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Predator-prey eddy in heterotrophic nanoflagellate-bacteria relationships in a coastal marine environment: a new scheme for predator-prey associations

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ABSTRACT: Seasonal and short-term variations in abundance of bacteria and heterotrophic nanoflagellates (HNF) together with environmental variables including chlorophyll a (chl *a*) were monitored in Onagawa Bay on the northeastern Pacific coast of Japan. Bacterial abundance varied within a narrow range throughout the year, while HNF abundance showed marked seasonal changes. Short-term observations revealed that peaks of bacterial abundance were usually followed by increases in HNF abundance with a lag of 2 to 6 d and both abundances changed cyclically with a 4 to 10 d period, indicating so-called predator-prey oscillations. These predator-prey oscillations appeared as circular orbits, or 'predator-prey eddies', in phase space during a period shorter than ca 1 mo. Considering the seasonal and short-term trends, we propose a new schematic diagram to describe seasonal changes in this predator-prey relationship. The relationship appears as a HNF-bacterial eddy during the shorter period, while the location and magnitude of the eddy in phase space differ with the seasons. Therefore, the annual cycle of the HNF-bacteria relationship is formed by a continual migration of the predator-prey eddy in phase space. A possible relationship between HNF and chl *a* is also discussed.

KEY WORDS: Heterotrophic nanoflagellates · Marine bacteria · Seasonal and short-term variations · Predator-prey eddy · Chlorophyll *a*

INTRODUCTION

Heterotrophic nanoflagellates (HNF) are widely distributed in marine and freshwater systems (e.g. Sanders et al. 1992 and references therein) and have a large capacity to prey upon bacteria (Haas & Webb 1979, Fenchel 1982a–d). It has been reported for bacteria that their growth is often balanced by predation by e.g. HNF (Sherr et al. 1986, McManus & Fuhrman 1988a, Sanders et al. 1989, Vaqué et al. 1992). This indicates either that a close predator-prey relationship is established between HNF and bacteria, or that HNF is the major agent controlling bacterial abundance in many aquatic systems.

Classical predator-prey models usually describe a simple relationship between 2 species or 2 populations (e.g. Lotka 1925, Volterra 1926, 1931). Such models suggest that abundances of a predator and a prey cyclically change, with a certain phase lag, which is called predator-prey oscillations. Rosenzweig & MacArthur (1963) illustrate predator-prey associations in a simple graphic model, which identifies 3 basic types of predator-prey oscillations: (1) stable oscillations where the magnitude of the oscillations is constant, or the predator-prey system is neutrally stable; (2) damped oscillations where the magnitude decreases with time, or the system proceeds toward a steady state; (3) amplified oscillations where the magnitude increases with time, or the predator completely consumes the prey and then the system will vanish. Although a variety of external factors modify the level of the predator and prey populations, the classical predator-prey models are useful to identify an underlying tendency and to predict the fate of a certain predator-prey system.

So-called predator-prey oscillations between HNF and marine bacteria have been observed for natural

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assemblages (Fenchel 1982d, Andersen & Sørensen 1986, Nakamura et al. 1994, Tanaka & Taniguchi 1996) and in laboratory cultures of a single predator-prey coupling as well (Andersen & Fenchel 1985). Fenchel (1982d) successfully simulated the natural predator-prey oscillations between HNF and bacteria with his model which involves some experimentally determined parameters. However, his run was limited to short time durations. Therefore, how predator-prey relationships between HNF and bacteria vary on an annual basis in nature has not yet been shown.

In this work, we discuss how the numerical relationship between HNF and bacteria can be graphically explained, by referring to Rosenzweig & MacArthur's (1963) model. The data set used was collected by seasonal monitorings in Onagawa Bay on the northeastern Pacific coast of Japan. We propose a new schematic diagram to illustrate the relationship on an annual basis.

MATERIALS AND METHODS

Samplings. Samples were obtained at Stn 1 in the innermost part of Onagawa Bay (38° 26.12' N, 141° 27.62' E, 5 to 6.5 m depth) for the period from December 1993 to March 1995. Samples were collected basically once a week from 3 layers, i.e. the 0, 2 and 5 m layers. In addition to this regular sampling, 2 intensive samplings to monitor the 'short-term variations' were done on every other day during the periods from 1 to 31 July 1994 at the 3 layers and from 5 February to 6 March 1996 at the 2 m layer. Temperature and salinity were recorded at every sampling time at the 3 layers. Water samples were taken with a Kitahara water bottle for nutrient (NO_2, NO_3, NH_4, PO_4, Si) and chlorophyll a (chl *a*) analyses and microscopic enumerations of bacteria and HNF.

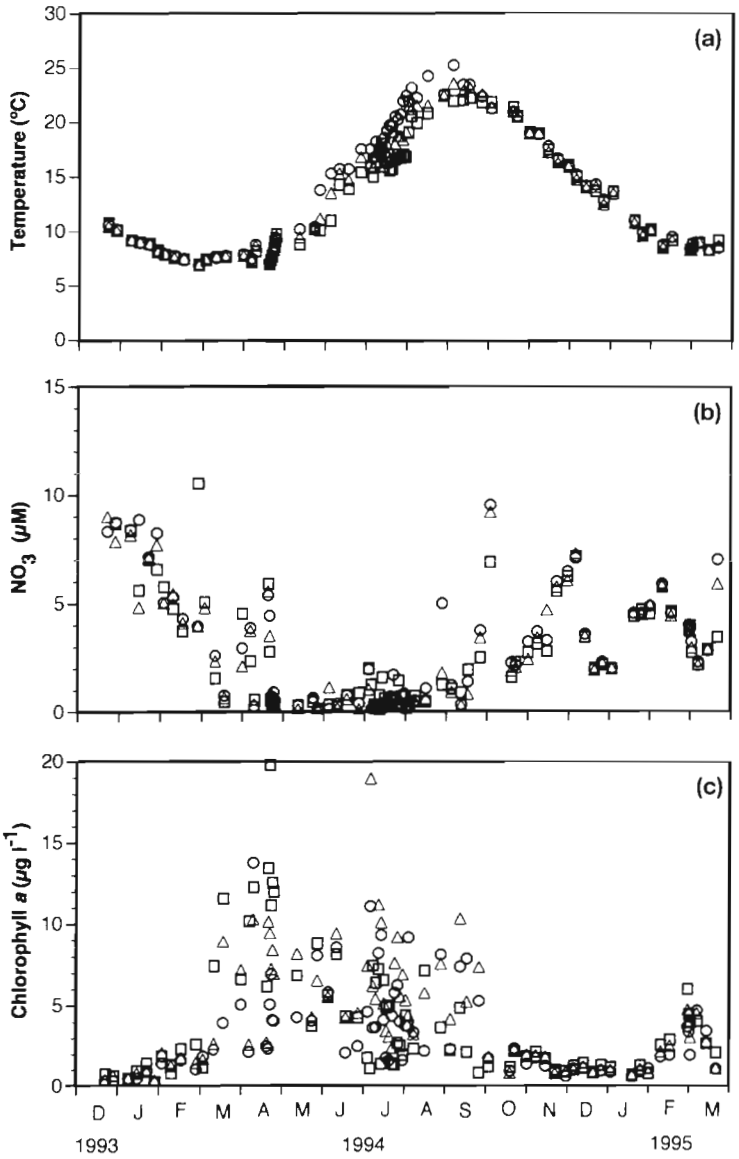

Fig. 1. Seasonal changes in (a) temperature, (b) NO_3 and (c) chl *a* at 0 (○), 2 (△) and 5 m (□) at Stn 1 during the period from December 1993 to March 1995

Samples were always carried back to Onagawa Marine Laboratory within 30 min and processed as described below. Chl *a* was fractionated into 3 size categories of 0.2–2, 2–10 and >10 μm by filtering a 500 ml aliquot through filters of different pore sizes, extracted in 90% acetone and determined by the method of Yentsch & Menzel (1963) with a Hitachi 139 spectrofluorometer. In this study, however, we took the total of the 3 size categories as the chl *a* concentration. In February/March 1996, the total chl *a* was determined without size fractionation by filtering through a Whatman GF/F glass fiber filter. Concentrations of 5 nutrients in the final filtrates (<0.2 μm in 1993 to 1995 or ca <0.7 μm in 1996) were determined with a Flow Solution spectrophotometer system. NO_3 data is presented here to illustrate seasonal changes in nutrient concentration.

Enumeration of plankton. In 1993 to 1995, 10 and 100 ml aliquots of water samples were fixed with glutaraldehyde (final conc. 0.9%) and kept refrigerated (ca 5°C) for enumeration of, respectively, bacteria and heterotrophic nanoplankton, including HNF. Preparation of slides was carried out within 24 h of sampling.

Bacteria were stained with 4',6-diamidino-2-phenylindole (DAPI; final conc. 0.4 µg ml^{-1}) for 5 min and then subsamples (1 to 3 ml) were filtered onto a 25 mm Nigrosin-stained Nuclepore filter of 0.2 µm pore size (Porter & Feig 1980). Each subsample (15 to 50 ml) taken from 100 ml aliquots for HNF enumeration was concentrated into ca 10 ml on a 25 mm Nigrosin-stained Nuclepore filter of 0.6 µm pore size and stained with DAPI for 5 min (final conc. 0.2 µg ml^{-1}) and thereafter with 3,6-diamino-acridine hemi-sulfate (proflavine; final conc. 0.06 µg ml^{-1}; Haas 1982) and finally filtered off. In 1996, the final concentration of DAPI used to stain both bacteria and heterotrophic nanoplankton was modified to 1 µg ml^{-1}.

In 1996, duplicate 100 ml aliquots were fixed and stored in the same way. One filter for enumeration of bacteria and one for HNF was prepared for each aliquot, 4 filters in total. We represent abundances of bacteria and HNF in 1996 as the mean of 2 values.

All the filters were examined under a Nikon epifluorescence microscope equipped with a 50 W mercury lamp at 1000× magnification. Bacterial cells were counted under a UV excitation in at least 10 fields up to ≥400 cells. Both HNF and other heterotrophic nanoplankton, which emit green fluorescence under blue excitation and blue fluorescence under UV excitation, were counted in at least 25 fields, and sized with an ocular micrometer. Cell volume and equivalent spherical diameter (ESD) of these heterotrophs were then calculated by assuming their shape to be spherical or ellipsoidal.

RESULTS

Seasonal changes in temperature and concentrations of NO_3 and chl *a* observed during the period from December 1993 to March 1995 are shown in Fig. 1. Annual range of temperature through the water column was 6.9 to 25.2°C (Fig. 1a). The water column was stratified between May and early September with occasional destratifications due to storms, and vertically mixed between October and April. NO_3 concentrations varied mostly in a range of 0.1 to 10 µM, being higher from fall to winter (Fig. 1b). Chl *a* concentration was in the range 0.2 to 19.8 µg l^{-1}, and was higher and fluctuated markedly from spring to summer (Fig. 1c). No concurrent changes in the vertical profiles of NO_3 and chl *a* with summer stratification of the water column were observed.

Throughout the whole study period, flagellates of 2 to 5 µm ESD dominated in abundance, comprising 59 to 100% (mean 84%) of the total cell number of the heterotrophic nanoplankton of 2 to 20 µm ESD. Since most bacterivores have been reported to be smaller than 5 µm in size (Sherr & Sherr 1991), we considered

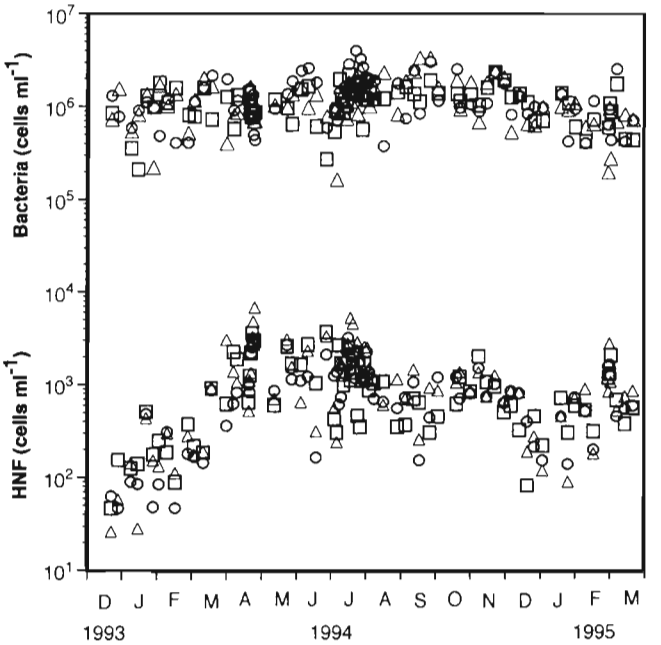

Fig. 2. Seasonal changes in abundance of bacteria and HNF at 0 (○), 2 (△) and 5 m (□) at Stn 1 during the period from December 1993 to March 1995

the flagellates of 2 to 5 µm ESD to be bacterivores. Although it has been reported that heterotrophic nanoplankton larger than 5 µm could also be bacterivores (e.g. Fenchel 1982a, Goldman & Caron 1985, Sherr & Sherr 1987), the general trend of the present results will not be affected due to predominance of the flagellates of 2 to 5 µm ESD. Hereafter, we refer to the flagellates of 2 to 5 µm ESD as 'HNF'. Density of bacterial populations during the period from December 1993 to March 1995 was generally in a range of 0.4×10^6 to 4×10^6 cells ml^{-1} with some exceptions observed at the 2 and 5 m layers, where unusually low values of 2×10^5 to 3×10^5 were recorded (Fig. 2). HNF density ranged from 0.03×10^3 to 6.7×10^3 cells ml^{-1}. It is apparent that both groups of organisms fluctuated in abundance. Although absolute abundance of bacteria was relatively higher in summer to fall, the magnitude of the temporal fluctuations was rather constant throughout the year.

In summer, when samples were obtained every other day to monitor short-term variations, water temperature was 15.0 to 23.1°C and mean (± SD) chl *a* concentration was 5.3 ± 3.4 µg l^{-1} (Fig. 1a, c). Peaks of bacterial abundance were usually followed by increases of HNF with a lag of 2 to 6 d and both HNF and bacterial abundances changed cyclically with a 4 to 10 d period at all 3 layers (Tanaka & Taniguchi 1996). Fig. 3a represents the short-term variation in abundance of HNF and bacteria at the 2 m layer in July 1994. In winter, when water temperature was 5.8 to 7.1°C and mean (± SD) chl *a* concentration was 3.3 ± 1.6 µg l^{-1} (data not

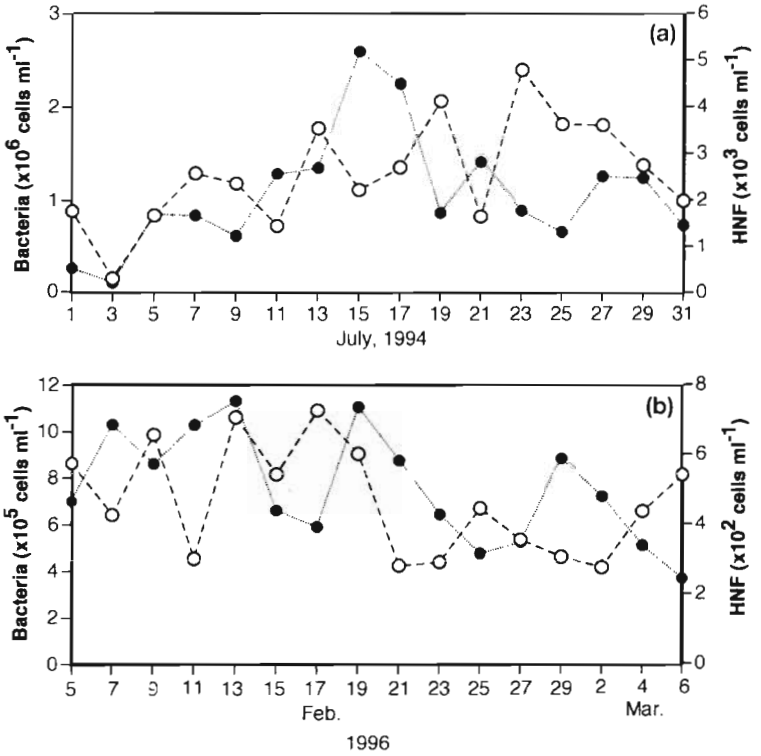

Fig. 3. Temporal changes in abundance of bacteria (○) and HNF (●) at 2 m at Stn 1 during the periods (a) from 1 to 31 July 1994 and (b) from 5 February to 6 March 1996

shown), similar predator-prey oscillations were also observed with a 6 to 10 d period and a lag of 2 to 4 d at the 2 m layer (Fig. 3b).

DISCUSSION

Seasonal and short-term variations

Environmental variables monitored in this study suggest that the trophic condition of Onagawa Bay is typical of embayments in a temperate zone with clear seasonal changes (Fig. 1). Among such changes, it is expected that growth rate and thus abundance of bacteria change seasonally too. However, the bacterial abundance was observed to be mostly in a narrow range of 0.5×10^6 to 2×10^6 cells ml^{-1} throughout the year (Fig. 2). This range is equivalent to the feeding threshold for HNF on bacteria which has been reported in previous studies (e.g. Fenchel 1982b, Andersen & Fenchel 1985, Wikner & Hagström 1991). The same trend of little seasonal variation in bacterial abundance in spite of large environmental variations has been observed in other aquatic systems (Wright & Coffin 1984, Iwamoto et al. 1994, Mostajir et al. 1995). On the other hand, HNF abundance showed marked seasonal variation, being high in warm seasons and low in winter (Fig. 2). From the ecological point of view taken in e.g. classical predator-prey models, this discrepancy in the magnitude of seasonal variation in abundance of the predator (HNF) and the prey (bacteria) is not expected.

Since generation times of HNF and bacteria are of the order of several hours to several days (e.g. Ducklow 1983, Eccleston-Parry & Leadbeater 1994), intensive samplings with short time intervals should be used to monitor changes in abundances. We observed predator-prey oscillations for HNF and bacteria at 2 d intervals in summer (Tanaka & Taniguchi 1996) and in winter. The closely coupled oscillations in temporal scales were observed in both seasons or at both extremes of the seasonal environmental fluctuation in Onagawa Bay (Fig. 3). This indicates that bacterial growth was probably roughly balanced by ingestion by bacterivores as suggested by previous studies (reviewed by McManus & Fuhrman 1988b, Sanders et al. 1992). Among the bacterivores, HNF might be the most important component in this bay as in other environments (cf. Sherr et al. 1986, Sanders et al. 1989). Thus, the short phase lag of 2 to 6 d between the two suggests that HNF quickly respond to increases of bacterial abundance and/or growth rate. It is interesting to note that bacterial abundance in Onagawa Bay seems to be kept within a very narrow range, corresponding to the reported feeding threshold for HNF throughout the year. Therefore, we can speculate that the feeding threshold for HNF may play an important role in determining the minimal bacterial abundance in the bay.

Based on the data sets obtained using short-term observations in summer and winter (Fig. 3), HNF abundance was plotted against bacterial abundance in a phase space (Fig. 4). Each of the seasonal data sets showed a circular orbit, which was roughly similar to Rosenzweig & MacArthur's (1963) graphic diagram. The direction of these orbits, however, alternated between clockwise and anti-clockwise in both seasons, unlike a regular anti-clockwise orbit suggested theoretically by Rosenzweig & MacArthur (1963). The observed circular orbits sometimes showed wide protrusions, indicating that the HNF-bacteria system was destabilized. Although the behavior of the system seemed to have a tendency to return to the original cycles, which are well known as 'stable limit cycles', the orbits showed very complicated, or chaotic, motion. Such drift from the theoretical model was possibly

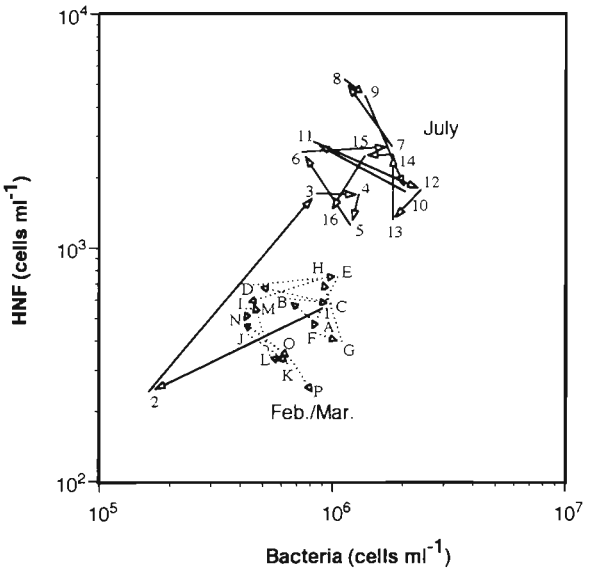

Fig. 4. Behavior of the HNF-bacteria system in each short-term observation given in a 2-dimensional phase space (see Fig. 3). The arrows with solid line and number (July) and the arrows with dotted line and letter (February/March) are shown to mark the direction of the change

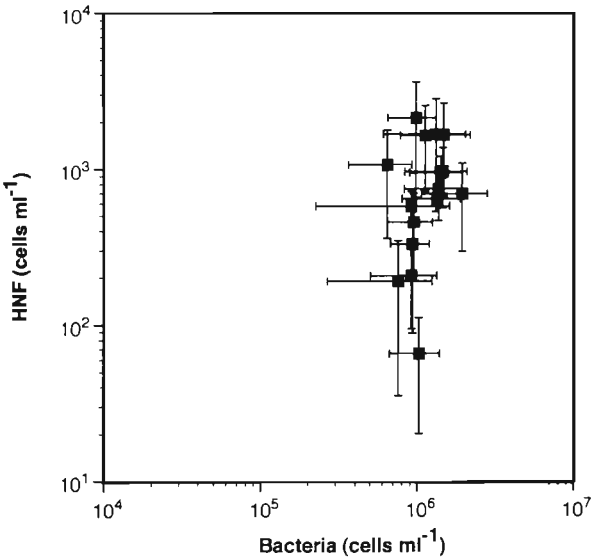

Fig. 5. Seasonal relationship between abundance of HNF and bacteria from monthly means with standard deviations for all individual points at 0, 2 and 5 m at Stn 1 during the period from December 1993 to March 1995

caused by (1) different sets of species that 'bloomed and crashed' over a season or alternatively even in a week, which is different from the theoretical model which deals with just a single pair of predator and prey, (2) a continual changing of relative abundance of several predators and prey with different niches (e.g. Wikner & Hagström 1988), (3) technical difficulty in monitoring the succession of the same predator-prey populations due to physical disturbances (e.g. current, storms and advection), (4) counting error which could become noisier when comparing the relatively small differences, and (5) influence of organisms other than bacteria and HNF.

Location and magnitude of the orbit were apparently different between summer and winter, because abundances of bacteria and HNF were mostly within the ranges of 0.5×10^6 to 3×10^6 and 0.3×10^3 to 3×10^3 cells ml^{-1} in summer and 0.4×10^6 to 0.9×10^6 and 0.3×10^3 to 0.7×10^3 cells ml^{-1} in winter, respectively (Fig. 4). Thus, even though the periodicity and phase lag in HNF-bacteria oscillations were similar in both seasons (see Fig. 3), turnover rate and level of material cycling through the HNF-bacteria system might have been much higher in summer than those in winter.

HNF-bacteria system

Based on the data shown in Fig. 2, the relationship between HNF and bacteria in Onagawa Bay could be illustrated by calculating their monthly means. Because of relatively small seasonal change of bacterial abundance, the relationship was confined to a vertically elongated elliptical region in phase space (Fig. 5). Although a simple linear regression has commonly been adapted to similar relationships within a system for various sites (Imai & Itoh 1984, Sherr et al. 1984, Davis et al. 1985, Wright et al. 1987, Iwamoto et al. 1993, 1994, Tzaras & Pick 1994), the typical linear relationship of 1000 bacteria:1 HNF was not apparent for Onagawa Bay on an annual basis. Data obtained by the short-term observations in summer and winter revealed that a circular orbit was also the case, on a monthly basis, in Onagawa Bay whose position and magnitude were different between seasons (Fig. 4).

Based on these results, we propose a schematic diagram to interpret the seasonal change of numerical relationship between HNF and bacteria (Fig. 6). Restricting observations to each 1 mo period, location of each orbit in phase space is probably confined in a particular region, in spite of sporadic and sometimes drastic changes of environmental variables (see Fig. 4). Such a behavior of each orbit is basically similar to Rosenzweig & MacArthur's (1963) model. However, as shown in Fig. 4, the HNF-bacteria orbit is chaotic, rather than neutrally stable or stable limit cycles. Nevertheless, since the main body of the orbit is confined to a certain region in phase space on a monthly basis and looks like an eddy, we term it 'predator-prey eddy'. The predator-prey eddy probably shifts in phase space with seasonal changes of certain environmental factors. The annual cycle of the

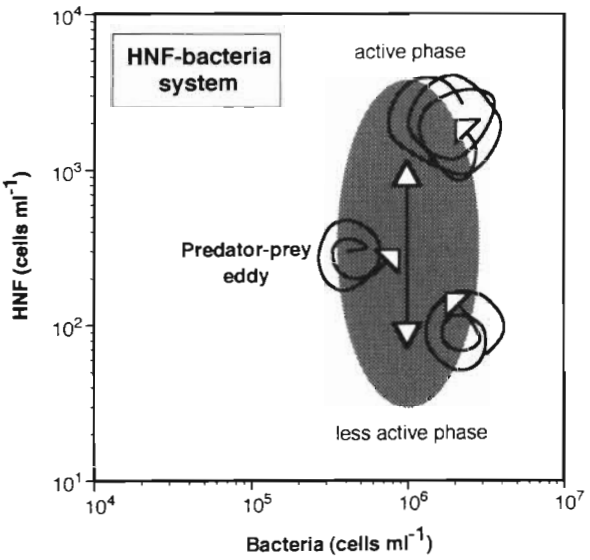

Fig. 6. Schematic diagram of the numerical relationship between HNF and bacteria. See 'Discussion' for details

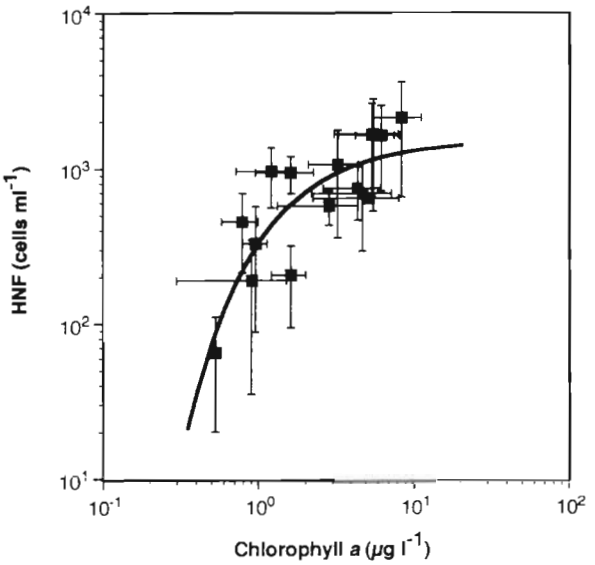

Fig. 7. Seasonal relationship between HNF abundance and chl *a* concentration from monthly means with standard deviations for all individual points at 0, 2 and 5 m at Stn 1 during the period from December 1993 to March 1995. The line shows the non-linear regression (equation in text)

HNF-bacteria relationship is a continuous migration of the predator-prey eddy, whose extension is probably confined to a particular elliptical region in phase space that is determined by the trophic condition of each habitat.

Relationship between HNF and chl *a*

According to the concept of the microbial loop (Azam et al. 1983), close couplings among microbial components, e.g. organic matter excreted by phytoplankton, bacteria and HNF, can be expected. However, as is apparent from Figs. 2 & 5, bacterial abundance showed little seasonal change. On the other hand, the relationship between HNF abundance (HNF) and chl *a* concentration in Onagawa Bay could be described by a non-linear regression ($r^2 = 0.678$, n = 16) on monthly means which were calculated from the data shown in Figs. 1 & 2 (Fig 7):

$$\log \mathrm{HNF} = 3.18\{1 - \exp[-2.31(\log \mathrm{chl} + 0.69)]\}$$

Although there is no significant inflow of freshwater, only very small streams pour into Onagawa Bay, influence of allochthonous organic matter on their relationships cannot be ignored, especially at a near-coast site (e.g. White et al. 1991). The HNF-chl *a* relationship observed in this study might be interpreted as follows: (1) contribution of phytoplankton to bacterial substrate was primarily important; and (2) coupling between HNF and bacteria was close in Onagawa Bay. If so, the observed relationship between HNF and chl *a* is established by a very efficient material transfer through 3 components in this semi-enclosed embayment.

On the other hand, the relationship between HNF and chl *a* could also be fitted by a linear regression ($r^2 = 0.647$, n = 16). Considering data on abundances of HNF and bacteria from a wide range of freshwater and marine environments, Sanders et al. (1992) and Gasol & Vaqué (1993) concluded that resource-dependence of HNF abundance (bottom-up control) is common under most oligotrophic situations and top-down control is common under eutrophic situations. Top-down control should exist in Onagawa Bay when trophic conditions are rich. Therefore, we consider that a non-linear fitting with an upper limit of HNF abundance may better represent the bay. At present, we cannot fully elucidate the relationship, because only a few environmental variables and abundances of bacteria and HNF at community level without species identification were monitored in this study.

CONCLUSION

A closely coupled relationship between HNF and bacteria has been reported universally from freshwater to marine and from oligotrophic to eutrophic environments. Therefore, the following can be assumed: (1) the so-called predator-prey eddy of HNF-bacteria system as shown in Fig. 6 is probably common; (2) location and magnitude of the eddy in phase space on shorter temporal scales are determined by seasonal environ-

mental factors; (3) region of the annual cycle of the eddy in phase space, or annual range of the seasonal migration of the eddy, is determined by local environmental factors particular to each system; and (4) each system seems to have an 'attractor' which attracts the eddy into a particular region in phase space (cf. Farmer et al. 1983).

Numerical relationships between HNF and bacteria in natural systems have frequently been described by a linear regression or a single ratio, e.g. 1000:1. However, our data reveal that such a single ratio is probably a simplification. The HNF-bacteria system is much more dynamic on both short and annual temporal scales as illustrated in Fig. 6.

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