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Seasonal changes in micro-zooplankton grazing on phytoplankton assemblages in the Oyashio region, western subarctic Pacific

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Abstract: Seasonal surveys were made for assessing grazing impacts of micro-zooplankton on phytoplankton assemblages in the Oyashio region in July and October 1997 and January, March and May 1998. Surface chlorophyll-*a* concentrations ranged from 0.51 to 7.15 $\mu g\,l^{-1}$ and diatom blooms were observed in October 1997 and May 1998. Over the study period as a whole, the major micro-zooplankton component was naked ciliates, although naked and thecate flagellates were most abundant during diatom-blooming periods. Phytoplankton growth rates and micro-zooplankton grazing rates ranged from 0.22 to 0.65 d^{-1} and from 0.09 to 0.57 d^{-1}, respectively. Water temperature (range: 1.5–12.1°C) was not related significantly to the seasonal variations in these rates. Neither chlorophyll-*a* nor micro-zooplankton biomass determined the seasonal variations in micro-zooplankton grazing rates. Seasonal changes in size composition of phytoplankton and micro-zooplankton assemblages are considered major factors contributing to the seasonal variations in grazing rates. Prey size was more favorable for micro-zooplankton during the winter but not during the periods of diatom blooming in the spring and fall. Despite a moderate biomass, the grazing rate ($<0.09\,d^{-1}$) of micro-zooplankton on phytoplankton was at a minimum in the summer (July), perhaps due to poor quality of their phytoplanktonic food. To fulfil the nutritional requirements of micro-zooplankton, a food pathway such as that of heterotrophic bacteria–heterotrophic nanoflagellates–micro-zooplankton may be important in July. These results suggest that the magnitude of micro-zooplankton grazing on phytoplankton in the Oyashio region depends mainly on the seasonal change in micro-zooplankton composition, and size and quality of phytoplankton.

Key words: Micro-zooplankton, dilution method, Oyashio region

Introduction

Micro-zooplankton, including heterotrophic flagellates, ciliates and copepod nauplii can represent a significant proportion of the total zooplankton biomass of the oceans (Odate & Maita 1988; Tsuda et al. 1990; Booth et al. 1993; Boyd et al. 1995a). The roles of micro-zooplankton in pelagic ecosystems, include those of consumers of pico- to nano-sized phytoplankton and rapid regenerators of nutrients (Paasche & Kristiansen 1982; Goldman & Caron 1985). Further, the micro-zooplankton are considered to play an intermediary role in trophic exchanges between the pico- to nano-phytoplankton and meso-zooplankton (Gifford 1991).

Recently, high nutrient and low chlorophyll (HNLC) conditions have been observed in various marine systems, where primary production and phytoplankton biomass are relatively low in spite of high concentrations of macro-nutrients such as phosphorus and nitrogen (Frost 1991). Instability of the water column, deficiency of micronutrients such as iron and micro-zooplankton grazing have been proposed as possible causes of the HNLC conditions (Smith & Nelson 1985; Martin & Fitzwater 1988; Frost 1991; Miller et al. 1991). Furthermore, the significant impacts of micro-zooplankton grazing on phytoplankton communities has

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been well documented in many regions of the world's ocean (Capriulo & Carpenter 1983; Burkill et al. 1987; Paranjape 1987; Gifford 1988; Odate & Maita 1988; Verity et al. 1993; Froneman & Perissinotto 1996; Tsuda & Kawaguchi 1997).

The Oyashio Current (temperature: <2°C) is a western boundary current in the subarctic circulation, originating from the East Kamchatka Current of the southwestern Bering Sea, and flowing southwestward along the Kuril Islands in the subarctic Pacific (Ohtani 1970). From a fisheries view point, the Oyashio region (Oyashio Current and its peripheral regions) is known as one of the most highly productive areas in the world ocean (FAO 1997), as is evidenced by its high primary production (Taniguchi & Kawamura 1972) and high zooplankton biomass (Hattori 1991; Odate 1994). In waters around the Oyashio region, incidental information is available about micro-zooplankton biomasses (Dohi 1982; Taniguchi 1984,1999) and vertical distributions (Suzuki & Taniguchi 1998) of naked ciliates and tintinnids. However, little is known about dynamic function of micro-zooplankton, such as their grazing impacts on phytoplankton throughout the year.

In this study, we determined both micro-zooplankton grazing rates on phytoplankton and phytoplankton growth rates during various seasons of the year and discuss the balance between micro-zooplankton and phytoplankton in order to evaluate the quantitative trophic role of micro-zooplankton in the planktonic food web of the Oyashio region.

Materials and Methods

Shipboard experiments were carried out at stations (A3–A11) along a transect (A-line) across the Oyashio current off southeastern Hokkaido (Fig. 1) in July and October 1997, and January, March and May 1998. In each experiment, 20-liter polycarbonate bottles were filled with surface seawater pre-filtered through 183-μm mesh netting to remove meso-zooplankton. One half of the seawater in the bottles was filtered through Whatman GF/F filters and used for the 'dilution' experiments detailed below. Dilution series of unfiltered to filtered seawater (1 : 5, 1 : 2, 1 : 1 and 1 : 0) were prepared in 1.2-liter polycarbonate bottles in duplicates. All the bottles were shaded to ca. 50% of surface light intensities with a black cloth to prevent photo-inhibition, and incubated for 24 h on a deck incubator with a throughout of the running surface seawater.

The 'dilution' technique allows simultaneous estimation of algal growth rates and the grazing loss rates due to micro-zooplankton with minimal manipulation of the natural plankton assemblages (Landry & Hassett 1982; Gifford 1988; Paranjape 1990). One of the potential sources of error associated with the technique is nutrient limitation during experiments. However, this source of error will be minimal in the present experiments, as nutrient exhaustion never occurs in Oyashio waters at any time of year (cf. Saito et al. 1998). According to Gifford (1988), nutrient addition may damage the delicate micro-zooplankton in the bottles. For these reasons, no nutrient additions were made during the present experiments.

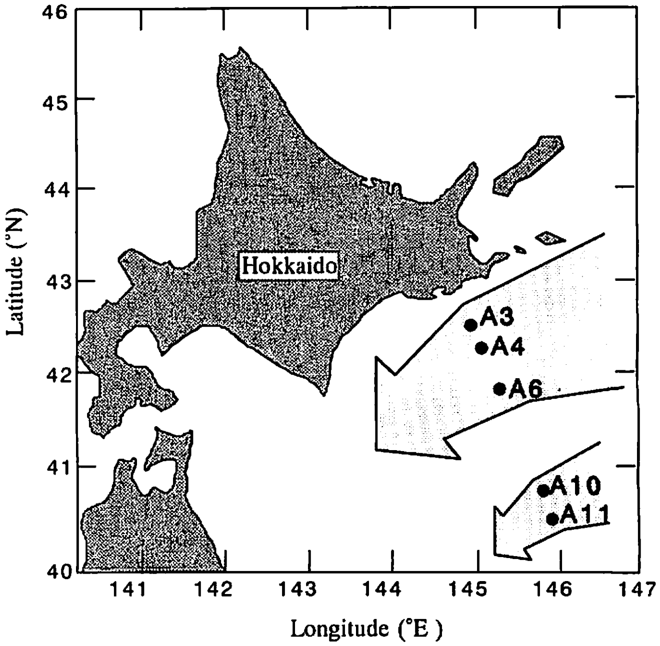

Fig. 1. Location of sampling stations (A3–11) in the Oyashio region, the western subarctic Pacific Ocean. *Arrow* denotes Oyashio Current.

Prior to the dilution experiments, chlorophyll-*a* (Chl-*a*) concentrations of non-diluted natural seawater were determined. At the end of the incubation, Chl-*a* concentrations were measured for all experimental bottles. Water subsamples (100–200 ml) were withdrawn from each bottle and filtered through Whatman GF/F filters. The filters were placed each separately into disposable tubes containing 6 ml of n,n dimethylformamide (Suzuki & Ishimaru 1990) and kept cool (−30°C) in a freezer until analysis. Subsamples (1000 ml) of non-diluted seawater (meso-zooplankton were already removed) were taken and preserved in 1% acid Lugol's solution for later counting of the micro-zooplankton.

Chlorophyll *a* was determined with a fluorometer (Turner Designs, model 10-AU), taking readings before and after acidification (Holm-Hansen et al. 1965). Apparent phytoplankton growth (μ_{net}, d^{-1}) and micro-zooplankton grazing rates (g, d^{-1}) on phytoplankton were estimated using Landry & Hassett's (1982) model:

$$\mu_{net}=\mu_{max}-g\cdot x,$$

where x and μ_{max} are the proportion of diluted seawater ($x=1$ is non-diluted treatment) and potential growth of phytoplankton, respectively. Apparent growth rate of phytoplankton was calculated for each bottle as

$$\mu_{net}=\ln(N_t/N_0)/t,$$

where N_0 and N_t are the initial and final Chl-*a* concentrations, and t is the incubation time (d), respectively. In analyzing the data, we noticed a nonlinearity in μ_{net} with decreasing x (see Results), as was observed previously by Gallegos (1989). Gallegos (1989) interpreted this as the result of prey levels exceeding the incipient limiting concentration (ILC) for micrograzers, a violation of one of the assumptions of Landry & Hassett's (1982) model. Bearing this in mind we analyzed the functional response carefully by using a piecewise regression technique in the NLIN (nonlinear models) procedure of SYSTAT (SYSTAT, Inc.) to fit a Model I regression (Sokal & Rohlf 1995), following the precedent set by (Elser & Frees 1995):

$$\mu_{net}=\mu_{max}-s\cdot x, \quad \text{when } x<\text{ILC},$$

and

$$\mu_{net}=\mu_{max}-s\cdot \text{ILC}, \quad \text{when } x\geq\text{ILC},$$

where s is the slope of the linear portion of the functional response. Grazing rates were then derived as:

$$g=s\cdot \text{ILC}.$$

Percentages of the initial standing stock of phytoplankton lost to micro-zooplankton grazing (Ig, d^{-1}) was calculated as

$$\text{Ig}=[1-\exp(-g)]\cdot 100.$$

The proportion of the potential production of the phytoplankton that had been grazed upon by the micro-zooplankton (Pg, d^{-1}) was given as

$$\text{Pg}=[1-\{\exp(\mu_{max}-g)-1\}/\{\exp(\mu_{max})-1\}]\cdot 100.$$

Micro-zooplankton were settled in a chamber and enumerated under an inverted microscope. As organisms were preserved in iodine fixative it was impossible to distinguish autotrophs from heterotrophs. Of the marine planktonic ciliates, *Myrionecta rubrum* is the only species known to be strictly autotrophic, whereas others are mixotrophs or heterotrophs (Pierce & Turner 1992) as is also the case for most flagellates (Gaines & Elbrächter 1987; Jones 1994). In this study, we assumed micro-zooplankton to all be heterotrophs. The biovolume of each micro-zooplankton specimen was estimated by measuring various body parts, and converted to carbon units using the appropriate conversion factors or equations listed in Table 1.

Correlations between various parameters including phytoplankton growth rates, micro-zooplankton grazing rates, micro-zooplankton biomass, temperature and Chl-*a* concentrations were explored (correlation analysis). Chlorophyll-*a* data were transformed to the logarithm scale (base 10) prior to the analysis.

Results

Over the entire survey period, the surface water temperatures ranged from 1.5 to 12.1°C. The lowest temperatures (<4°C) were recorded in January and March 1998 (Table 2), and water temperatures increased in late May onward, reaching >10°C in July. Chlorophyll-*a* concentrations varied from 0.43 to 7.15 $\mu g\,l^{-1}$. High Chl-*a* values (>3 $\mu g\,l^{-1}$) were observed at Stn A3 in October 1997 and at Stns A3 and A4 in May 1998, where diatoms consistently dominated the phytoplankton assemblages (A. Shinada, unpublished data). On other occasions, Chl-*a* values were low (0.4–0.7 $\mu g\,l^{-1}$).

Micro-zooplankton biomass ranged from 4.2 to 149 $\mu g\,C\,l^{-1}$ (Fig. 2). The highest micro-zooplankton biomass was seen at Stn A3 in May 1998, where naked flagellates consti-

Table. 1. Conversion factors or formulae for converting the biovolumes of each taxon of micro-zooplankton to carbon biomasses.

Micro-zooplankton	pg C μm^{-3}	Reference
Naked flagellates	0.11	Edler 1979
Thecate flagellates	0.13	Edler 1979
Naked ciliates	0.19	Putt & Stoecker 1989
Tintinnids	$444.5+0.053^{l*}$	Verity & Langdon 1984
Nauplii	0.05	Mullin 1969

* *l*: lorica volume in μm^3.

Table 2. Summary of the results of the dilution experiments, including the surface water temperatures and chlorophyll-*a* concentrations at the start of the experiments, phytoplankton growth rates (μ_{max}) and micro-zooplankton grazing rates (g). Ig and Pg represent fractions of the initial phytoplankton stock and primary production consumed by micro-grazers, respectively.

Year	Date	Station	Temperature (°C)	Initial Chl *a* ($\mu g\,l^{-1}$)	μ_{max} (d^{-1})	g (d^{-1})	Ig (% d^{-1})	Pg (% d^{-1})
1997	2 Jul	A11	12.1	0.72	0.47	0.09	8.3	22.3
	3 Jul	A6	11	0.51	0.45	0.10	9.7	28.0
	5 Jul	A3	7.8	0.65	0.49	0.25	21.7	56.0
	17 Oct	A3	12.1	7.07	0.44	0.31	26.7	74.3
1998	15 Jan	A4	3.8	0.52	0.25	0.18	16.5	74.5
	12 Mar	A10	1.5	0.61	0.22	0.37	30.9	156.6
	14 Mar	A3	1.6	0.43	0.65	0.57	43.4	90.9
	12 May	A3	4.3	7.15	0.47	0.23	20.5	54.8
	12 May	A4	5.6	3.19	0.48	0.27	23.7	62.2
	14 May	A11	8.3	0.59	0.62	0.38	31.9	69.1

tuted the major component (64% of the total micro-zooplankton biomass), followed by naked ciliates (21%) and thecate flagellates (11%). In October 1997, the biomass of naked and thecate flagellates was high at Stn A3. On other occasions, naked ciliates were 21–80% of the total micro-zooplankton biomass. A positive correlation was found in the relationship between the total micro-zooplankton biomass and Chl-*a* concentrations ($n=10$, $r=0.786$, $p<0.05$; Fig. 3).

In 4 out of 10 experiments, a non-linear regression of μ_{net} on x was found (Fig. 4). The rectilinear model was therefore applied to solve for g and μ_{max}. ILC was found to be between 0.41 and 0.56 as a fraction of the unfiltered seawater in these four experiments. Maximum growth rates of phytoplankton assemblages (μ_{max}) ranged from 0.22 to 0.65 d^{-1} (Table 2, Fig. 4), which equate to 0.32–0.94 doublings per day in terms of Chl-*a*. Both the lowest μ_{max} (0.22 d^{-1}), recorded at Stn A10 on 12 March 1998, and the highest μ_{max} (0.65 d^{-1}) at Stn A3 on 14 March 1998, were associated with low temperatures (1.5 and 1.6°C, respec-

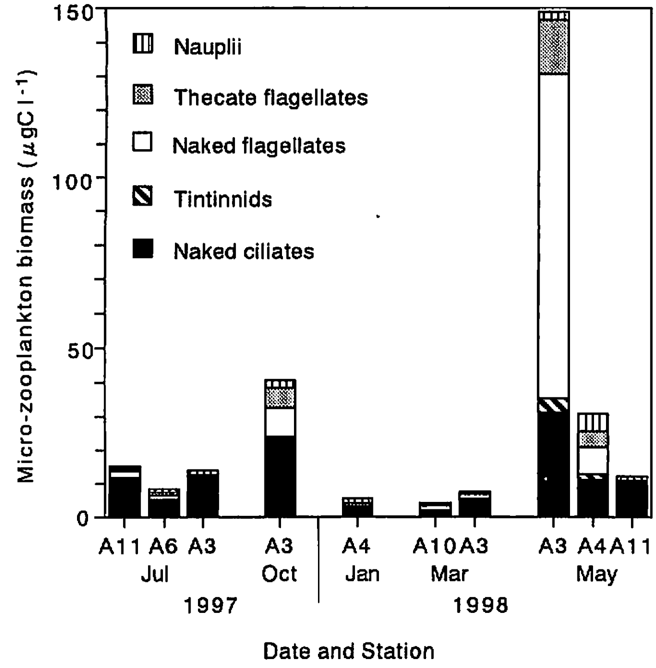

Fig. 2. Biomass and composition of micro-zooplankton in the natural seawater used for dilution experiments at each station and season.

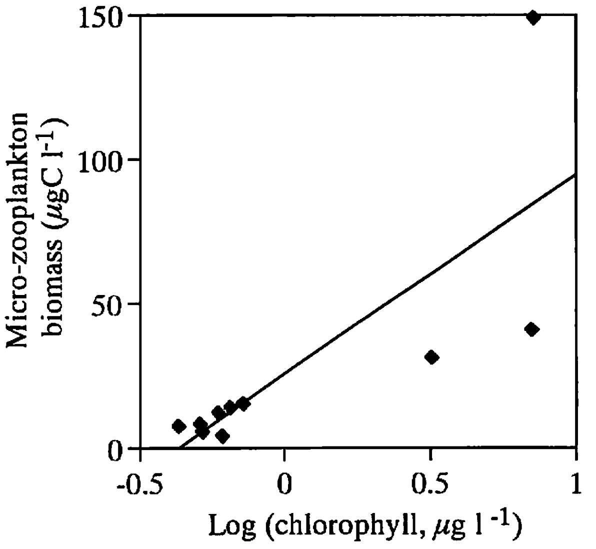

Fig. 3. Relationships between micro-zooplankton biomass and chlorophyll-*a* concentration ($r=0.786$, $p<0.05$).

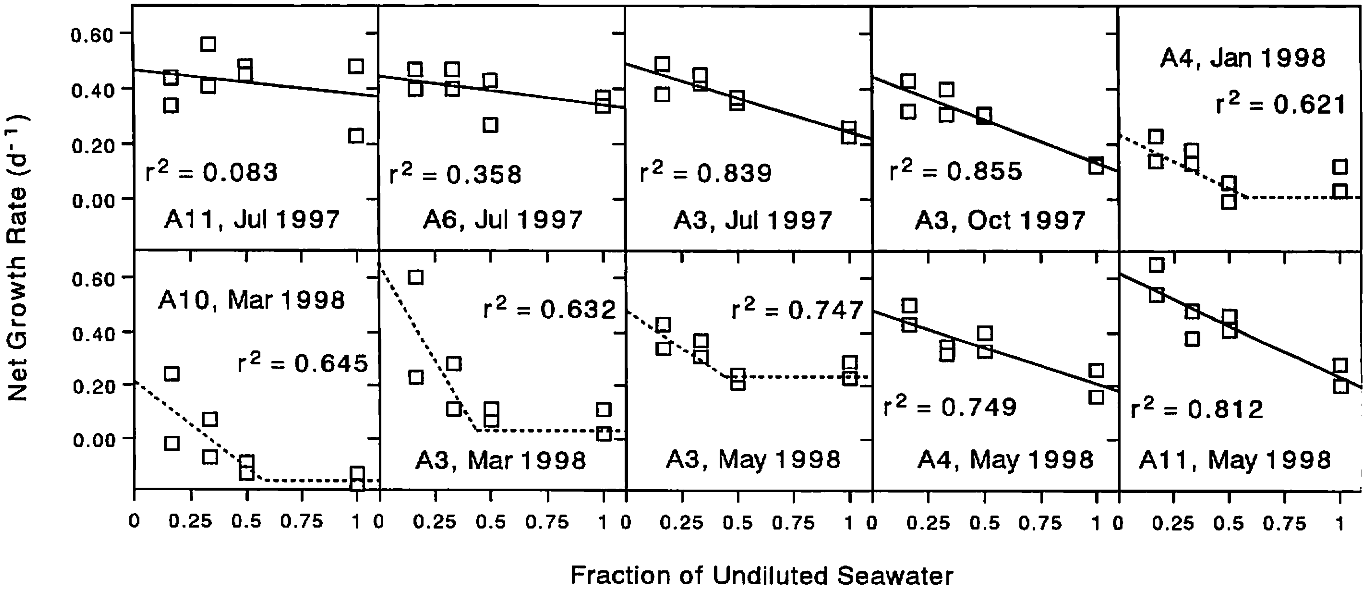

Fig. 4. Relationships between apparent growth rates of phytoplankton and the degree of dilution of natural seawater with filtered seawater at Stns A3 to A11. Solid and broken lines are linear and rectilinear fits of the data points, respectively. Note that the rectilinear fits assume grazing saturation at a certain level of dilution (=ILC).

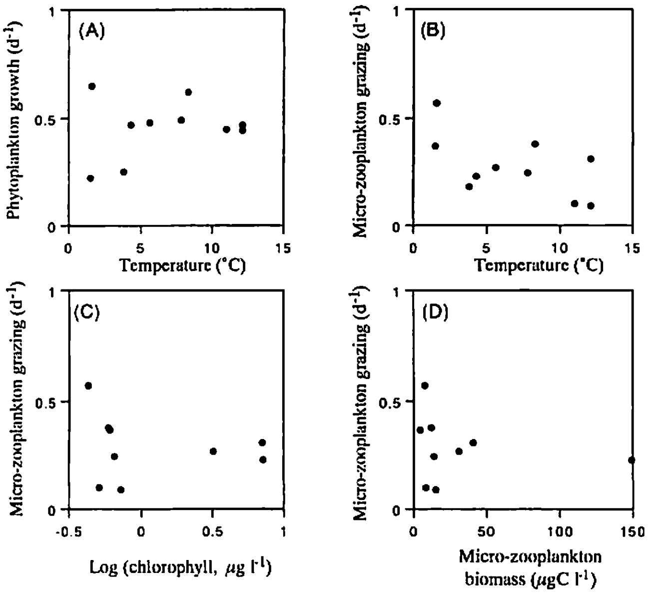

Fig. 5. Relationships between maximum growth rates of phytoplankton and surface temperatures ($r=0.214$, $p>0.05$) (**A**), between micro-zooplankton grazing rates and surface temperatures ($r=0.578$, $p>0.05$) (**B**), between micro-zooplankton grazing rates and chlorophyll-*a* concentrations ($r=0.149$, $p>0.05$) (**C**), and between micro-zooplankton grazing rates and micro-zooplankton biomass ($r=0.167$, $p>0.05$) (**D**).

tively), indicating that the phytoplankton growth rates were not correlated with water temperature ($n=10$, $r=0.130$, $p>0.05$; Fig. 5). Grazing rates (g) of micro-zooplankton ranged from 0.09 to 0.57 d^{-1} and were correlated weakly to surface water temperatures ($n=10$, $r=-0.578$, $p=0.08$; Fig. 5). Correlation analyses revealed no significant relationships between micro-zooplankton grazing rates and the initial Chl-*a* concentrations or the micro-zooplankton biomass. Igs and Pgs ranged from 8.3 to 43.4% (mean 31.1%) and from 22.3 to 156.6% (mean 78.7%), respectively (Table 2). Lower Pgs (22.3–56%) were observed in July, while higher Pgs (>74.5%) occurred in January and March (Table 2).

Discussion

The present results show clearly that the impact of micro-zooplankton grazing on phytoplankton in the Oyashio region varies greatly with season, and that a number of factors are involved in the observed variation. In order to evaluate region-specific characteristics of micro-zooplankton grazing in the Oyashio region, the present results were compared with those from high latitude seas such as the NE subarctic Pacific (Landry et al. 1993; Boyd et al. 1995b), the North Atlantic (Burkill et al. 1993; Verity et al. 1993) and the Southern Ocean (James & Hall 1998; Froneman & Perissinotto 1996) during similar seasons.

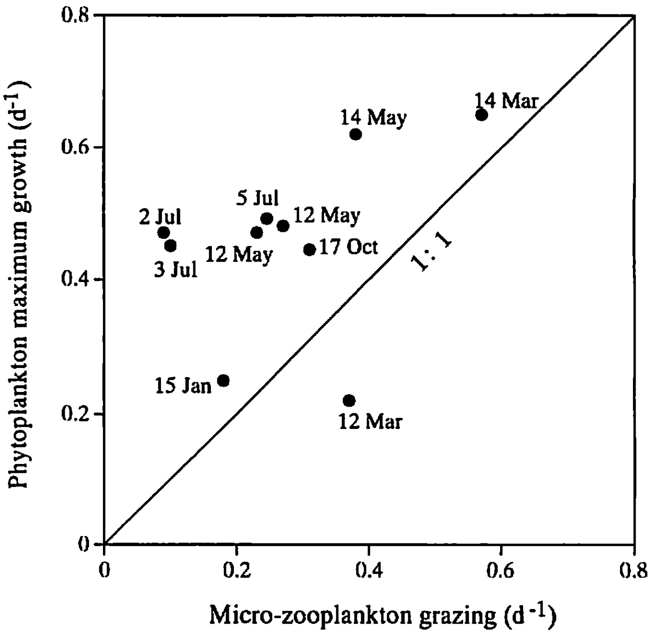

Fig. 6. Relationships between phytoplankton growth rates and microzooplankton grazing rates.

During the winter season (January and March), the micro-zooplankton grazing rates (g: 0.18–0.57 d^{-1}) obtained in this study fell well within the ranges reported from other high latitude seas in winter, such as the NE subarctic Pacific (0.17–0.21 d^{-1}, Boyd et al. 1995b), the subantarctic Pacific (0.25–0.78 d^{-1}, James & Hall 1998) and the South Atlantic (0.38–0.70 d^{-1}, Froneman & Perissinotto 1996) and nearly balanced or exceeded phytoplankton growth rates (Fig. 6). Earlier studies have shown that phytoplankton cell size (Hansen 1992; Peters 1994), species compositions of phytoplankton and micro-zooplankton (Burkill et al. 1987; Strom & Welschmeyer 1991; Kamiyama 1999) and ambient temperature (Peters 1994) affect grazing rates of micro-zooplankton. Micro-zooplankton are known to prefer nano-size phytoplankton prey (2–10 μm) (Rassoulzadegan & Etienne 1981; Capriulo 1982). Although we did not examine phytoplankton species composition in this study, nano-phytoplankton were reported to be abundant at Stn A3 in winter in 1998 (Shinada 2000). Further, micro-zooplankton were demonstrated to graze on phytoplankton at high rates in cold waters (ca. 1.5°C) during this study (Fig. 5). Similar findings have been reported from the northern Baltic Sea (Kivi & Setälä 1995). Presumably, micro-zooplankton species occurring during winter in the Oyashio region might be those adapted to low temperatures. Therefore, we consider that the relatively high grazing impact on phytoplankton in winter, also observed in other high latitude seas, may be attributable to the phytoplankton being of the optimum food size for micro-zooplankton adapted to low temperatures.

During the period of diatom blooming in spring (Stns A3 and A4 in May) and fall (Stn A3 in October), phytoplankton growth rates exceeded micro-zooplankton grazing rates (Fig. 6). In these seasons, grazing losses to the phytoplankton was 55–74% of primary production (Table 2). These impacts on primary production due to grazing were lower than those reported from the North Atlantic (82–119%) during the spring phytoplankton bloom (Verity et al. 1993). In the Oyashio region, the diatom bloom is composed of micro-sized, not nano-sized, diatoms ($>10\,\mu$m) such as *Thalassiosira* spp. and *Chaetoceros* spp. (Shinada et al. 1999a, b), in contrast to the dominance of nano-sized (2–10 μm) phytoplankton such as prymnesiophytes in the North Atlantic (Sieracki et al. 1993). Micro-zooplankton usually prey mainly on nano-sized particles (Rassoulzadegan & Etienne 1981; Capriulo 1982).

In summer (July), micro-zooplankton grazing rates were low (g: 0.09–0.25 d^{-1}). Grazing rates in July fell somewhere in the lower range of those reported from the North Atlantic (0.34–0.57 d^{-1}, Burkill et al. 1993) and the NE subarctic Pacific during the same season (0.12–0.71 d^{-1}, Landry et al. 1993). Despite the lower grazing rates, micro-zooplankton may require more food during summer to meet the elevated metabolic rates expected due to summer temperatures. Bacteria are known to be grazed primarily by heterotrophic nanoflagellates (HNFs), which in turn are cropped mainly by micro-zooplankton (Azam et al. 1983; Sherr & Sherr 1988; Weisse & Scheffel-Möser 1991), or the bacteria are grazed directly by the micro-zooplankton (Sherr & Sherr 1987; Sherr et al. 1989a, b; Bernard & Rassoulzadegan 1990). In the Oyashio region, high biomasses of heterotrophic bacteria and HNFs have been observed at Stn A3 in summer in the euphotic zone (50.9 and 40.4 mg C m^{-3}, respectively; Shinada 2000). As discussed by Shinada (2000), bacterial and HNF biomasses during summer in the North Atlantic (14 and 12.8–18.3 mg C m^{-3}, respectively; Harrison et al. 1993; Zubkov et al. 1998) and NE subarctic Pacific (1–6 and 1.2–9.7 mg C m^{-3}, respectively; Booth et al. 1993; Kirchmann et al. 1993) are much lower than those in the Oyashio region during summer. As food for micro-zooplankton, bacteria and HNFs have been demonstrated to be superior to phytoplankton in terms of nutritional value (cf. review of Stoecker & Capuzzo 1990). Thus, it is speculated that the major food source of micro-zooplankton in summer in the Oyashio region is bacteria and/or HNFs rather than phytoplankton. If this speculation is correct, the proposed food energy deficit in micro-zooplankton in the summer can be counteracted by grazing on bacteria and HNFs.

In conclusion, seasonal changes in micro-zooplankton grazing pressure on phytoplankton assemblages are primarily due to the effects of cell size and quality of phytoplankton food in the Oyashio region. As a result, reduced micro-zooplankton grazing on phytoplankton during spring and fall phytoplankton blooms and during the summer season is a feature observed in the Oyashio region, but not in other high latitude seas.

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