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Predation pressure of *Noctiluca scintillans* on diatoms and thecate dinoflagellates off the western coast of Kyushu, Japan

Toshikazu Suzuki*, Kingo Yamamoto & Tetsuya Narasaki

Faculty of Fisheries, Nagasaki University, Nagasaki 852–8521, Japan

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Abstract: Predation pressure of *Noctiluca scintillans* on diatoms and thecate dinoflagellates was investigated off the western coast of Kyushu, Japan by a comparison between the taxonomic composition of prey in the food vacuoles of *N. scintillans* and that in the ambient water. The ratios of total diatoms and centric diatoms in the food vacuoles were higher than those in the ambient water, while thecate dinoflagellates and pennate daitoms showed a reverse trend. These results indicate that predation pressure of *N. scintillans* on total diatoms is higher than on thecate dinoflagellates, and that the pressure on centric diatoms is stronger than that on pennate ones. Among the centric diatoms, *Chaetoceros* and *Bacteriastrum* were dominant in the food vacuoles and their respective ratios were higher than in the ambient water. Their chain-forming colonies with long setae appear to be easily trapped by *N. scintillans* tentacles and this is probably the cause of the high predation pressure of *N. scintillans* on centric diatoms.

Key words: diatoms, predation pressure, *Noctiluca scintillans*, thecate dinoflagellates

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Introduction

The dinoflagellate *Noctiluca scintillans* (Macartney) Kofoid & Swezy is frequently observed in temperate to tropical marine areas and it sometimes forms red tides, especially in coastal areas (Enomoto 1956, Le Fèvre & Grall 1970, Uhlig & Sahling 1990, Tada et al. 2004, Miyaguchi et al. 2006). Its temperate form does not possess endosymbiotic algae and it is an obligate heterotroph (Harrison et al. 2011). Although they feed on various suspended particles such as copepods, chaetognaths, fish eggs and fecal pellets (Enomoto 1956, Prasad 1958, Kiørboe 2003), their main prey organisms are reported to be diatoms (Prasad 1958). Kiørboe & Titelman (1998) observed under incubation conditions that the clearance rates of *N. scintillans* were higher when the diatom *Conticribra weissflogii* (Grunow) K. Stachura-Suchoples & D. M. Williams was provided as prey than when the dinoflagellate *Heterocapsa triquetra* (Ehrenberg) F. Stein was provided. Under natural conditions where various prey organisms coexist, however, it has rarely been reported whether prey selection of *N. scintillans* is actually occurring or whether any kind of prey is favorably fed upon. In this study, we focused on ubiquitous scaled plankton, i.e. diatoms and thecate dinoflagellates, as feeding tracers, as these are observable under a light microscope even in the food vacuoles of *N. scintillans*, in order to try to comprehend the predation pressure on each group by comparing taxonomic composition in the food vacuoles and in the ambient water.

Materials and Methods

A total of 25 samples of *Noctiluca scintillans* were collected at 16 stations off the western coast of Kyushu, Japan on cruises of the T/S *Kakuyo-maru* and *Nagasaki-maru* from April to August 2009 (Fig. 1). A Norpac-net (330 μm mesh size) equipped with a flow meter was towed horizontally for one minute at about 1 m sec^{-1} speed in the surface layer. Temperature and salinity were measured with a handheld conductivity meter (YSI Model 30, YSI Inc.). Chlorophyll *a* concentration was estimated following Suzuki & Ishimaru (1990) by filtering a 100 mL water sample through a Whatman GF/F filter. Samples were immediately fixed with formalin (5% final concentration). After returning to the laboratory, more than 40 individuals of *N. scintillans* were randomly selected from each sample

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[*] Corresponding author: Toshikazu Suzuki; E-mail, tsuzuki@nagasaki-u.ac.jp

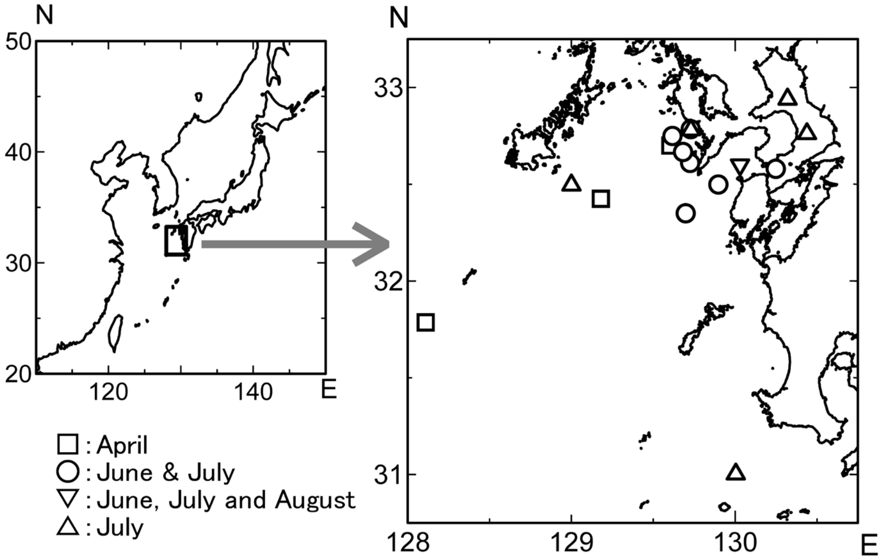

Fig. 1. Sampling stations for *Noctiluca scintillans* on cruises of the T/S *Nagasaki-maru* and *Kakuyo-maru* from April to July, 2009. Squares: single samplings in April, circles: duplicate samplings in June and July, inverted triangles: triplicate samplings in June, July and August, and triangles: single samplings in July.

when a sufficient number of individuals were collected. When *N. scintillans* was rare (less than 40 individuals) in a sample, all individuals were examined. *Noctiluca scintillans* cells were transferred into a Sedgwick-Rafter cell and sealed with a cover glass (Guillard 1978). Then diatom frustules and dinoflagellate thecae in the food vacuoles were observed and enumerated under an inverted microscope with 20 to 60x objective lenses using the bright field and differential interference contrast methods (Edler & Elbrächter 2010). Ingested diatoms were divided into the two orders Centrales and Pennales, and the centric diatoms *Bacteriastrum* and *Chaetoceros* were separately identified. Ingested thecate dinoflagellates were not divided into subgroups.

Surface water was collected simultaneously to net sampling using a bucket and fixed immediately with formalin (5% final concentration). After returning to the laboratory, the specimens were concentrated in a settling chamber (Sukhanova 1978) and transferred into a Sedgwick-Rafter cell. Diatoms and thecate dinoflagellates were observed under an inverted microscope. More than 200 cells (mean 373 cells) in total were identified and enumerated according to the aforementioned method.

Numerical composition of each taxonomic group distinguished in this study was calculated both in the food vacuoles of *N. scintillans* and in the ambient water. The statistical analysis was carried out using the Wilcoxon's signed-ranks test (Sokal & Rohlf 1987).

Results

Water temperature, salinity and chlorophyll *a* concentration varied greatly among the sampling stations, ranging from 17.9–26.9°C, 9.3–34.5 and 0.4–24.8 μg L^{-1}, respectively (Table 1). In ambient waters, diatoms comprised more than half (55.9–99.9%, mean 87.8%) of the scaled plankton cells, and centric diatoms frequently exceeded pennate ones in abundance. *Noctiluca scintillans* was 6.0×10^{-1}–1.6×10^{4} cells m^{-3} in abundance, and its scaled-plankton feeding ratio was 7.8–85.7%. These ratios were not significantly correlated with the chlorophyll *a* concentrations ($p>0.05$).

In the food vacuoles of *N. scintillans*, diatom frustules were neither crushed nor crunched and composed 98.1–100.0% (mean 99.8%) of the scaled plankton (Fig. 2), which was significantly higher than the ratio of these groups in the ambient water as noted above ($p<0.01$).

The ratio of centric diatoms in the food vacuoles of *Noctiluca* was 60.0–100.0% (mean 93.9%) of the scaled plankton, which was significantly higher than the ratio in the ambient water (20.7–96.1%, mean 68.7%) ($p<0.01$) (Fig. 3a). In contrast, pennate diatoms showed an inverse relationship (Fig. 3b), that is, ratios in the food vacuoles (0.0–40.0%, mean 5.9%) were significantly lower than in the ambient water (3.4–48.8%, mean 19.0%) ($p<0.01$).

Chaetoceros and *Bacteriastrum*, which are easily distinguishable by their long spines, were the dominant centric diatoms in the food vacuoles of *N. scintillans*, comprising 0.0–100.0% (mean 84.5%) of the centric diatoms. The ratio of *Chaetoceros* in the vacuoles (0.0–100% mean 65.0%) was significantly higher than that in the ambient water (1.6–91.4%, mean 43.1%) ($p<0.05$) (Fig. 4a). The ratio of *Bacteriastrum* in the vacuoles (0.0–97.8%, mean 15.2%) was also significantly higher than that in the ambient water (0.0–18.2%, mean 4.6%) ($p<0.05$) (Fig. 4b).

Thecate dinoflagellates were less common than diatoms

Table 1. List of sampling times, locations (latitude and longitude), environmental factors (surface temperature, salinity and chlorophyll *a* concentrations), composition of the scaled plankton, *Noctiluca scintillance* abundance, number of individuals examined, and ratio of individuals fed scaled-plankton.

							Plankton composition (%) in the sea water					*Noctiluca scintillans*		
							Diatom							
							Centrales							
Date	Time	Latitude (N)	Longitude (E)	Temp. (℃)	Sal.	Chl-a (μg L^{-1})	*Ch.*	*Bac.*	Others	Pen-nales	Thecate dinof.	Abundance (ind. m^{-3})	No. of ind. ex-amined (ind.)	Ratio of ind. fed scaled-plankton (%)
April														
13	16:00	32°42.0′	129°36.2′	17.9	34.3	0.5	13.5	0.0	7.2	35.1	44.1	1.6×10^{4}	51	7.8
13	19:00	32°25.5′	129°10.8′	19.8	34.1	0.5	27.5	0.0	2.5	27.5	42.5	1.0×10^{4}	67	53.7
13	17:00	31°47.1′	128°06.6′	19.7	34.2	0.7	1.6	1.6	29.0	41.9	25.8	2.6×10^{1}	43	27.9
June														
24	09:15	32°47.1′	129°43.7′	23.1	34.3	1.1	77.4	3.4	10.1	6.7	2.4	9.1×10^{2}	76	38.2
25	10:36	32°34.8′	130°14.9′	21.8	34.5	1.0	20.9	0.0	30.8	42.3	6.0	1.0×10^{2}	60	43.3
25	11:35	32°36.0′	130°01.9′	22.9	34.3	1.1	57.2	0.0	22.9	12.4	7.5	3.9×10^{2}	63	52.4
25	12:30	32°30.0′	129°53.9′	24.1	34.1	0.5	30.9	2.7	12.8	30.3	23.4	1.0×10^{4}	77	42.9
25	13:57	32°21.0′	129°41.9′	24.9	34.5	0.4	34.8	18.2	21.2	13.6	12.1	1.9×10^{3}	67	34.3
25	15:59	32°36.6′	129°43.5′	23.5	34.2	1.1	36.8	0.0	4.5	23.2	35.5	1.2×10^{2}	66	63.6
25	16:28	32°40.0′	129°40.9′	23.9	33.9	0.8	41.4	0.0	3.6	12.7	42.3	3.3×10^{3}	60	83.3
25	17:02	32°45.0′	129°37.0′	22.7	34.1	0.4	22.4	0.0	45.9	14.2	17.5	1.6×10^{2}	107	43.9
July														
22	09:49	32°47.1′	129°43.8′	26.8	34.3	1.7	91.4	1.3	3.3	3.8	0.1	1.7×10^{0}	28	30.8
22	12:51	32°29.8′	129°00.0′	24.6	32.9	1.7	72.1	3.9	16.4	6.0	1.6	4.3×10^{0}	41	65.9
23	00:16	31°00.1′	130°00.2′	26.9	33.3	0.3	62.4	15.1	10.6	10.6	1.4	6.0×10^{-1}	10	80.0
28	10:01	32°21.0′	129°42.0′	24.9	33.7	1.0	73.1	7.1	9.9	8.8	1.1	1.6×10^{2}	44	31.8
28	11:28	32°30.0′	129°54.0′	25.5	33.8	1.2	56.2	11.1	3.5	19.0	10.2	7.9×10^{2}	62	27.4
28	12:22	32°36.0′	130°02.0′	24.7	33.6	3.0	5.5	0.0	89.0	3.4	2.1	4.3×10^{2}	135	22.2
28	13:27	32°34.8′	130°15.2′	23.3	32.9	12.1	82.2	7.3	4.7	4.3	1.6	1.1×10^{2}	65	40.0
28	15:03	32°45.7′	130°26.4′	26.1	16.6	24.8	1.8	0.0	68.1	26.4	3.7	6.2×10^{1}	61	26.2
28	16:27	32°56.4′	130°19.2′	26.0	9.3	21.3	1.7	0.0	90.2	7.7	0.4	2.3×10^{1}	56	44.6
30	08:34	32°36.6′	129°43.5′	25.4	33.6	0.9	61.0	6.1	9.3	17.1	6.5	2.0×10^{2}	61	49.2
30	09:19	32°40.0′	129°40.8′	25.2	33.8	0.5	56.2	13.7	11.3	18.0	0.8	1.7×10^{2}	57	28.1
30	09:59	32°47.1′	129°43.7′	25.6	33.4	1.4	74.6	6.0	2.1	16.9	0.4	7.9×10^{1}	52	26.9
30	10:32	32°45.0′	129°37.0′	25.6	33.8	0.4	52.1	13.9	1.9	23.9	8.1	9.8×10^{1}	65	29.2
August														
25	13:30	32°36.0′	130°01.8′	26.1	33.4	1.5	21.9	4.0	15.9	48.8	9.3	7.0×10^{-1}	14	85.7

Ch.: *Chaetoceros*, *Bac.*: *Bacteriastrum*

in the ambient water (0.1–41.1%, mean 12.2%) (Fig. 5). When their composition was substantial (>10%), Peridiniales and/or Gonyaulacales were the major components. The ratio of thecate dinoflagellates in the vacuoles was 0.0–1.9% (mean 0.2%), which was significantly lower than that in the ambient water (p<0.01).

Discussion

Predation pressure of *Noctiluca scintillans* has usually been evaluated based on the growth, ingestion and clearance rates on each prey species. Most of these studies have been carried out in laboratory incubation experiments (e.g. Nakamura 1998a, b, Tada et al. 2003). This study is the first case in which feeding intensity of *N. scintillans* was investigated by comparing prey compositions in the food vacuoles and the ambient water. Plankters observed in the vacuoles were those actually ingested in the field and their ingestion was not subjected to artificial influences that are sometimes inherent in laboratory incubations. Although traceable prey plankton species were limited to diatoms and thecate dinoflagellates, this study provides useful information on the predation pressure of *N. scintillans* on each of these prey groups.

In this study, the ratio of total diatoms to other plankters in the food vacuoles of *N. scintillans* was significantly higher than that in the ambient water, while thecate dinoflagellates showed the opposite trend. Among the diatoms, the ratio of centric diatoms to others in the food vacuoles was significantly higher than that in the ambient water,

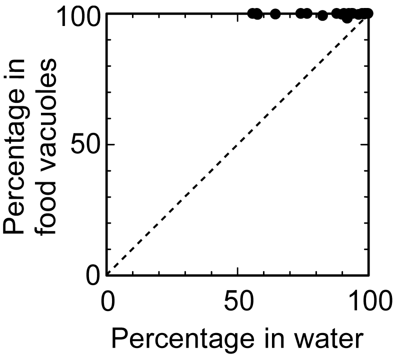

Fig. 2. Percentage composition of diatoms vs total scaled plankton (diatoms and thecate dinoflagellates) in ambient water (horizontal axis) and in the food vacuoles of *Noctiluca scintillans* (vertical axis). The dashed line indicates equivalence in percentage.

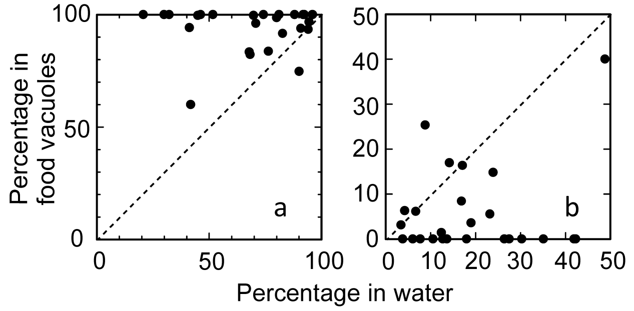

Fig. 3. Percentage composition of centric diatoms (a) and pennate diatoms (b) vs total scaled plankton (diatoms and thecate dinoflagellates) in ambient water (horizontal axes) and in the food vacuoles of *Noctiluca scintillans* (vertical axes). Dashed lines indicate equivalence in percentages.

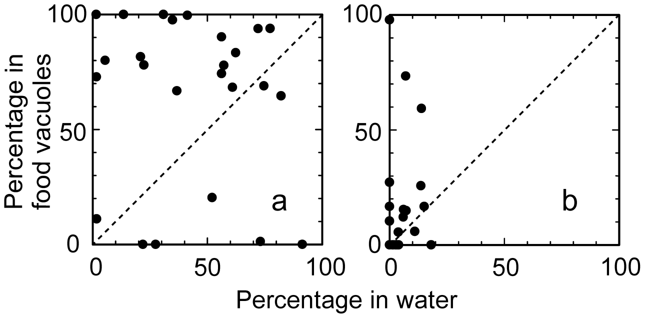

Fig. 4. Percentage composition of *Chaetoceros* spp. (a) and *Bacteriastrum* spp. (b) vs total scaled plankton (diatoms and thecate dinoflagellates) in ambient water (horizontal axes) and in the food vacuoles of *Noctiluca scintillans* (vertical axes). Dashed lines indicate equivalence in percentages.

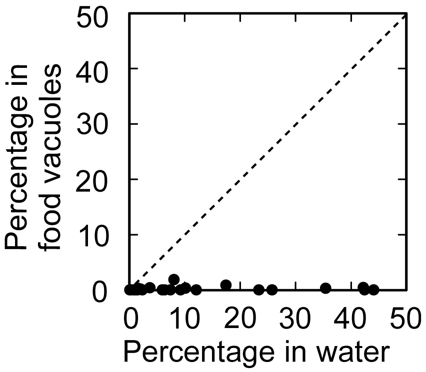

Fig. 5. Percentage composition of thecate dinoflagellates vs total scaled plankton (diatoms and thecate dinoflagellates) in ambient water (horizontal axis) and in the food vacuoles of *Noctiluca scintillans* (vertical axis). The dashed line indicates equivalence in percentages.

while pennate diatoms showed the opposite trend. These results indicate that predation pressure of *N. scintillans* on total diatoms is greater than that on thecate dinoflagellates, and moreover, the pressure on centric diatoms is greater than that on pennate ones.

Buskey (1995) reported that growth rates of *N. scintillans* were higher when diatoms were provided as prey. Kiørboe & Titelmann (1998) reported that clearance rates of *N. scintillans* feeding on the diatom *Conticribra weissflogii* were higher by about one order than those when it fed on the dinoflagellate *Heterocapsa triquetra* and this trend remained even when the two prey species were offered in a mixture. On the other hand, Nakamura (1998b) and Tada et al. (2003) suggested that feeding selectivity of *N. scintillans* on diatoms was not significantly different from that on dinoflagellates. Frangópulos et al. (2011) reported that even the toxic dinoflagellate *Alexandrium minutum* Halim was a good prey item for *N. scintillans*. All these results, which are not always consistent with each other, were obtained in laboratory incubation experiments. However, this study focuses on a natural population and indicates that the predation pressure of *N. scintillans* is greater on diatoms, especially centric diatoms.

Among the centric diatoms, the ratios of *Bacteriastrum* and *Chaetoceros* in the food vacuoles of *N. scintillans* were higher than those in the ambient water. This indicates that these two genera are preferentially ingested by *N. scintillans*. *Bacteriastrum* spp. and most *Chaetoceros* spp. have long setae and occur in chain-forming colonies. Their colony size, including setae, is much greater than those of solitary pennate diatoms and dinoflagellates. Kiørboe & Titelman (1998) revealed that clearance rates of *N. scintillans* on latex beads of 5–80 μm increased with particle size. This indicates that high predation pressure on these diatom genera is probably attributable to their large size, in having long setae and forming chains. Furthermore, their long setae may be easily entangled by the mucus strings extending from a *N. scintillans* tentacle. Once one cell in a colony is entangled, all the other cells of the colony would also be trapped. This feeding method in *N. scintillans* is advantageous, especially in coastal waters from temperate to tropical regions, since colony-forming centric diatoms having long setae such as *Chaetoceros* and *Bacteriastrum*, which are easily trapped by *N. scintillans*, are generally the dominant phytoplankton there.

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