotrophic and heterotrophic dinoflagellates to their initial abundance in 12- and 24-hour incubation experiments.

Ingestion rates estimated from clearance rates, abundances and cell volumes during 24- hour incubation experiments ranged from mean values of 46-114 ng C copepod^{-1} d^{-1} for ciliates, 50-136 ng C copepod^{-1} d^{-1} for autotrophic dinoflagellates and 1-38 ng C copepod^{-1} d^{-1} for heterotrophic dinoflagellates (Fig. 8). Although *Dioithona oculata* has generally higher clearance rates on ciliates (Fig. 5), autotrophic

dinoflagellates may comprise a similar or slightly larger proportion of their ingested food. Heterotrophic dinoflagellates, while often very abundant in these experiments, had both lower clearance rates and were of generally smaller size and, therefore, account for a smaller fraction of the estimated carbon ingested by *D. oculata.* Combined ingestion on these three food categories was ca. 200 ng C copepod^{-1} d^{-1} for each of the four experiments.

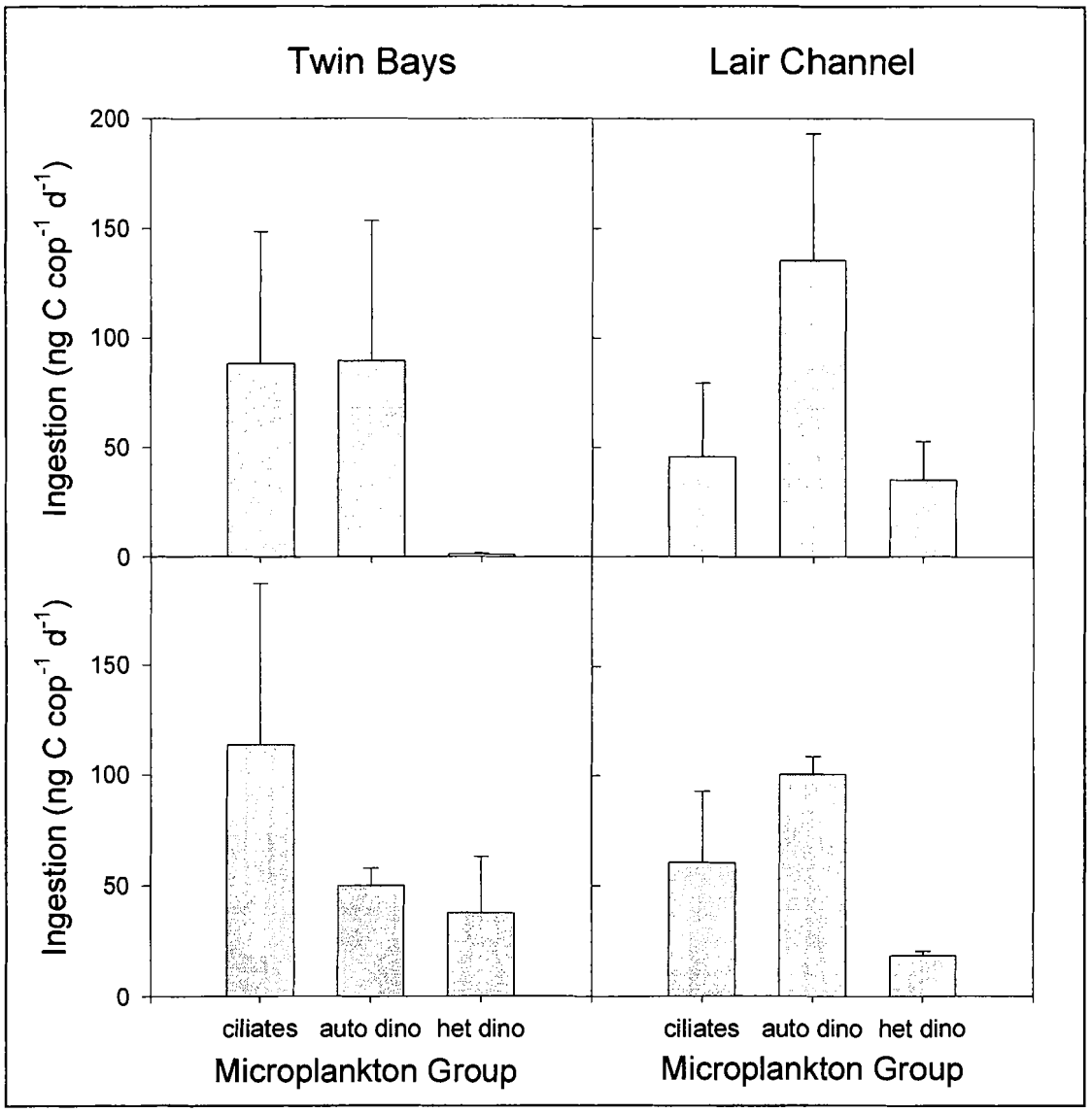

Figure 8. Estimates of carbon ingested by *Dioithona oculata* as ciliates, autotrophic dinoflagellates (auto dino) and heterotrophic dinoflagellates (het dino) for 24-hour incubation experiments carried out during two days with samples collected in Twin Bays and during two days with samples collected in Lair Channel.

Predation rates of *Dioithona oculata* on its own nauplii increased linearly over the range of prey densities tested (0.2–8 nauplii ml^{-1}, Fig. 9). Maximum predation rates were ca. 2.5 nauplii $copepod^{-1}$ h^{-1}. However, there is no evidence of saturation in the functional response relationship so higher predation rates may be achieved at higher densities of nauplii. By comparing the size distributions of the natural prey distributions before and after feeding by copepods during the 24-hour incubation experiments, it is apparent that copepods feed preferentially on larger prey (>14 μm equivalent spherical diameter, Fig.10).

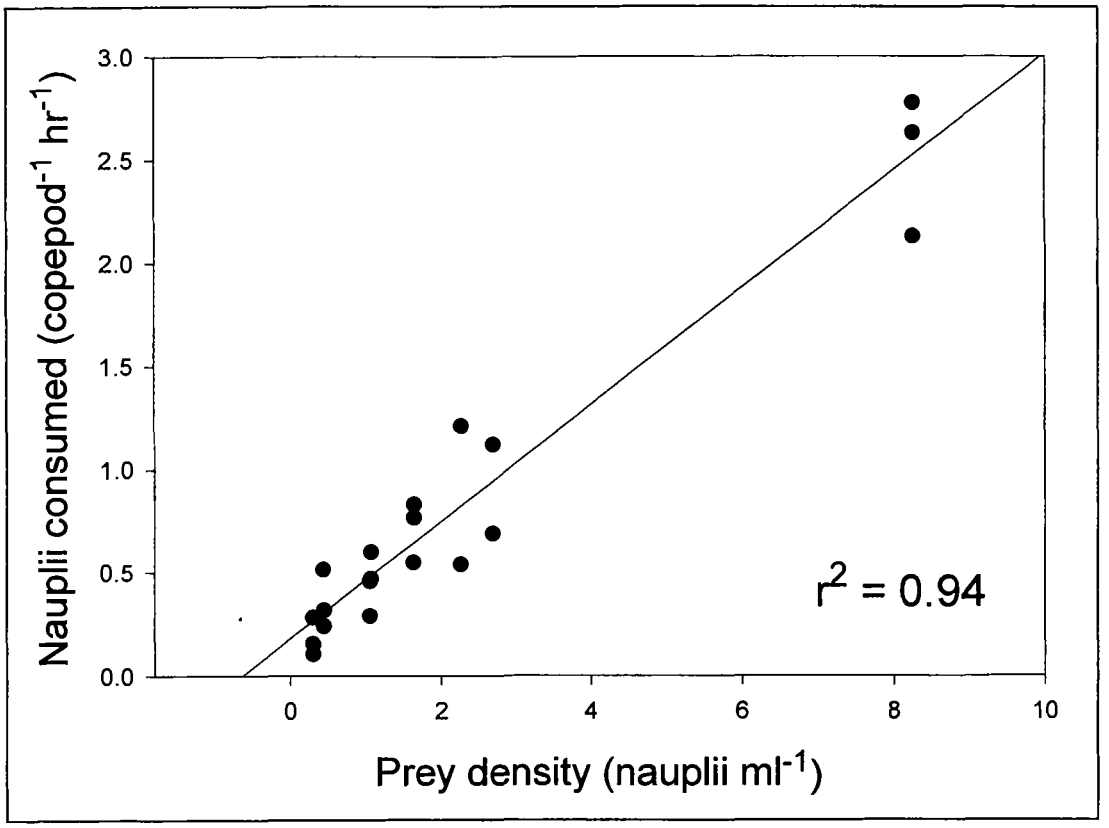

Figure 9. Ingestion rates of adult *Dioithona oculata* on newly hatched nauplii of *D. oculata* as a function of prey density.

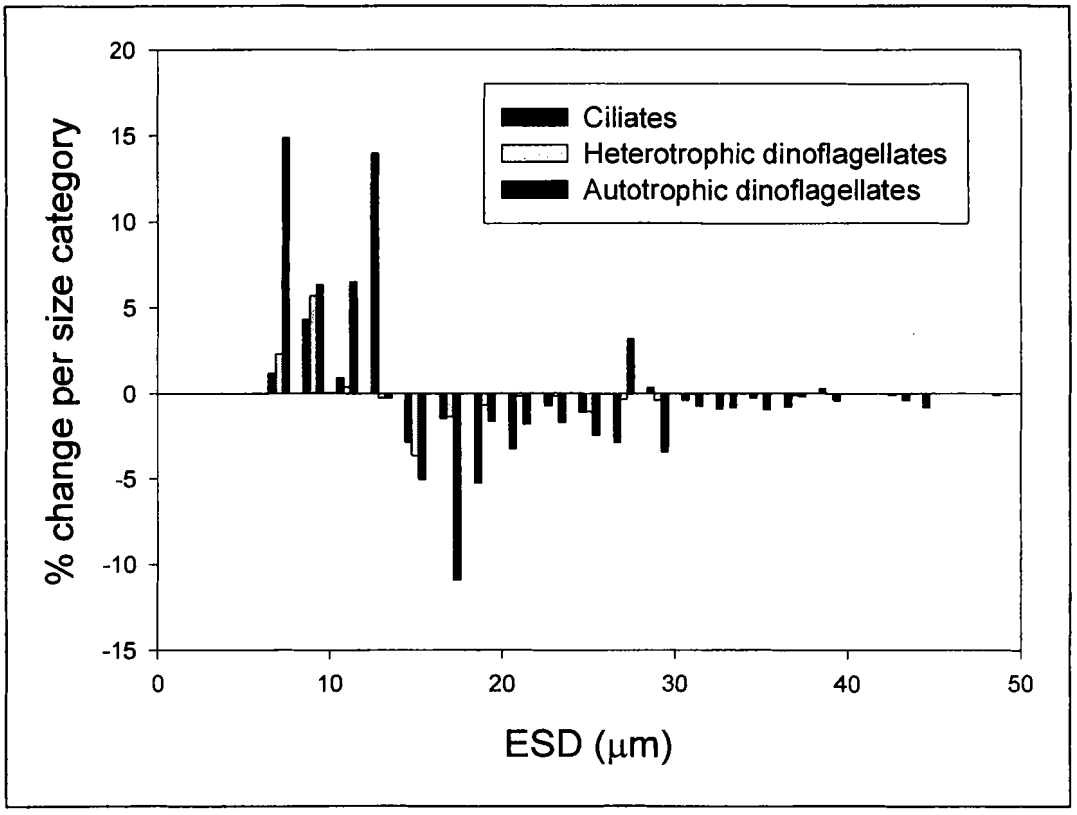

Figure 10. Percentage change in size categories of microplankton between the beginning and end of 24-hour feeding experiments with *Dioithona oculata*. Decreases in size categories indicate that copepods were removing cells through grazing.

DISCUSSION

Microzooplankton are abundant in the mangrove channels of Twin Cays and they are an important trophic link between the pico- and nanoplankton-sized organisms they feed on and the larger zooplankton that in turn feed on them. For broad categories of protists, heterotrophic dinoflagellates were most abundant, followed by aloricate ciliates and tintinnids (Fig. 2). Abundances of heterotrophic dinoflagellates and ciliates in this study (mean ca. 2-20 ml $^{-1}$) are comparable to those found in other studies of coastal regions in tropical and subtropical environments (e.g. Lynn et al., 1991; Buskey, 1993; Strom and Strom, 1996). Few studies have been published on the microzooplankton of mangrove channels but similar densities of ciliates are found in undisturbed mangrove creeks of North Queensland, Australia (McKinnon et al., 2002). Likewise, the low densities of tintinnids found in this study (mean < 1 ml^{-1}) are comparable to the densities reported for mangrove waters on the southeast coast of India (Godhantaraman, 2001).

It is now generally accepted that microzooplankton are the major grazers of phytoplankton throughout much of the world's oceans (Strom, 2002 and references therein). Based on our studies, the microzooplankton community in the mangrove channels of Twin Cays is a major consumer of phytoplankton, consuming ca. 60-90% of the potential phytoplankton production per day (Table 1). In this study, apparent growth of phytoplankton exceeded grazing by the microzooplankton community in all four experiments. In contrast, in a study of mangrove creeks with higher phytoplankton biomass than in the mangrove channels of Twin Cays (McKinnon et al., 2002), phytoplankton growth and grazing were found to be roughly in balance although microzooplankton grazing usually exceeded phytoplankton primary production. The grazing rates we measured with the dilution method are more comparable to measurements made in other less eutrophic coastal environments (e.g. Tamigneaux et al., 1997).

The phytoplankton community of the mangrove channels of Twin Cays appears to be highly productive. Phytoplankton growth rates estimated from changes in chlorophyll *a* concentrations in our dilution incubations indicate rapid phytoplankton growth equivalent to a range of 0.9 to 1.8 doublings per day (Table 1). Low concentration nutrient additions to dilution incubations (equivalent to f/200) caused a pronounced increase in phytoplankton growth rates (Fig. 4, Table 1) indicating that phytoplankton populations of Lair Channel were nutrient-limited. Nutrient additions are recommended for studies in oligotrophic waters where dilution may reduce the availability of recycled nutrients to phytoplankton (Landry et al., 1995). Nutrient additions are typically omitted in studies of more eutrophic coastal waters where it is assumed or known that nutrients are not limited (e.g. Gallegos, 1989; McKinnon et al., 2002). Given the evidence for nutrient limitation of phytoplankton growth in the mangrove channels of Twin Cays, nutrient additions are appropriate for these dilution experiments.

The dominant copepod in the mangrove channels of Twin Cays, *Dioithona oculata*, forms dense swarms along the fringes of the mangrove channels. Given the extremely high densities of copepods within these swarms (over 30 copepods ml^{-1}, Buskey et al., 1996) it seems likely that competition for food within swarms is intense. Previous attempts to compare the feeding behavior of swarming copepods during the day to that of dispersed copepods at night using the gut pigment method (Dagg, 1983) indicated that copepods within swarms generally had lower levels of chlorophyll *a* in their guts than dispersed copepods at night (Buskey et al., 1996). This difference could be due to higher competition for food in the dense swarms during the day compared with that of dispersed copepods at night, or due to a diel feeding behavior of the copepods where feeding is most intense at night (Mackas and Bohrer, 1976; Stearns, 1986). In addition there are a number of potential problems with interpretation of feeding rates using the gut pigment method (e.g. Baars and Helling, 1985; Conover et al., 1986) although this method can still be used to indicate relative feeding rates on phytoplankton

if it is assumed that gut passage rates and pigment destruction rates are the same under the conditions being compared. However, the gut pigment method only provides information for feeding rates on chlorophyll-containing cells (phytoplankton) and yields no information on the feeding rate on heterotrophic organisms. Many copepods are omnivorous in their diets and consume both phytoplankton and heterotrophic microzooplankton (Gifford and Dagg, 1988; Tiselius, 1989).

The results of our grazing experiments clearly indicate that *Dioithona oculata* is omnivorous and feeds on a mixture of microplankton including copepod nauplii (Fig. 9), ciliates and both autotrophic and heterotrophic dinoflagellates (Fig. 5). Relatively few detailed studies have been made of the feeding behavior of marine cyclopoid copepods compared with that of calanoid copepod species. The most common and best-studied marine cyclopoid copepods belong to the closely related genus *Oithona*. However, the overall behavior pattern of most *Oithona* species is in sharp contrast to the behavior of *D. oculata*. Species of *Oithona*, such as *O. nana*, *O. plumifera* and *O. similis,* have behavioral patterns that are characterized by long periods of inactivity during which they sink slowly (Hwang and Turner, 1995; Svensen and Kiorboe, 2000; Paffenhofer and Mazzocchi, 2002). In contrast, *D. oculata* swims nearly continually with a jerky motion and is capable of swimming at sustained speeds of up to 2 cm s^{-1} (Buskey et al., 1996). Marine cyclopoid copepods, such as *Oithona* species, are thought to feed only on moving prey and to detect their prey primarily through mechanoreception (Svensen and Kiorboe, 2000; Paffenhofer and Mazzocchi, 2002). It seems unlikely that *D. oculata* could feed in this manner because of the difficulty in detecting prey based on mechanoreception within a dense swarm of actively swimming copepods. It is unknown how *D. oculata* detect and capture their food but it is clear that they are feeding within these dense swarms based on both gut pigment analysis (Buskey et al., 1996) and the ability to collect fecal pellets from copepods captured from swarms (unpublished observations).

There have been relatively few studies of feeding by marine cyclopoid copepods on natural plankton assemblages. *Oithona similis* has been shown to feed primarily on ciliates and dinoflagellates greater than 10 μm diameter (Nakamura and Turner, 1997) and to have average carbon ingestion rates similar to those we found for *Dioithona oculata*. However, the average clearance rates measured for this copepod in the rich coastal waters of Massachusetts were much lower than those we found for *D. oculata* in the mangrove channels of Belize. In a study of unidentified *Oithona* species in the Antarctic (Lonsdale et al., 2000), clearance rates on protozoa were more similar to those found this study. It does appear that *D. oculata* feed preferentially on larger-sized food particles which would be consistent with a more raptorial-feeding mode than a filter-feeding mode. Based on the change in size frequency distribution of microplankton before and after grazing by *D. oculata* (Fig.10), it is apparent that these copepods only have a grazing impact on particles larger than 14 μm equivalent spherical diameter. Higher clearance rates on ciliates and autotrophic dinoflagellates compared with

heterotrophic dinoflagellates also indicate a preference for classes of microplankton which include more large cells.

Although metazoan microzooplankton were not abundant enough in our incubation experiments to determine feeding rates of adult *D. oculata* on natural assemblages, it is clear that these copepods are capable of feeding on active metazoan prey such as copepod nauplii (Fig. 9). These rare, large prey could be important components of their diet in nature. Other marine cyclopoid copepods have been shown to feed readily on copepod nauplii (Lampitt, 1978; Nakamura and Turner, 1997) including cannibalistic feeding on their own nauplii (Uchima and Hirano, 1986). *D. oculata* females have evolved a diel periodicity in the timing of egg production and egg hatching; egg clusters are produced during the day while the copepods swarm but the eggs hatch from these clusters (attached to the female body) when the copepods are dispersed at night (Ambler et al., 1999). This is highly useful as an antipredator adaptation for both adult females and newly hatched nauplii. Females bearing egg clusters are more visually conspicuous and are preyed on preferentially by planktivorous fish when not in swarms (Collumb, 2000); nauplii would be heavily preyed upon if they were hatched within high-density swarms during the day (Fig. 9).

Feeding of *Dioithona oculata* swarms will have an important impact on microplankton populations in mangrove channels. Average clearance rate of these copepods on ciliates is 40 ml per copepod per day. Thus a population density of 25 copepods per liter can potentially consume all ciliates in the water column. However, the average density within swarms of *D. oculata* can exceed 30 copepods per ml (Buskey et al., 1996); at this density a swarm potentially can clear the water of ciliates in less than two minutes. However, average current speeds in prop-root environments are ca. 1 cm s^{-1} (Buskey, unpublished data) so since swarms hold position within light shafts the food to swarms is continually renewed. Average densities of copepods throughout the entire mangrove channel, based on population density estimates taken at night when copepods are dispersed from swarms, are ca. three copepods per liter (Ferrari et al., 2003). At this density, *D. oculata* could consume ca. 10% of the ciliate population per day. However, given the slow growth rates measured for heterotrophic protozoa in our experiments, copepods could still play an important role in structuring the microzooplankton community, especially given their apparent size-selective feeding behavior (Fig. 10).

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