Multitrophic Interactions as a Trigger of the *Gyrodinium aureolum* Bloom in Reeves Bay, New York

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미국 뉴욕 Reeves만에서 쌍편모조류인 *Gyrodinium aureolum*의 대발생에 영향을 미친 먹이연쇄내의 상호작용

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Multitrophic interactions among gelatinous planktivores, zooplankton, and phytoplankton were investigated in Reeves Bay, New York from mid-March to July in 1989 to evaluate the top-down effect by gelatinous macrozooplankton on the *Gyrodinium aureolum* bloom through cascading trophic interactions. Zooplankton abundances reached maximal density following a decrease in gelatinous macrozooplankton (hydromedusae and scyphomedusae) abundances, and phytoplankton biomass was low at this time. Subsequently, as ctenophore populations increased, zooplankton abundances decreased sharply, and the cell concnetration of *G. aureolum* began to increase. This field observation supports that the top-down control by gelatinous macrozooplankton on grazers, resulting in low grazing pressure on phytoplankton, can cause an algal bloom. The minimal zooplankton grazing measured using ^{14}C tracer technique during the bloom period indicated that zooplankton did not prefer *G. aureolum* as a food source.

해파리류의 동물플랑크톤에 대한 포식 파급효과가 식물플랑크톤의 대발생에 어떠한 영향을 미치는 가를 연구하기 위해, 해파리류, 동물플랑크톤, 식물플랑크톤으로 이어지는 먹이연쇄에서의 상호작용을 미국 뉴욕주에 있는 Reeves만에서 쌍편모 조류인 *Gyrodinium aureolum*의 대발생이 있었던 기간을 전후한 1989년 3월 중순에서 7월 초순사이에 조사하였다. 동물플랑크톤의 최대 개체수는 해파리류의 개체수가 감소하기 시작한 4월 중순에서 5월 초사이에 관찰되었으며, 이때 식물플랑크톤의 생물량은 낮게 나타났다. 한편 해파리류의 개체수가 다시 증가하였던 5월 중순부터 동물플랑크톤은 개체수의 감소를 보인 반면, 식물플랑크톤은 대발생을 시작하였다. 이와 같은 결과는 2차 소비자인 해파리류의 포식이 1차 소비자인 동물플랑크톤의 식물플랑크톤에 미치는 섭식압력의 감소 효과에서 비롯된 것으로 나타났다. 한편, 탄소동위원소를 사용하여 측정한 동물플랑크톤의 섭식률은 대발생 전후에 비해 대발생 중에 현저하게 낮아, 동물플랑크톤들이 대발생을 일으킨 *G. aureolum*을 먹이로서 선호하지 않는 것으로 밝혀졌다.

INTRODUCTION

A phytoplankton bloom of *Gyrodinium aureolum* was observed in Reeves Bay, New York in 1989. Potential causes of *G. aureolum* blooms have included environmental conditions (Negri *et al.*, 1992), hydrological structure (Jimenez *et al.*, 1992), inhibitory exclusion (Gentien and Arzul, 1990), and lack of zooplankton grazing pressure (Kim *et al.*, in preparation). A change in the trophic structure of planktonic food webs due to predation by gelatinous macrozooplankton can also cause algal blooms (Lindahl and Hernroth, 1983).

Trophic relationships have been intensively investigated especially in freshwater pelagic food webs, and many hypotheses such as "biomanipulation" (Shapiro *et al.*, 1982;' Shapiro and Wright, 1984), "cascading trophic interactions" (Carpenter *et al.*, 1985), and "bottom-up vs. top-down control" (McQueen *et al.*, 1986; McQueen *et al.*, 1989) have been proposed. Such hypotheses mainly have been tested in freshwater ecosystems using enclosures and developed in an attempt to understand environmental problems such as algal blooms (Shapiro *et al.*, 1982).

It is well known that a rise in piscivore biomass results in decreased planktivore biomass, increased herbivore biomass, and consequently, decreased phytoplankton biomass in freshwater ecosystems. An analogous observation (ctenophore-zooplankton-phytoplankton) was reported in the coastal environments (Deason and Smayda, 1982a). However, in general, information on cascading trophic interaction in marine planktonic ecosystems is limited.

Gelatinous macrozooplankton such as ctenophores, scyphomedusae and hydromedusae are important predators in controlling herbivorous zooplankton populations (Bishop, 1967; Burrell and Van Engel, 1976; Kremer, 1979; Lonsdale, 1981; Deason and Smayda, 1982a; Deason and Smayda, 1982b; Stoecker *et al.*, 1987a; Stoecker *et al.*, 1987b; Monteleone, 1988; Kim and Lonsdale, 1992). In turn, herbivorous zooplankton play an important role in controlling the size and species composition of phytoplankton populations (Riley,

1946, Lampert *et al.*, 1986; Frost, 1987). High grazing rates of herbiovorous zooplankton contribute to the decline of algal blooms (Riley *et al.*, 1949) and to the suppression of bloom development (Watras *et al.*, 1985), while the lack of grazing pressure can allow algal blooms to take place (Huntley, 1982). Therefore, an increased gelatinous macrozooplankton populations can regulate phytoplankton population dynamics indirectly through predation on herbivorous zooplankton (Huntley and Hobson, 1978; Deason and Smayda, 1982a; Lindahl and Hernroth, 1983).

This study was performed to investigate the multitrophic interactions among planktivorous macrozooplankton, zooplankton and phytoplankton that may affect phytoplankton bloom dynamics, through both structural and functional approaches.

MATERIALS AND METHODS

The structural approach was taken by measuring the standing stocks of phytoplankton and zooplankton in terms of abundance, and the functional approach was done by measuring primary productivity and zooplankton grazing rates in Reeves Bay, Long Island, New York, U.S.A.

Study Area

Reeves Bay is a part of Flanders Bay in the Peconic Bay estuarine system, and is located at the head of the estuary which receives discharge of the Peconic River (Fig. 1). This bay is a very shallow (average depth : 1.5 m), eutrophic and well-mixed region where vertical gradients, in such physical characteristics as temperature and salinity, appear small or absent due to the strong tidal circulation, and where high concentrations of soluble nitrogen and orthophosphate exist (Hardy, 1976). Even during the phytoplankton bloom, major nutrient levels remained relatively high (Bruno *et al.*, 1980; Cosper *et al.*, 1987). Recently, this bay has experienced various algal blooms (Bruno *et al.*, 1980; Cosper *et al.*, 1987; Cosper *et al.*, 1990; Kim and Chang, 1992a; Kim *et al.*, in preparation).
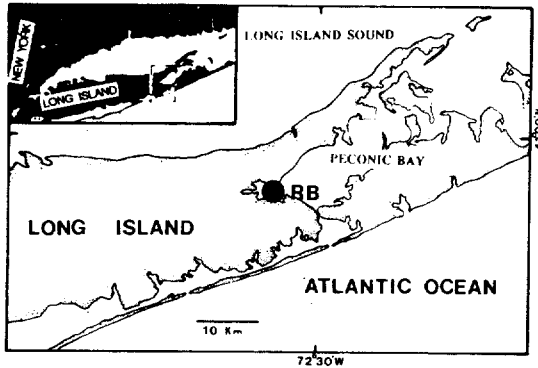
Fig. 1. Map of the study area (RB: Reeves Bay).

Fig. 2. Temperature (°C), salinity (ppt), and Secchi depth (m) at Reeves Bay from mid-March to early July, 1989.

Field Sampling

Surface water samples were collected in Reeves Bay weekly or biweekly from mid-March to July in 1989. Water temperature, salinity, and Secchi disk depth were measured with a mercury thermometer, a refractometer, and a white 30 cm Secchi disk, respectively. Phytoplankton enumeration and identification was performed on 10 m*l* Lugol's fixed subsamples under a light microscope (Zeiss, Axiophot). Quantitative zooplankton samples were collected in replicate by filtering 40 liters of ambient seawater through a 64-μm Nitex screen, and preserved in 4% neutralized formalin solution for enumeration and identification. Ambient seawater (20 liters) was collected in a polyethylene cubitainer kept in a cooler, and brought to the laboratory for measuring primary productivity and zooplankton grazing.

Laboratory Experiments

Phytoplankton biomass was estimated by measuring chlorophyll *a* concentrations with a Turner Designs fluorometer on 90% acetone extracts of glass fiber filtered samples (Strickland and Parsons, 1972; Cosper *et al.*, 1989). Primary productivity was measured using uptake of ^{14}C-HCO_3 during 4 hour incubations of 100 m*l* samples under natural sunlight (see Cosper *et al.*, 1989 for detail procedures).

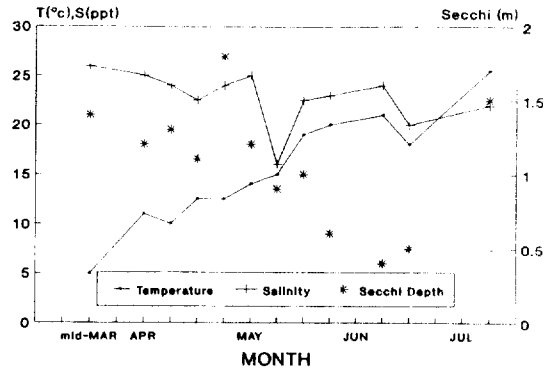Zooplankton grazing rates were measured using

^{14}C as a tracer (Haney, 1971; Daro, 1978); Griffiths and Caperon, 1979; Roman and Rublee, 1981; Lampert, 1985) weekly from mid-April to early July Grazing experiments were conducted in 2-liter glass bottles in triplicate by adding 1 m*l* of ^{14}C bicarbonate solution (100-200 μCi m*l*$^{-1}$) to the ambient seawater (2 liters) with natural phytoplankton and zooplankton populations (see Kim and Chang, 1992a for detail procedures).

RESULTS AND DISCUSSION

Hydrography

Surface water temperature ranged from 5.0°C in March to 25.5°C in July, salinity changed from 13 parts per thousand (ppt) to 26 ppt, and Secchi disk depth ranged from 0.3 m to 1.8 m throughout the study period (Fig. 2). Temperature increased continuously in a predicatable seasonal mode, and salinity slightly decreased in the summer and showed fluctuation depending on rainfall. Secchi disk depth was minimal during the dinoflagellate bloom of *Gyrodinium aureolum* in June. Temperature (about 20°C) and salinity (about 22 ppt) during the bloom period were the optimal conditions in which growth rate of *G. aureolum* in culture was maximum (Nielsen and Toenseth, 1991).

Phytoplankton Community

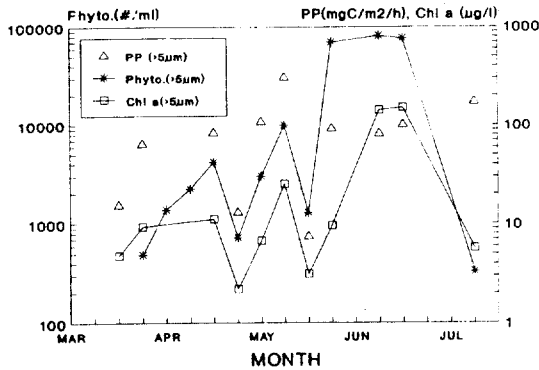Phytoplankton cell numbers varied from 328 to

Fig. 3. Phytoplankton cell numbers (#/m*l*), primary production (mgc/m²/h), and chl *a* concentration (µg/*l*) at Reeves Bay from mid-March to early July, 1989.

Fig. 4. Chl *a* of >5 µm size-fraction and zooplankton (>64 µm) abundance at Reeves Bay from mid-March to early July, 1989.

Table 1. Dominant species of phytoplankton in Reeves Bay during the study period.

Date	Species	Cells/m*l*	%
Mar. 16	*Leptocylindrus danicus*	176	36.2
Apr. 5	*Chroomonas amphioxieia*	680	49.4
	Leptocylindrus danicus	460	33.4
Apr. 12	*Leptocylindrus danicus*	956	43.0
Apr. 20	*Skeletonema costatum*	2966	70.7
Apr. 27	ND		
May 3	*Chroomonas amphioxieia*	1740	56.5
	Gyrodinium aureolum	1040	33.7
May 17	*Gyrodinium aureolum*	9566	95.8
May 23	*Gyrodinium aureolum*	424	33.3
May 31	*Euglena pumila*	70050	98.9
Jun. 9	*Gyrodinium aureolum*	80925	99.9
Jun. 15	*Gyrodinium aureolum*	42100	54.8
	Euglena pumila	34575	45.0
Jul. 12	ND		

ND: no dominant species

81,001 cells/m*l* (average: 22,798 cells/m*l*), and reached a peak in early June when the dinoflagellate bloom was found (Fig. 3). The fast succession of dominant phytoplankton species, which was characteristic of this study area (Bruno, 1980), was also observed during the study period (Table 1). Dominant species were the short chain form diatoms, *Leptocylindrus danicus* and *Skeletonema costatum*, in mid and late April, a small-sized (3-5 µm) cryptomonad, *Chroomonas amphioxieia*, in early May, and a relatively small (15-20 µm) dinoflagellate, *G. aureolum*, in mid and late May. An eugle-
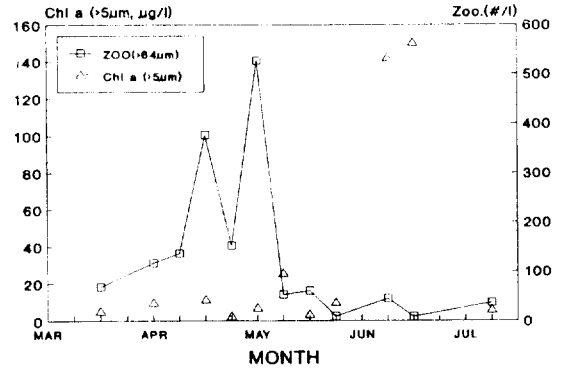
noid, *Euglena pumila*, composed 98.9% of the total cell numbers at the end of May, and *G. aureolum* formed a bloom in early June. Thereafter, both *G. aureolum* and *E. pumila* were dominant species which composed 54.8% and 45.0% of the total cell numbers, respectively.

The overall pattern of phytoplankton community succession was that diatoms were replaced by relatively small-sized dinoflagellates and euglenoids in mid-May. The temporal variation in phytoplankton cell numbers was coincident with that of chlorophyll *a* concentrations and primary productivity (Fig. 3). However, the highest primary productivity in July, despite relatively low chl *a* concentrations and cell numbers, seemed to be due to the temperature effect when temperature increased by 6°C (Raymont, 1980).

Zooplankton community

Zooplankton was most abundant from mid-April to early May, and the abundance declined quickly from mid-May and remained low through July (Fig. 4). Total copepod populations, including adults, copepodites and nauplii, were dominant numerically throughout the study period except occasional abundance peak of rotifers or polychaete larvae. The organisms which contributed to the zooplankton abundance peaks were polychaete larvae (296 individuals/*l*) in mid-April, copepod nauplii(127 individuals/*l*) in late April, and
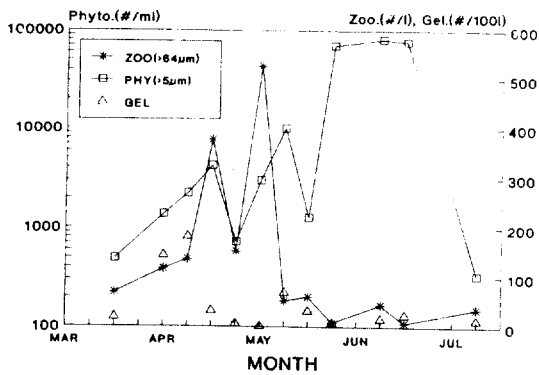
Fig. 5. Phytoplankton (>5 μm) cell numbers. zooplankton abundance (#/l), and gelatinous macrozooplankton abundance (#/100 l) at Reeves Bay from mid-March to early July, 1989.

rotifers (516 individuals/l) in early May. Microzooplankton (64-202 μm) was numerically more abundant than mesozooplankton (>202 μm).

Planktivorous macrozooplankton-zooplankton interactions

The peak of zooplankton abundance were found following a decrease in the abundance of a anthomedusa *Sarsia* sp. and a scyphomedusa *Aurelia aurita* (Fig. 5). The impact of *Sarsia* predation on copepod populations in the Dutch coastal area was reported to be generally negligible (Danna, 1986), however, negative relationship between medusan biomass and that of zooplankton (Matsakis and Conover, 1991) indicates a significant zooplankton population control by gelatinous macrozooplankton. Low copepod standing stocks were often found, when *A. aurita* was abundant in a small estuary near the study area from April until mid-June (Stoecker *et al.*, 1987b). Therefore, the released predation pressure from gelatinous macrozooplankton appeared to lead to an increase of zooplankton.

Zooplankton biomass decreased when ctenophore *Mnemiopsis leidyi* increased again in mid-May (Fig. 5). Although the density of ctenophores was less than that of hydromedusae in April, their predation impact on zooplankton may be greater than hydromedusae predation because of their re-

latively large body size and high ingestion rates (Deason and Smayda, 1982a). A ctenophore, *M. leidyi*, is an abundant predator in this study area throughout the warmer period (Turner *et al.*, 1983), and is known as a keystone predator to control the density of copepod populations and to cause significant changes in the structure of plankton community (Deason and Smayda, 1982a). Their predation impact on microzooplankton (20-200 μm) is especially important, when copepod standing stocks are low (Stoecker *et al.*, 1987a). This field observation of the maximal zooplankton abundance between two peaks of gelatinous macrozooplankton abundance indicated that zooplankton populations could be controlled from the above trophic level of gelatinous planktivores.

In addition to indirect influence of gelatinous macrozooplankton on enhancing phytoplankton populations by predation on grazers, they can directly contribute to an increase of phytoplankton by nutrient recycling (Deason and Smayda, 1982a). Nutrient-mediated effects of planktivores may exceed trophic-cascade effects associated with reduced grazing pressure (Threlkeld, 1987). However, nutrient regeneration by ctenophore and macrozooplankton, accounted for 1 to 3% of nitrogen requirements of phytoplankton, seems not to be important in the coastal embayment near the study area, especially in summer when primary productivity is high (Park and Carpenter, 1987).

Zooplankton-phytoplankton interactions

Zooplankton grazing can be affected by food concentration, food particle size, and food quality (Raymont, 1983). It is generally accepted that clearance rate rises with food concentrations to the optimal concentration, but gradually declines thereafter (Corner *et al.*, 1972). The decreased grazing pressure and ingestion rate during the bloom period (Figs. 6 and 7) showed that algal concentration in the middle of the bloom was so high that zooplankton could not consume efficiently. The algal cell size of *G. aureolum* (15-20 μm) was large enough for copepods to handle (Poulet, 1976), therefore it was not likely to affect zooplankton gra-
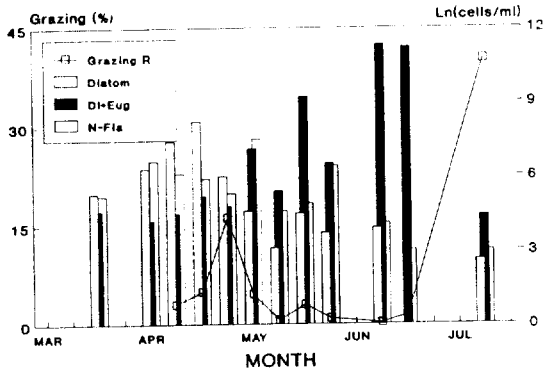
Fig. 6. Total zooplankton community grazing (% of the hourly primary production), and the cell numbers of dominant phytoplankton groups at Reeves Bay from mid-March to early July, 1989.
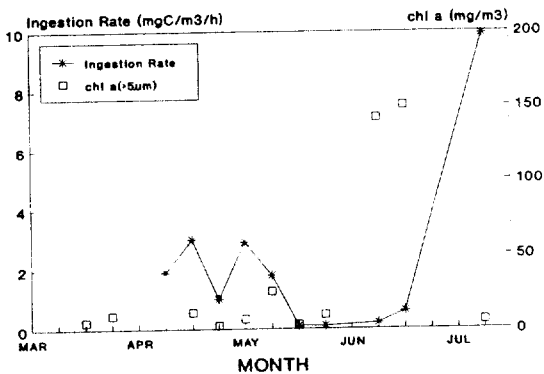

Fig. 7. Ingestion rate (mgC/m³/h) and chl *a* (mg/m³) at reeves Bay from mid-March to early July, 1989.

zing.

Copepods can shift their grazing pressure according to the phase of the peaks in food particle concentration (Poulet, 1978). However, low zooplankton grazing rate on *G. aureolum*, despite its high cell concentration, seems to be due to a toxic effect of this dinoflagellate. A dinoflagellate, *G. aureolum*, has been known as a toxic species (Denn *et al.*, 1990) to change the feeding behavior of copepods (Gill and Harris, 1987), to reduce zooplankton abundance (Bjoernsen and Nielsen, 1991), and to be involved in massive fish kills (Yasumoto *et al.*, 1990). The toxicity of some dinoflagellates can have an adverse influence on copepods (Kim and Chang, 1992b), which may result in reduced community grazing rates. In the middle of the

bloom, individual clearance rates of zooplankton were also much reduced (kim *et al.*, in preparation) as well as zooplankton abundance, community grazing rates, and ingestion rates (Figs. 5, 6, and 7).

Zooplankton community grazing rates were related more closely to the zooplankton species than to the total abundance. For example, grazing rate was recorded higher in late April when the copepod nauplii were most abundant than when the abundances of polychaete larvae and rotifers were higher than that of copepod nauplii in mid-April and early May, respectively (Figs. 5 and 7). This mismatch may be due to the differences in the individual clearance rates among these organisms. The highest grazing rate in July seemed to be due to an increase in the abundance of adult copepods of which clearance rate is much higher copepod nauplii or polychaete larvae (Kim and Chang, 1992a) and to an increase in temperature. Such an increased grazing rate may contribute to suppress an increase in phytoplankton populations despite high primary production in July (Figs. 3 and 7).

Trophic interaction studies in Korea

Phyto- and zooplankton communities are controlled through both bottom-up control by producers and top-down control by consumers, however, bottom-up control has been emphasized to explain the variation of phyto- and zooplankton populations. Most of the plankton studies performed in the coastal waters of Korea have dealt with phytoplankton-zooplankton interactions superficially from a "bottom-up control" viewpoint. However, a couple of studies have suggested the importance of multitrophic interactions to understand planktonic community structure from a "top-down control" viewpoint. For example, Shim *et al.* (1984) suggested that low phytoplankton biomass in Kwangyang Bay was possibley due to the increased zooplankton qrazing during the summer season when the zooplankton was most abundant (Kim, 1984). Shim and Yun (1990) observed that ctenophore populations showed a negative correla-

tion with the copepod populations in Chonsu Bay during the summer and fall, possibly implying the predator control of ctenophores. Pae and Yoo (1991), however, suggested that zooplankton grazing had little effects on diminishing phytoplankton populations in Masan Bay.

As planktonic ecosystems are controlled by both producers and consumers, the question remains, which force, top-down force or bottom-up force, is dominant to construct planktonic community structure. In eutrophic waters, top-down forces may be stronger than bottom-up forces (McQueen *et al.*, 1986). Therefore, when plankton community structure was investigated especially in such eutrophic waters as estuarine and coastal waters, both bottom-up and top-down controls should be considered. Whether zooplankton grazing impact is significant or not, trophic interactions have been often emphasized without any direct measurements. Recently, direct measurement of zooplankton grazing impact using radioactive tracer, however, was attempted in Korean waters (J.-K. Choi, Inha Univ. personal communication). We suggests that direct measurement of consumer impacts are necessary to better understand plankton community structure.

CONCLUSION

The results based on both field observation of community structure and laboratory measurement of zooplankton grazing were in agreement with previous microcosm experiments (Deason and Smayda, 1982a), and showed that gelatinous predator could contribute to the changes in phytoplankton populations. The factors that initiated *G. aureolum* bloom in Reeves Bay were low zooplankton grazing pressure combined with favorable temperature and salinity conditions. Low grazing pressure was due to declined zooplankton abundance by the predation of gelatinous macrozooplankton and reduced individual clearance rate possibly by toxic effect of *G. aureolum*. The dinoflagellate bloom in Reeves Bay provides an evidence showing that "cascading trophic interactions" among gelatinous planktivores, zooplankton, and

phytoplankton can cause a phytoplankton bloom in eutrophic estuarine waters.

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