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EXPERIMENTAL MANIPULATIONS OF PHYTOPLANKTON + ZOOPLANKTON + CTENOPHORE COMMUNITIES, AND FOODWEB ROLES OF THE CTENOPHORE, Mnemiopsis leidyi

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ABSTRACT

50 L mesocosm experiments incubated outdoors using various combinations of phytoplankton + zooplankton (= *Acartia tonsa*) + ctenophores (= *Mnemiopsis leidyi*) evaluated the effect of various herbivore/carnivore combinations on phytoplankton species composition, succession and abundance. It also tested the Greve-Parsons hypothesis that small flagellates favor energy flow to ctenophores (= jellyfish) leading to their predominance, whereas diatom predominance favors young fish. The experiments show that ctenophores can markedly regulate phytoplankton community structure, abundance, and ratio of diatoms : flagellates through their grazing on zooplankton. Ctenophores themselves influence phytoplankton size structure and subsequent energy flow, independent of whether their occurrences/swarms are a consequence of whether flagellates or diatoms predominated as a result of other environmental regulation, including in response to nutrient or climatic changes suggested by Greve and Parsons. Ctenophores are both a consequence of and regulators of energy flow via their selective predation on zooplankton and associated influence on phytoplankton community structure. It is shown that the role of ctenophores (= jellyfish) in establishing foodweb patterns is diverse and even favorable to fish production and influenced by the ratios of ctenophores : zooplankton, diatoms : flagellates, and other trophic components The balance between the ctenophore : zooplankton ratio particularly influences whether the presence of ctenophores is favorable to finfish and/or (in shallow areas) shellfish, or is detrimental to recruitment of these trophic levels. Various energy flow pathways incorporating these elements are diagrammed in emendation of the Greve-Parsons hypothesis.

INTRODUCTION

In Narragansett Bay, Rhode Island, USA, population dynamics of the ctenophore *Mnemiopsis leidyi* influence summer phytoplankton dynamics in two ways: through predation on zooplankton and through excretion of nutrients during grazing (Deason & Smayda, 1982a,b). Although experiments indicate that *Mnemiopsis leidyi* does not graze phytoplankton ranging in size up to circa 80 µm (the maximum size tested), nutritionally superfluous capture and destruction of phytoplankton on mucus secreted by *Mnemiopsis* occur (Deason & Smayda), 1982b). This paper presents experimental evidence from small scale mesocosms that, although not herbivorous, *Mnemiopsis leidyi* can influence phytoplankton species composition and bloom dynamics through its grazing on zooplankton. Two experimental series (A,B) are described here.

METHODS

50 L of seawater collected from Narragansett Bay were placed into 110 L mesocosms incubated outdoors in a running sea water tank at temperatures ranging from 20°-23°C. Screening placed over the mesocosms reduced incident irradiance to approximately 60%, which ranged from 137 to 682 ly d^{-1}. Mesocosms, stirred twice daily with a small paddle, were sampled daily at 0900 hr after thorough mixing; experiments lasted from three to five days. Treatments set up were phytoplankton control (P) and various grazing combinations: phytoplankton + ctenophores (P+C), phytoplankton + zooplankton (P+Z), and phytoplankton + zooplankton + ctenophores (P+Z+C). In experimental series B, ammonia, phosphate and silicate were added daily (0900 hr) to all mesocosms at a rate approximating their daily excretion release from the benthic *Nephthys - Nucula* community found in Narragansett Bay (Hale, 1975) assuming a mean water column depth of 10 m and continuous 24 hr nutrient excretion. Concentrations added yielded 0.34 µM ammonia, 0.048 µM phosphate, and 0.52 µM silicate. Seawater pumped directly from Narragansett Bay into the mesocosms at the beginning of the experiments provided a natural phytoplankton assemblage. The diatoms *Rhizosolenia fragilissima* and *Thalassionema nitzschioides* dominated in experiment A, and microflagellates and the diatoms *Cerataulina pelagica* and *Skeletonema costatum* in experiment B. *M. leidyi* was hand dipped from Narragansett Bay for experimental use. Zooplankton were collected with a 153 µm mesh net tow, transferred to 50 L of unfiltered seawater, and reconcentrated for addition to the mesocosms.

The following parameters were measured daily: nutrients, phytoplankton species composition and abundance, chlorophyll, primary production and ctenophore length converted to weight using the equations of Kremer and Nixon (1976). Zooplankton abundance in each treatment was determined at the initiation and termination of the experiments to estimate grazing rates on phytoplankton. In the presence of ctenophores, zooplankton grazing rates were estimated assuming the phytoplankton losses were due entirely to zooplankton feeding. Ctenophore predation of zooplankton was estimated based on a "volume swept clear" procedure using the P + Z treatment as a control and the daily *Mnemiopsis* dry weight estimates. Apparent grazing selection was estimated using Vanderploeg and Scavia's (1979) electivity index. This paper focuses on the changes in phytoplankton community structure in the various mesocosm treatments and their foodweb implications.

RESULTS

Experiment A

Experiment A, lasting four days, focused on diatom responses (Fig.1). Initial diatom populations in the replicated treatment varied from 251 to 371 cells ml^{-1}. Initial zooplankton populations, dominated by *Acartia tonsa* (9 to 18 animals L^{-1}), varied from 16 to 27 animals L^{-1}. Crab zoea, other benthic larvae and cladocerans were secondary components. Five ctenophores (i.e., 1 per 10 L) were added to the P+C and P+C+Z treatments, corresponding to a wet weight biomass of 483 to 579 mg L^{-1}. In experiments without added zooplankton *M.*

leidyi remained predominantly motionless on the bottom of the mesocosms. In the presence of zooplankton, *Mnemiopsis* swam with lobes extended and food visible in the gut. In the mesocosms containing phytoplankton and zooplankton (P+Z+C), *Mnemiopsis* produced eggs.

Nutrients were not initially limiting to phytoplankton growth in any mesocosm, but NH_4 was depleted by day 3 and NO_3 by day 4, with levels decreasing more slowly in the presence of zooplankton (P+Z and P+Z+C). Expressed as numerical abundance (Fig.1), the total diatom population increased above initial levels (305 cells ml^{-1}) by approximately 50-fold in mesocosms from which zooplankton and ctenophores were excluded (P); by 42-fold when ctenophores, but not zooplankton, were added (P+C); by 30-fold in the presence of both zooplankton and ctenophores (P+C+Z), but only 7-fold in the presence of zooplankton alone (P+Z). Relative to abundance (14,814 cells ml^{-1}) in the control (P), terminal diatom abundance in P+Z was 86% lower, 40% lower in P+C+Z and 14% lower in P+C. Relative to the P+Z treatment (2124 cells ml^{-1}) diatom abundance increased about 4-fold when ctenophores were added to graze upon zooplankton (P+Z+C). The diatom community growth rate was 0.70 d^{-1} in the presence of zooplankton (P+Z), corresponding to a population doubling time (G) of 34 hrs. Adding ctenophores to prey upon the zooplankton (P+Z+C) increased the diatom community growth rate to 1.21 d^{-1}, corresponding to G = 20 hrs. The latter rates are similar to those for diatoms grown alone (P), $k = 1.40\ d^{-1}$, G = 17 hrs, and in the diatom + ctenophore treatment (P+C), $k = 1.35\ d^{-1}$, G = 18 hrs.

With regard to individual species: *Rh.fragilissima*, initially dominant, increased in the control (P) the first two days, then declined; in contrast, the other species grew throughout the experiment. *Rh. fragilissima's* behavior in the zooplankton and/or ctenophore mesocosms was that of a naturally declining population exposed to variable predation pressure. The abundance and growth patterns of the other diatoms, excluding *Cerataulina pelagica*, mirrored those of the total community (Fig. 1). Final abundance was least in P+Z, intermediate in P+Z+C and greatest in P and/or P+C. The similar final abundance of *C. pelagica* in all mesocosms suggested minimal predation of it by zooplankton. Maximal growth rates of all species exceeded $k = 2.25\ d^{-1}$: *Skeletonema* (5.18 d^{-1}), *Thalassiosira* sp. (4.61), *Cyclotella* sp. (3.94), *Phaeodactylum tricornutum* (3.68), *Thalassionema nitzschioides* (3.27), *Cerataulina pelagica* (2.68), *Rhizosolenia setigera* (2.32), *Thalassiosira decipiens* (2.26).

Significant differences in diatom species' dominance occurred among mesocosms (Fig.1) which reflected the degree and type of grazing pressure. In the control (P), after four days, *S. costatum* replaced *Rh. fragilissima* as the dominant species. The relative importance of *T. nitzschioides* (12%) increased slightly, as it did for the species grouped as "other" (27%): *Thalassiosira* sp., *Cyclotella* sp., *P. tricornutum*, *Rh. setigera* and *C. pelagica*. In the zooplankton mesocosm (P+Z), however, the relative importance of *Skeletonema* (7%) remained similar to that in the initial population, and *Rh. fragilissima* (30%) persisted as the dominant species. This increased zooplankton grazing pressure also led to an increased relative importance of *T. nitzschioides* (22%) and, especially, that of "other" diatoms (41%). *Cyclotella* sp. and *C. pelagica* represented about 17% and 10%, respectively, of the population. The P+Z mesocosm had the most equitable phytoplankton species composition of any experimental treatment. Zooplankton presence tended to reduce overall community abundance and that of individual species, but increase phytoplankton species diversity.

The effect on diatom community structure of adding ctenophores to the zooplankton + phytoplankton mesocosm (P+C+Z) was equally dramatic. The terminal community composition was similar to that which evolved in the control (P). *S. costatum* (41%) overwhelmingly dominated and *Rh. fragilissima* (8%) became relatively unimportant (Fig. 1). The primary difference from control populations was the greater predominance of *T. nitzschioides* (29%). The obvious explanation for the P+Z+C mesocosm results is that ctenophore predation on zooplankton reduced grazing pressure on the diatoms, notably *Skeletonema*. Similar responses in the P+C mesocosms support this conclusion. Electivity indices indicate zooplankton "selection" for *S. costatum* and *T. nitzschioides* in the P+Z mesocosms, but were negative for ctenophore removal of *Rh. fragilissima* and *S. costatum*.

Experiment B

The six unreplicated mesocosms in experiment B were inoculated with natural phytoplankton populations which ranged from 48 to 87 cells ml^{-1} (excluding microflagellates). The dinoflagellate *Prorocentrum redfieldii* (17%) and the diatoms *S. costatum* (13%), *C. pelagica* (13%), *Chaetoceros curvisetus* (13%), and *Coscinodiscus* spp. (13%) co-dominated, accompanied by lesser abundances (6%) of *Rh. fragilissima* and *T. nitzschioides*. Microflagellates, ranged from 11 to 68 cells ml^{-1}. Initial zooplankton populations (inoculated into four mesocosms) ranged from 15 to 23 animals L^{-1}, dominated by *Acartia tonsa*. *Centropages spp.*, cladocerans, crab zoea and other mero-planktonic larvae were also present. One, two and three adult *Mnemiopsis* were added to mesocosms containing phytoplankton and zooplankton, e.g., PN+Z+C, PN+Z+2C, PN+Z+3C, respectively. Two mesocosms (P, PN) contained only phytoplankton, but PN differed in having daily additions of ammonia, phosphate and silicate to simulate benthic excretion rates (see METHODS). Nutrients were also added daily to the PN+Z, PN+Z+C, PN+Z+2C and PN+Z+3C mesocosms.

As in experiment A, nutrients progressively decreased in this three day experiment. The pattern of decrease, particularly in silicate levels, reflected the patterns of phytoplankton activity in a given mesocosm. Terminal Si concentrations in the P and PN mesocosms, ca. 1.2 to 1.8 μM, decreased by about 10- and 8-fold from initial levels. Terminal Si concentrations, higher in the other treatments, reflected the degree of ctenophore predation on zooplankton. In P+Z+2C and P+Z+3C, terminal Si concentrations were about 6.5 μM; in P+Z and P+Z+C about 10 μM. These differences in Si concentrations reflected diatom growth (Figs. 2,3) which, in the presence of zooplankton, progressively increased with ctenophore numbers. Thus, ctenophore presence influences Si dynamics, favoring diatoms in the experiments.

The responses of the microflagellates and diatoms + dinoflagellates, whose mean initial abundances were 37 and 64 cells ml^{-1}, respectively, differed significantly among mesocosms (Figs. 2, 3). In P and PN, diatoms, which accounted for 56% to 74% of the total population, increased by 16-fold ($k = 1.18\ d^{-1}$) and 48-fold ($k = 1.53\ d^{-1}$), respectively, but decreased to 49 cells ml^{-1} in the various zooplankton + ctenophore combinations and comprised less than 5% of total phytoplankton abundance. The taxonomically diverse microflagellates overwhelmingly dominated in all mesocosms to which zooplankton were added, irrespective of ctenophore abundance. Terminal microflagellate populations accounted for 96 to 99% of the total phytoplankton population *vs.* 33% in the initial inoculum (Fig. 2). Clearly, the absence of grazers in the P and PN mesocosms favored diatom predominance, particularly in the mesocosm (PN) enriched with nutrients daily, just as the presence of zooplankton + ctenophores favored microflagellate predominance. Microflagellates contributed only 44%

and 26%, respectively, of the total abundance in P and PN treatments, with mean growth rates of 1.38 and 1.22 d^{-1}, respectively. In the zooplankton+ctenophore mesocosms, microflagellate growth rates ranged from 1.22 to 1.71 d^{-1}, with explosive growth occurring between experimental days 2 to 3. In P+Z+C and P+Z+3C, microflagellate doubling times were about 10 hrs, compared to 27 and 17 hrs in PN and P, respectively.

Significant diatom successional trends and differences in species composition between mesocosms accompanied the remarkable proliferation of microflagellates in the four treatments containing grazers (Fig. 3). In the unenriched mesocosm (P), the initial community, characterized by a more or less equal distribution of species, remained basically unchanged after three days. *Skeletonema, Cerataulina* and Ch. *curvisetus* became relatively more important, the other species less so. The daily addition of nutrients (PN) stimulated considerable growth of *Skeletonema;* its relative importance progressively increased from 13% to 54% over the three day period. The relative importance of *C. pelagica* remained unchanged; progressive decreases characterized *Prorocentrum redfieldii, Ch. curvisetus* and the *Coscinodiscus* spp. The addition of zooplankton (PN+Z) progressively led to the elimination of *Skeletonema*, with *Prorocentrum*, *Cerataulina*, *Ch. curvisetus* and *Rh. fragilissima* disappearing after only one day. The result was that *Coscinodiscus* spp. (11%), *T. nitzschioides* (22%), *P. tricornutum (=Nitzschia closterium)* (22%), along with a number of "other" species (45%), dominated the community.

The addition of *one* ctenophore (PN+Z+C) resulted in the reappearance of *Rh. fragilissima,* although *Coscinodiscus* spp., *T. nitzschioides* and *P. tricornutum* remained dominant. The addition of *two* ctenophores (PN+Z+2C) was accompanied by a significant change. Except for the continued absence of *Ch. curvisetus*, a community similar to that in the initial inoculum and unenriched mesocosm (P) developed. *P. redfieldii, S. costatum* and *C. pelagica* reappeared, the latter species progressively increasing over the three day period leading to its co-dominance (25%) with *Rh. fragilissima* (23%), which also progressively increased in importance. Concurrent with these changes, *T. nitzschioides* was considerably less important, *Coscinodiscus spp.* progressively decreased, and *Phaeodactylum* remained important. The addition of *three* ctenophores (PN+Z+3C) produced a floristic pattern and trend similar to that in the PN+Z+2C mesocosm, except that *Cerataulina* was absent or very sparse.

These results indicate, therefore, that *S. costatum, C. pelagica* and *P. redfieldii* were the character species in unenriched or enriched mesocosms containing a natural phytoplankton assemblage relatively free of zooplankton predation. The addition of zooplankton eliminated the dinoflagellate, *P. redfieldii*, and predominant centric diatoms; and shifted the dominant character species to large *Coscinodiscus* species and the pennate diatoms *T. nitzschioides* and *P. tricornutum.* However, the addition of two or more ctenophores shifted the phytoplankton community structure back towards that characterizing mesocosms free of zooplankton.

In addition to these floristic changes, *Mnemiopsis* via its predation on zooplankton also influenced total phytoplankton biomass, its distribution among different size classes, and assimilation number. Terminal biomass levels (> 20 mg^{-3} Chl) were similar in the P, PN and PN+Z+3C mesocosms, exceeding levels in the other zooplankton + ctenophore treatments. Terminal zooplankton populations in the mesocosms ranged from 0 to 23 animals L^{-1}. The proportion of total community chlorophyll in the < 20 μm phytoplankton size class increased linearly from 40% to 90% with increasing zooplankton abundance. The primary production assimilation number (µg C fixed µg Chl^{-1} hr^{-1}) also progressively increased with microflagellate abundance (i.e. < 20 µm size class) concomitant with increased zooplankton abundance.

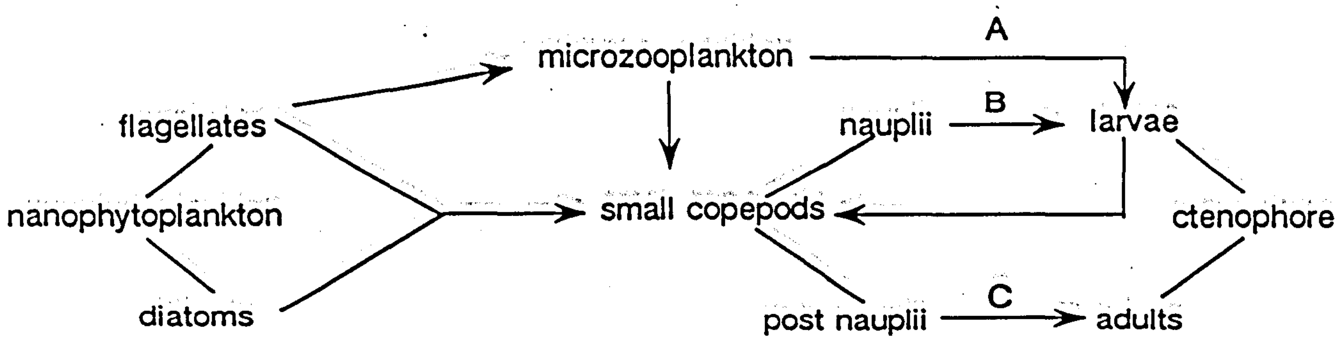
DISCUSSION

My experiments reveal that *Mnemiopsis leidyi*, in top-down fashion, through its predation on herbivorous zooplankton modifies and influences phytoplankton community structure, successional patterns, bloom dynamics, size class, diatom:flagellate ratio, nutrient levels and herbivorous grazing. Greve and Parsons (1977) have suggested that changes in the diatom : flagellate ratio accompanying proliferation of flagellates due to increased nutrification or climatic change may influence gelatinous zooplankton behavior, the effects of which may be to deflect energy flow from fish to ctenophores, or medusae, and thereby decrease fish production. Their hypothesis is rooted in their assumption that two principle pelagic food chains occur in the sea:

Nanoflagellates (e.g. small flagellates)→small zooplankton→ctenophores or medusae
and
Microphytoplankton (e.g. large diatoms)→large zooplankton→young fish

Given the apparent global increase in flagellate blooms in the sea (Smayda, 1990) and seemingly increasing abundance of gelatinous zooplankton in some marginal seas, such as *Pelagia noctiluca* in the Mediterranean and Adriatic Seas (Zavodnik, 1987) and *Aurelia aurelia* and *Mnemiopsis* in the Black Sea (Gomoiu, 1980), evaluation of the Greve-Parsons hypothesis is of increasing contemporary relevance.

Greve and Parsons' nanophytoplankton based foodweb is too restrictive in focusing on small flagellates as prey for small zooplankton. Diatoms, also an important functional group in this size class, can be of equal, if not greater dietary importance to small zooplankton, such as *Acartia tonsa* used in my experiments (see Durbin and Durbin, 1975). Greve and Parsons' diagrammed pathway from nanophytoplankton to small zooplankton also neglects the important microzooplankton (ciliates, tintinnids, etc.) loop, a trophic aspect found to be important after formulation of their hypothesis. Flagellates appear to be significantly preyed upon by ciliates and tintinnids (see Stoecker, et al. 1987a, b). Thus, the nanophytoplankton foodweb proposed by Greve and Parsons needs to include these linkages:

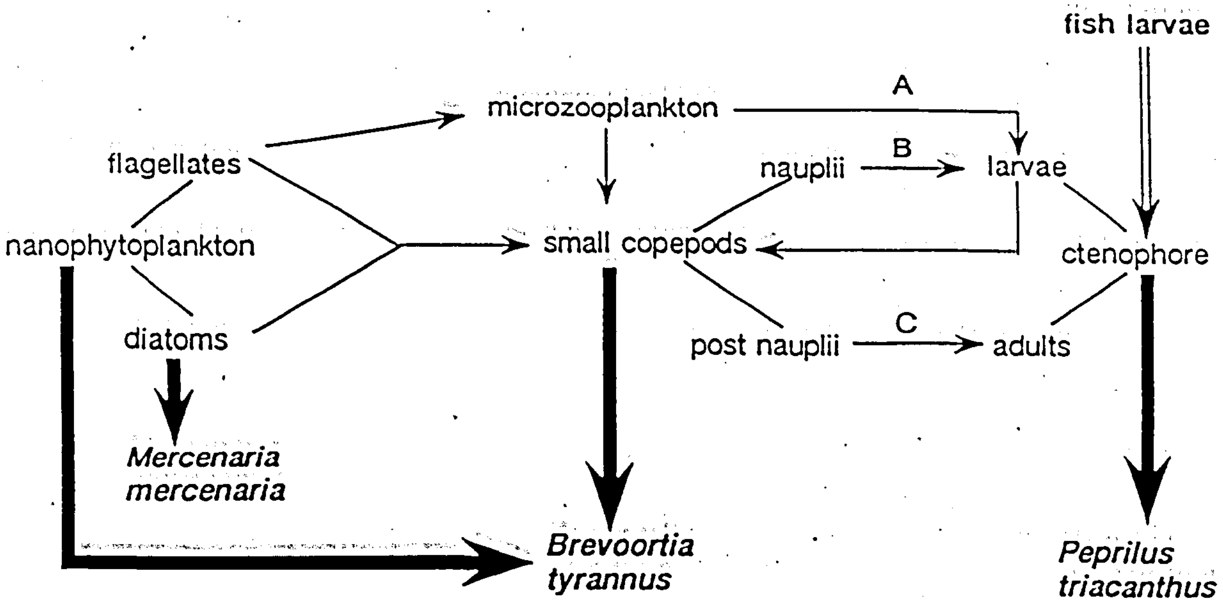


Given differential feeding behavior between larval/nauplii and adult stages of both zooplankton and ctenophores, these morphogenetic stages are also designated. Stoecker et al. (1987a) found *Mnemiopsis leidyi* larvae grew best when provided a mixture of ciliates and copepod nauplii, with adult *Mnemiopsis* preying upon a wide variety of micro- and macrozooplankton. *Aurelia aurelia* preferentially removed large oligotrichs (> 50 µm) and copepod nauplii in experiments (Stoecker et al. 1987b). It is also well established that high densities of adult copepods can physically damage ctenophore larvae, and copepod grazing reduces microzooplankton abundance (Reeve and Walter, 1978; Stanlaw et al., 1981; Stoecker et al., 1978a). These linkages are therefore also diagrammed in the emended Greve-Parsons foodweb.

Considering these planktonic components only, together with the experimental results, summer dynamics in Narragansett Bay, and ecophysiology of *Acartia tonsa* and *Mnemiopsis leidyi*, the following dynamics are expected. If *Mnemiopsis* is absent, *Acartia tonsa* decimates the diatomaceous component of the phytoplankton and nanoflagellates predominate; when *Mnemiopsis* is abundant, nanodiatoms thrive (Figs. 1-3; Deason & Smayda, 1982a, b). Ctenophore predation on copepods (route C in diagram) also favors increased ciliate abundance, which, in turn, is further regulated by larval ctenophore (predation) and flagellate (prey) abundances. Summer red tide blooms of the harmful rhaphidophycean flagellate, *Heterosigma akashiwo,* occur in Narragansett Bay which, based on experiments, leads to die offs of *A. tonsa* and microzooplankton (Tomas and Deason, 1981) and larval ctenophores (Stoecker et al., 1987a). The scyphomedusan *Aurelia aurelia* is a voracious feeder on microzooplankton (Stoecker et al., 1987b; Båmstedt, 1990). Båmstedt has speculated that reduced microzooplankton (e.g. ciliates) grazing pressure may have contributed to the devastating toxic *Chrysochromulina polylepis* bloom along the Scandinavian coast in 1988 (Granéli et al., 1993).

These interactions indicate that the ratios of abundance of nanodiatoms : small flagellates and their subsequent foodweb routing are influenced, *inter alia,* by the ratios of abundance of upper trophic level components, i.e., microzooplankton : small copepods; small copepods : ctenophores; microzooplankton : ctenophores, together with any allelochemic effects the flagellate components may have. That is, the proposed deflection of energy flow from harvestable fish stocks to gelatinous zooplankton, such as *Mnemiopsis*, does not follow a linear route, but is under complex regulation. However, whatever combination of trophic interactions contributes to ctenophore outbreaks, the salient issue is whether these blooms are indeed detrimental, directly or indirectly, to harvestable fishery stocks. Narragansett Bay dynamics will be considered prior to a more general assessment of this fundamental suggestion of the Greve-Parsons hypothesis.

During the frequent summer ctenophore outbreaks in Narragansett Bay (Deason and Smayda, 1982a, b), the experimental and field evidence indicates diatom blooms are favored. These blooms are beneficial to the commercially important clam, *Mercenaria mercenaria* (= quahog). Pratt and Campbell (1956) found statistically significant correlations between *Mercenaria* growth rates and the abundance of small diatoms < 15 µm, including *Skeletonema costatum*, whereas growth was negatively correlated with flagellate abundance. *M. leidyi* also produces mucoid boluses packed with diatoms and detrital material which sink to the bottom for benthic ingestion (Deason & Smayda, 1982b). In Narragansett Bay, at least, ctenophore outbursts provide an energy flow routing favorable to the growth and recruitment of harvestable clams. This pathway and those discussed below are diagrammed as follows:



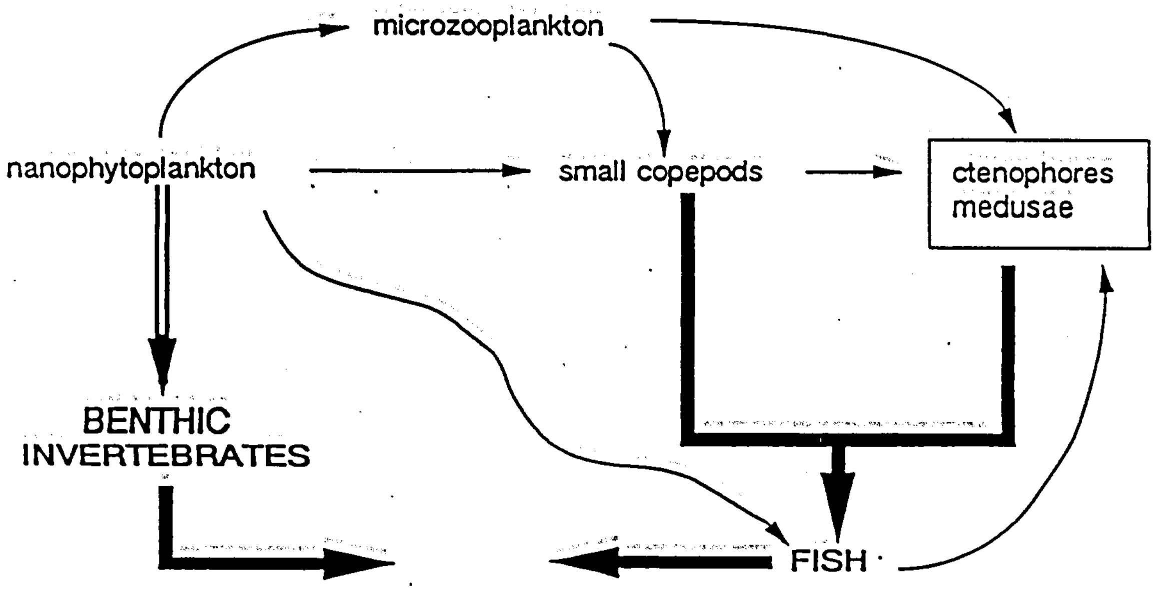
Summer ctenophore populations in Narragansett Bay compete with the commercially important planktivorous fish species *Brevoortia tyrannus* (= menhaden). Durbin and Durbin's (1975) experiments established that menhaden selectively graze upon both phytoplankton > 10 µm (including diatom colonies) and zooplankton, with preferential utilization of *Acartia tonsa*. They suggested that this size-selective grazing behavior, coupled with growth stimulation of nanophytoplankton from NH_4 excreted by menhaden, "may partly explain why small nanophytoplankters are so abundant during summer." Therefore, the ratio of ctenophore abundance to that of menhaden and other planktivorous fishes is an important determinant of their individual population dynamics and associated energy flow pathways. It also indicates that zooplankton species composition and abundance are a composite function of phytoplankton composition and abundance, presence or absence of both menhaden and ctenophores, and of other planktivorous fishes and gelatinous zooplankton.

An extensive literature corroborates Greve and Parsons' conclusion that jellyfish are often detrimental to younger stages of fish, usually because of voracious feeding. But, it does not follow that fish stocks, including harvestable species, will be decimated either because of larval predation by jellyfish, or unsuitability of the latter as fish prey. In Narragansett Bay, the commercially important butterfish, *Peprilus triacanthus*, as shown experimentally, is a voracious grazer on ctenophores (Oviatt and Kremer, 1977). Oviatt and Kremer concluded that the annual decline in ctenophore population levels in Narragansett Bay is probably attributable to butterfish grazing. Mansueti's (1963) literature review indicates that the butterfish and its congener *Peprilus alepidotus* (= harvestfish) are avid grazers of ctenophores, including *Chrysaora quinquecirrha*. Moreover, conspicuous fish-jellyfish associations are characteristic of four pelagic and three demersal families of fish, many of which are commercially important, including Atlantic cod, European whiting, haddock and hake. These associations include grazing upon jellyfish by juveniles and/or adult stages, or commensalisms in which the fish species seeks out jellyfish for shelter or to obtain food accompanying jellyfish grazing. Despite active jellyfish predation on fish larvae, there are numerous examples of commercially important fish species actively seeking out associations with venomous jellyfish which serve as passive hosts in providing shelter for crustacean and other invertebrates preyed upon by fish.

For example, Mansueti (1963) reported the occurrence of > 100 young horse mackerel (*Trachurus*) under a large *Rhizostoma*, 305 young mackerel and harvestfish under a 5 kg medusa, *Chrysopsalmus* sp., and 62 young European whiting and Atlantic cod under a *Rhizostoma* sp. 43 cm in diameter. Thus, one positive role of such jellyfish associations is 0-year class enhancement. Such attractions, which require a certain degree of nematocyst toxin immunity, contrast with avoidance reactions of species such as herring, whose catches are inversely correlated with jellyfish abundance (Lucas and Henderson, 1936; Mansueti, 1963). Mansueti also lists numerous examples of jellyfish predation by commercially important species, including the mackerel genera *Scomber* and *Trachurus*. Sea turtles, the ocean sunfish (*Mola mola*) and 11 bird species also prey upon jellyfish (Mansueti, 1963; Harrison, 1984). Clearly, there are numerous exceptions to the paradigm that jellyfish are a carbon dead end in marine foodwebs.

The key aspect of the Greve-Parsons' hypothesis, however, is whether jellyfish swarms decrease the harvest available for human consumption, nothwithstanding such beneficial fish-jellyfish associations and confirmed instances of grazing upon jellyfish. Catch statistic data needed for such an evaluation are very limited. However, Vucetic and Alegria-Hernandez (1988) assessed the annual trends in catch or stock densities of harvestable pelagic fishes in relationship to the outbursts of the jellyfish *Pelagia noctiluca* in the Adriatic and Mediterranean Seas. Remarkably, positive correlations between annual catches and the occurrence of "*Pelagia* years" were recorded for the following species known to feed on jellyfish: mackerel, *Scomber scombus*, *S. japonicus*; horse mackerel, *Trachurus* sp.; tuna, *Thunnus thynnus*, and *Auxis nochei* and *Sarda sarda*. In addition, catches of the planktivorous sardine (*Sardina pilchardus*), sprat (*Sprattus sprattus*) and anchovy (*Engraulis encrasicolus*) also increased. Augmentation of these latter, small planktivores during *Pelagia* years probably reflected alterations in foodweb energy flow accompanying jellyfish presence favorable to them rather than from their direct grazing on *Pelagia*.

The foregoing results collectively indicate that the basic Greve-Parsons paradigm - that energy flow to harvestable fishes or other stocks is blocked by jellyfish blooms - needs revision. That, indeed, ctenophore or medusae blooms are neither *a priori* detrimental, nor preclude beneficial recruitment of harvestable fishes. The following general emendation of the Greve-Parsons paradigm towards ultimate resolution of the complex foodweb interactions and consequences accompanying jellyfish blooms is accordingly suggested:



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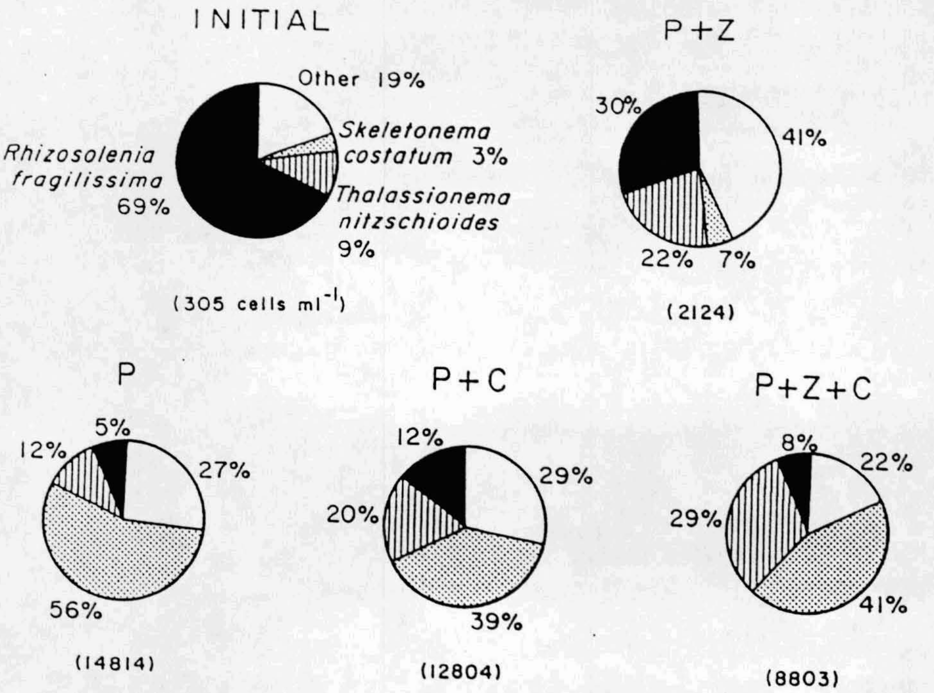

Figure 1. Dominant diatom species in the different mesocosm treatments as percent of total diatom abundance after four days in a replicate series of experiment A. Values in parentheses represent total diatom abundance as cells ml^{-1}. P = phytoplankton, Z = zooplankton, C = ctenophore *Mnemopsis leidyi* present in those mesocosms.

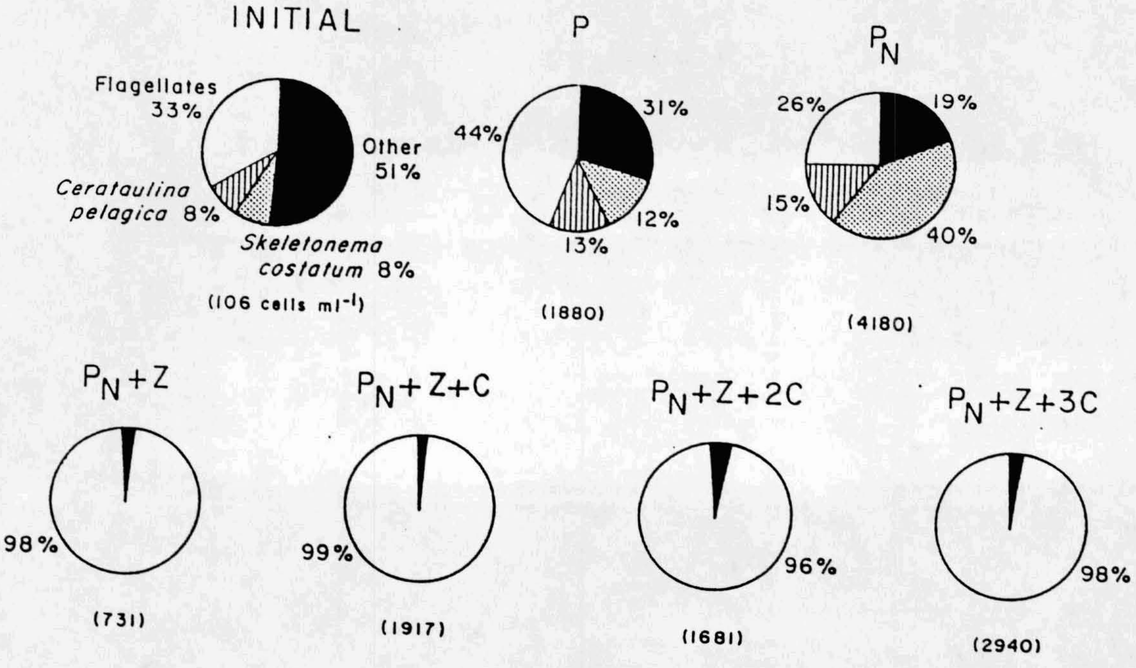

Figure 2. Representation, as percent of total phytoplankton, of diatoms, including dominant species, and microflagellates in the different mesocosm treatments after three days in experiment B. Values in parentheses indicate total phytoplankton abundance. See text for descriptions of various mesocosm treatments, and legend to Figure 1.

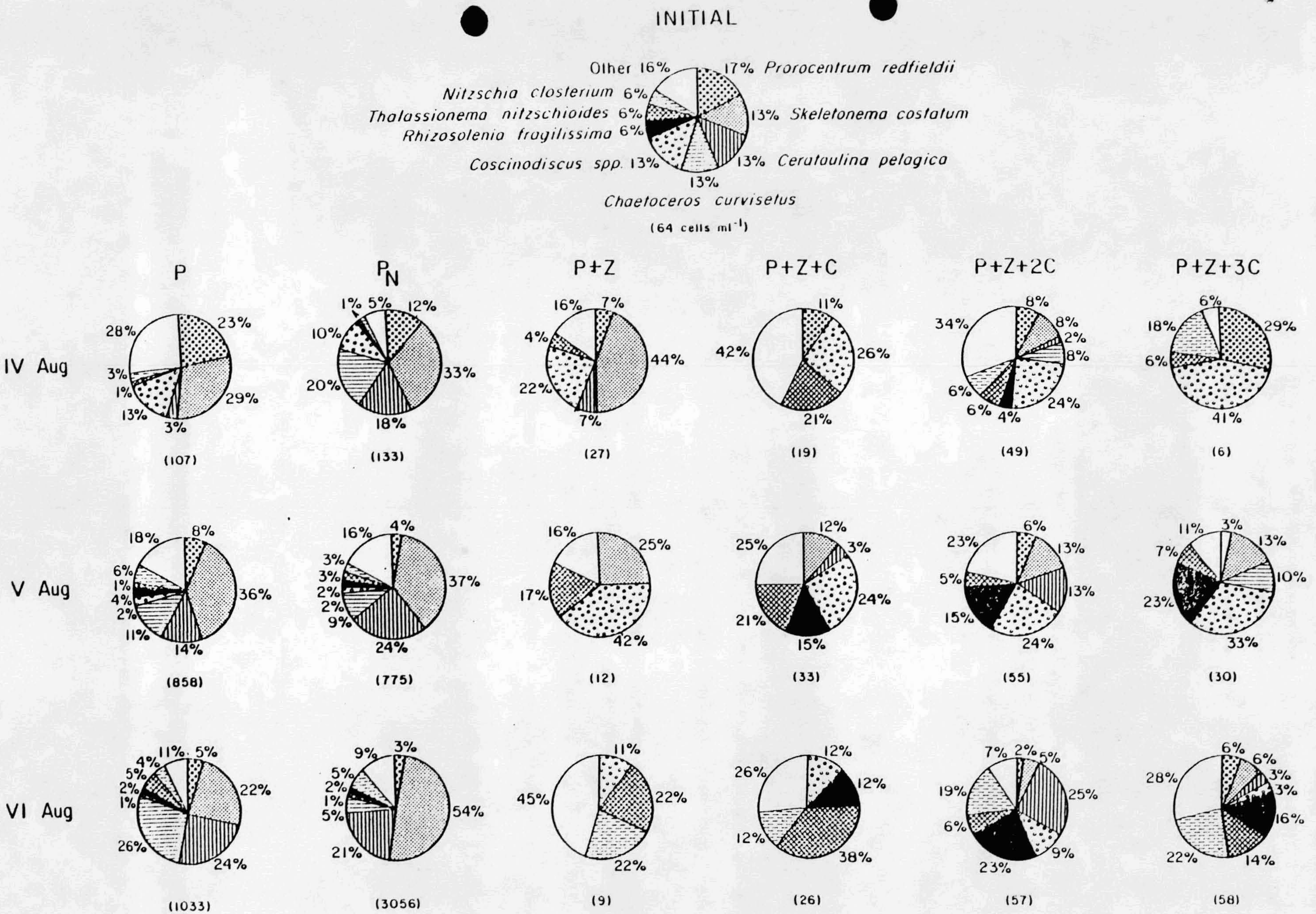

Figure 3. Day-to-day changes in the relative proportions and abundance of the major diatom and dinoflagellate species in the different mesocosms during experiment B. Values in parentheses represent total diatom and dinoflagellate abundance as cells ml^{-1}. Otherwise, as described in legend to Figure 1.