

# Mesozooplankton grazing in the coastal Gulf of Alaska: *Neocalanus* spp. vs. other mesozooplankton

Hongbin Liu, Michael J. Dagg, Jeffrey M. Napp, and Riki Sato

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Three species of large calanoid copepod, *Neocalanus flemingeri*, *Neocalanus plumchrus*, and *Neocalanus cristatus*, dominate the spring biomass of mesozooplankton in the Subarctic Pacific. We compared the grazing impact of *Neocalanus* species on phytoplankton with grazing by the remainder of the mesozooplankton community in the coastal and shelf waters of the Gulf of Alaska during spring and summer 2003. *Neocalanus* spp. and other mesozooplankton fed mainly on particles  $>20\ \mu\text{m}$ , and phytoplankton in the smaller size-fractions ( $<20\ \mu\text{m}$ ) increased in the presence of mesozooplankton, possibly because of a trophic cascade resulting from mesozooplankton consumption of microzooplankton. *Neocalanus* spp. accounted for most of the mesozooplankton biomass and herbivory in the shelf water of the Gulf of Alaska and in the Prince William Sound (PWS) during April/May. The biomass of other mesozooplankton (mostly small copepods) varied seasonally and spatially; it did not increase in summer after the descent of *Neocalanus* spp. from the surface layer. On the basis of the clearance rates obtained from our experiments, in spring, grazing by *Neocalanus* spp. and the remaining mesozooplankton consumed  $\sim 10\%$  of daily growth of phytoplankton  $>20\ \mu\text{m}$  in the outer-shelf region, where chlorophyll *a* concentrations were  $<0.5\ \text{mg m}^{-3}$ , and in PWS. Mesozooplankton consumed a smaller percentage of the  $>20\ \mu\text{m}$  daily phytoplankton production in the inner- and mid-shelf regions where chlorophyll *a* concentrations were typically  $>5\ \text{mg m}^{-3}$  with blooms of large diatoms. In summer, without *Neocalanus* spp. in the surface layer, mesozooplankton grazing accounted for a very small proportion of phytoplankton production across the whole shelf.

**Keywords:** grazing, Gulf of Alaska, mesozooplankton, *Neocalanus*, phytoplankton.

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H. Liu: Department of Biology, Hong Kong University of Science and Technology, Clear Water Bay, Hong Kong, and Atmospheric, Marine and Coastal Environment (AMCE) Program, Hong Kong University of Science and Technology, Clear Water Bay, Hong Kong. M. J. Dagg and R. Sato: Louisiana Universities Marine Consortium, Chauvin, LA 70344, USA. J. M. Napp: NOAA Alaska Fisheries Science Center, Seattle, WA, USA. Correspondence to H. Liu: tel: +1 852 23587341; fax: +1 852 23581559; e-mail: liuhb@ust.hk

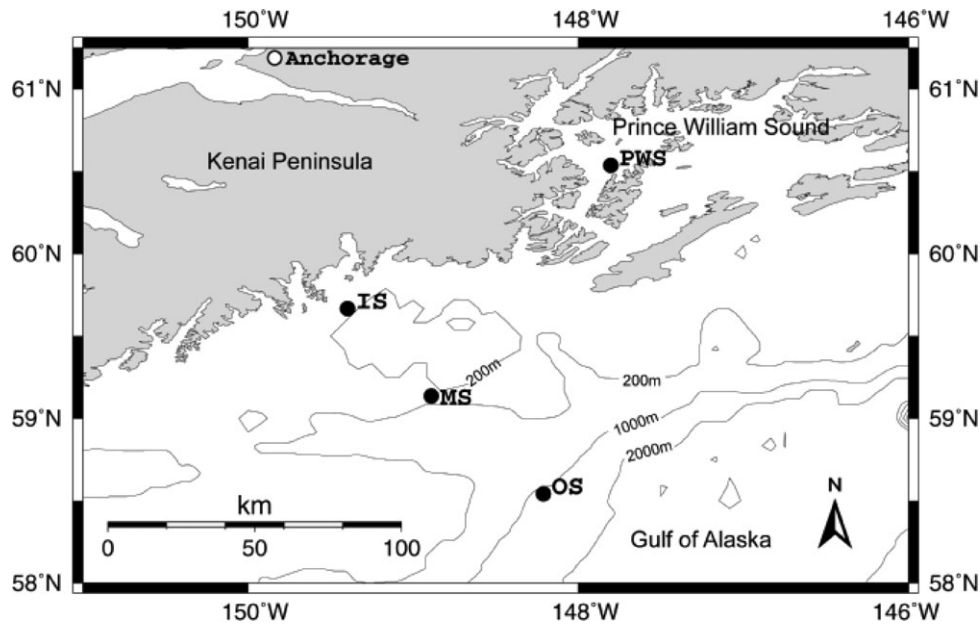
## Introduction

Three species of large calanoid copepod, *Neocalanus flemingeri*, *Neocalanus plumchrus*, and *Neocalanus cristatus*, commonly dominate the spring biomass of mesozooplankton in the coastal and shelf regions of the Gulf of Alaska (Cooney, 1986; Miller, 1993; Incze *et al.*, 1997; Coyle and Pinchuk, 2003). They have annual life cycles, except for a portion of the *N. flemingeri* population in the western Pacific and its marginal seas, which is biennial (Miller and Clemons, 1988; Miller and Terazaki, 1989; Mackas and Tsuda, 1999; Tsuda *et al.*, 1999). Each year, *Neocalanus* nauplii ascend from deep in the water column to the surface water in spring and complete their annual feeding, growth, and development in spring and early summer. Upon completing their growing season and accumulation of lipid stores in the upper ocean, *Neocalanus* spp. descend from the upper layer to spend late summer, autumn, and winter at 500–2000 m, where they mate, spawn, and die.

The absence of a spring phytoplankton bloom in the Subarctic North Pacific was originally attributed to grazing by *Neocalanus* spp. (Beklemishev, 1957; Heinrich, 1962; Frost, 1987; Parsons and Lalli, 1988). Egg production by *Neocalanus* spp. occurs very early in the year at depth, and it was suggested that the early

arrival of copepodites at the surface allowed them to control the bloom through grazing. It was later demonstrated that mesozooplankton grazing at ineffective at controlling total phytoplankton production (Dagg, 1993a; Tsuda and Sugisaki, 1994; Boyd *et al.*, 1999). However, mesozooplankton may still play an important role in regulating the abundance of micrograzers (Gifford, 1993) and therefore alter the size structure of the phytoplankton community (Landry and Lehner-Fournier, 1988; Landry *et al.*, 1993a; Shiimoto and Asami, 1999; Liu *et al.*, 2005).

Most studies of mesozooplankton feeding in the Subarctic Pacific have focused on *Neocalanus* spp., which are only present in surface waters for a few months of each year. Little is known about the grazing impact of other mesozooplankton at other times of the year (Frost, 1993), and almost no grazing studies for the coastal Gulf of Alaska have been published. In the coastal Gulf of Alaska, the abundance of mesozooplankton increases until autumn, although total biomass begins to decline after early summer when *Neocalanus* spp. descend (Incze *et al.*, 1997; Coyle and Pinchuk, 2003). In this paper, we compare the grazing impact of *Neocalanus* species and the rest of the mesozooplankton community on phytoplankton in the coastal and shelf waters of the Gulf of Alaska during spring and summer 2003.



**Figure 1.** Northern Gulf of Alaska experimental sites.

The purpose of this study was to (i) compare the relative importance of *Neocalanus* spp. and other components of the mesozooplankton community in consuming phytoplankton during spring, and (ii) to determine whether the biomass and grazing impacts of other mesozooplankton increase in summer after the ontogenetic descent of *Neocalanus* spp.

### Material and methods

During April/May 2003, grazing experiments were conducted at inner-shelf (IS), mid-shelf (MS), and outer-shelf (OS) stations along the Seward line in the coastal Gulf of Alaska and in the Prince William Sound (PWS) for three *Neocalanus* species (Figure 1, Table 1). Separate experiments were conducted for the non-*Neocalanus* mesozooplankton community during both the April/May and July/August cruises (there were no *Neocalanus* spp. in the surface layer in summer).

Live *Neocalanus* spp. were collected with a 202  $\mu\text{m}$  plankton net with a 20-l aquarium codend (Reeve, 1981) from the upper 50 m immediately before the experiments. CVs of *Neocalanus* spp. in good condition were sorted, and a variable number of each species was placed in 2.3 l polycarbonate bottles filled with seawater (prescreened through 200  $\mu\text{m}$  mesh), taken from the depth at which light levels were 50% that of the surface, and incubated on deck for 24 h. Typically, two *N. cristatus* and four *N. flemingeri* or *N. plumchrus* CV were added to each bottle. All experimental bottles were tightly capped, and one layer of neutral screen was applied to each bottle to decrease light by 50%. Incubation temperature was controlled by running seawater from the ship's seawater system. Bottles with no *Neocalanus* added were also prepared as controls. Typically, three control and four treatment bottles for each experimental species were prepared in each experiment. Chlorophyll *a* concentrations in three size-fractions (<5, 5–20, and >20  $\mu\text{m}$ ) were measured for each experiment. Initial chlorophyll concentration was obtained from the experimental water before it was added to the bottles, and final concentrations were determined from duplicate subsamples removed from each incubation bottle. Individual CV and CIV

*Neocalanus* spp. were collected, rinsed in distilled water, and dried in a 60°C oven on a precombusted and preweighed glass-fibre filter for dry weight measurements. For other mesozooplankton taxa, the same experimental design was used, except that an aliquot of live mesozooplankton (after removal of *Neocalanus* spp. CV and CIV, when they were present) mixture was added to each treatment bottle (Liu and Dagg, 2003). Dry weights of mesozooplankton from the same aliquots were measured, and mesozooplankton ingestion per unit dry weight was calculated. In addition, mesozooplankton biomass and abundance were determined at each experimental site.

At each experimental site, large zooplankton were collected with a 1-m<sup>2</sup> MOCNESS with 500  $\mu\text{m}$  mesh nets. The net was fished at midnight, and 6–7 oblique samples were collected from 100 or 150 m depth to the surface (0–10 m, 10–20 m, 20–40 m, 40–60 m, 60–80 m, 80–100 m, and 100–150 m). Copepodid stages III–V of the *Neocalanus* species were identified, staged, and enumerated.

Chlorophyll *a* was determined by placing the filters in 90% acetone for 24 h at –20°C. Chlorophyll *a* fluorescence from the

**Table 1.** Details of grazing experiments performed during the April/May cruise.

Region	Dates	Number of experiments	Clearance rates measured for
OS	25–28 April, 13 May	6	<i>Neocalanus flemingeri</i> CV, <i>N. plumchrus</i> CV, <i>N. cristatus</i> CV
MS	11–12 May	3	<i>Neocalanus flemingeri</i> CV, <i>N. cristatus</i> CV, MESO
IS	5–8 May	4	<i>N. flemingeri</i> CV, <i>N. cristatus</i> CV, MESO
PWS	30 April–3 May	4 <sup>a</sup>	<i>Neocalanus flemingeri</i> CV, <i>N. cristatus</i> CV, MESO

MESO, mesozooplankton without *Neocalanus* spp. CIV and CV.

<sup>a</sup>Two experiments using water from the deep chlorophyll maximum (16 m, ~3% of surface irradiance) were excluded.

resulting extract was measured with a Turner Designs fluorometer (Parsons *et al.*, 1984), which had been calibrated with a purified chlorophyll *a* extract (Sigma Chemicals).

Clearance rate,  $F$ , ( $\text{ml animal}^{-1} \text{d}^{-1}$  for *Neocalanus* spp. and  $\text{ml mg dry wt}^{-1} \text{d}^{-1}$  for mesozooplankton) on each size fraction of chlorophyll *a* was calculated using the formula of Frost (1972):

$$F = \frac{V(k_c - k_t)}{Z},$$

where  $V$  is the volume of the incubation bottle,  $Z$  is number of copepods (*Neocalanus* spp.) or dry weight (other mesozooplankton) in the incubation bottle,  $k_c$  and  $k_t$  are the net or apparent prey growth rates in the controls and treatments, respectively, which are calculated by

$$k(\text{d}^{-1}) = \ln\left(\frac{C_0}{C_e}\right)$$

for 24 h incubation, where  $C_0$  is the concentration of phytoplankton at time 0, and  $C_e$  is the concentration in the control and treatment bottles at the end of the incubation.

Ingestion rate ( $I$ ,  $\text{ng Chl animal}^{-1} \text{d}^{-1}$  for *Neocalanus* spp. and  $\text{ng Chl mg dry wt}^{-1} \text{d}^{-1}$  for mesozooplankton) is calculated by

$$I = CF,$$

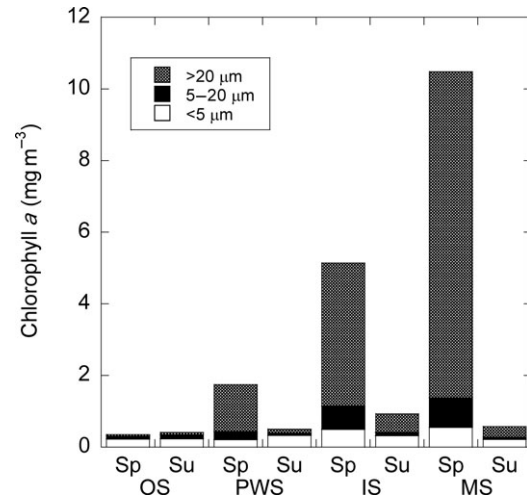
where  $C$  is the mean concentration of prey throughout the 24 h incubation period, which is calculated by

$$C = \frac{C_0(e^{k_i} - 1)}{K_t}.$$

Because we only measured feeding rates of *Neocalanus* CVs during the spring and summer 2003 cruises, we used the clearance rates of *N. cristatus* and *N. flemingeri* CIV, measured in 2001 at the same study sites, to estimate the ingestion of *Neocalanus* spp. CIV (Liu *et al.*, 2005; Dagg *et al.*, 2006). Measurement of the clearance rate for *N. cristatus* CIV were conducted on 19 and 20 April 2001 at OS and MS, respectively, where chlorophyll *a* concentrations were 0.31 and 0.37  $\text{mg m}^{-3}$  with 62% and 76% of that in  $<5 \mu\text{m}$  fraction, respectively. Average clearance rate was 182.6  $\text{ml copepod(s)}^{-1} \text{d}^{-1}$  ( $n = 10$ ,  $\text{s.d.} = 125.5$ ). Experiments with *N. flemingeri* CIV were conducted at the IS station on 25 April 2001 (chlorophyll *a* concentration = 3.75  $\text{mg m}^{-3}$  with 82% in  $>20 \mu\text{m}$  size fraction), with measured average clearance rate of 62.5  $\text{ml copepod(s)}^{-1} \text{d}^{-1}$  ( $n = 6$ ,  $\text{s.d.} = 13.4$ ).

## Results

During April/May, the shelf-break station (OS) had low total chlorophyll *a* and a large contribution from the  $<5 \mu\text{m}$  size-fraction, in contrast with other stations where spring chlorophyll *a* concentrations were high and dominated by large cells (Figure 2). During July/August, total chlorophyll *a* concentrations were  $<1 \text{ mg m}^{-3}$ , and small phytoplankton ( $<20 \mu\text{m}$ ) dominated at all stations except IS. *Neocalanus* spp. were abundant at OS and moderately abundant at MS, IS, and PWS during April/May. Virtually no *Neocalanus* spp. were found in the upper 50 m during July/August. In April/May, other copepods were more abundant in the inshore and PWS waters than in the offshore waters (Table 2). Abundance of other copepods increased at OS



**Figure 2.** Size-fractionated chlorophyll *a* concentrations at each experimental site in spring and summer.

and MS in summer after the ontogenetic descent of *Neocalanus* spp., mainly because of the increase in the abundance of *Oithona* spp. at OS and *Pseudocalanus* spp. at MS. In contrast, abundance of other copepods decreased at PWS in summer because of fewer *Metridia* spp. and *Oithona* spp. At IS, abundance of *Metridia* spp. and *Oithona* spp. also decreased, but the total copepod abundance remained largely unchanged as abundance of *Pseudocalanus* spp. doubled (Table 2).

Multidepth sampling by MOCNESS conducted during our cruises reveal that, despite variations between sampling locations, the CV of all three *Neocalanus* species were concentrated in the upper 20 m (often most abundant between 10 and 20 m, Figure 3), whereas stages CIII and CIV were mostly below 20 m (data not shown). Dry weights of *Neocalanus* spp. varied substantially, both temporally and spatially (Table 3). Using the dry weight data, the total biomass of *Neocalanus* spp. CIV and CV during April/May reached 62.6  $\text{mg dry wt m}^{-3}$  at OS. In contrast, the biomass of other mesozooplankton was only 2.5  $\text{mg dry wt m}^{-3}$  (Figure 4a). *Neocalanus* spp. CIV and CV accounted for more than 96% of total mesozooplankton biomass at this station. The biomass of *Neocalanus* spp. was lower at MS and IS than at OS, but its contributions to total mesozooplankton biomass were still 93% and 86%, respectively. PWS had the highest biomass of non-*Neocalanus* mesozooplankton (13.2  $\text{mg dry wt m}^{-3}$ , including *Neocalanus* spp. CI–CIII), but still, *Neocalanus* spp. accounted for 64% of total zooplankton biomass. In July/August, except for a small number of *N. plumchrus* at the OS, no *Neocalanus* spp. CIV and CV occurred in the upper 50 m water column of the study area. The biomass of other mesozooplankton varied largely in accordance to their abundance (Figure 4b, Table 2).

All three species of *Neocalanus* fed mostly on phytoplankton cells  $>20 \mu\text{m}$ ; only at the OS stations, where chlorophyll *a* concentration was low and dominated by small cells, were positive clearance rates on chlorophyll  $<20 \mu\text{m}$  occasionally observed (Table 4). Mean clearance rates for *N. flemingeri* and *N. cristatus* were low (or undetectable) in the high chlorophyll IS and MS water, higher in PWS, and the highest in the low chlorophyll OS. *Neocalanus plumchrus* clearance rate was measured only at OS, and its mean rate was similar to that of *N. flemingeri* (MJD, unpublished data). Therefore, clearance rates obtained

**Table 2.** Mesozooplankton abundance ( $m^{-3}$ ) at each experimental site.

	OS		PWS		IS		MS	
	April–May <sup>a</sup>	July–August	April–May	July–August	April–May	July–August	April–May	July–August
<i>Neocalanus</i> ( $m^{-3}$ )								
<i>N. cristatus</i> CV	37.0	–	3.0	–	4.6	–	7.1	–
<i>N. cristatus</i> CIV	3.4	–	0.4	–	6.9	–	4.8	–
<i>N. cristatus</i> CIII	1.1	–	0.01	–	0.8	–	0.8	–
<i>N. flemingeri</i> CV	67.1	–	27.3	–	113.4	–	108.8	–
<i>N. flemingeri</i> CIV	9.4	–	2.7	–	64.6	–	6.7	–
<i>N. flemingeri</i> CIII	0.8	–	0.5	–	0.8	–	–	–
<i>N. plumchrus</i> CV	12.0	0.1	2.2	–	25.7	–	69.5	–
<i>N. plumchrus</i> CIV	11.4	0.2	2.3	–	60.1	–	56.1	–
<i>N. plumchrus</i> CIII	6.0	0.3	0.6	–	25.0	–	16.7	–
<i>Neocalanus</i> spp. CI–CII	53.0	0.4	36.2	–	–	–	12.0	1.1
<i>Metridia</i> spp.	–	14.8	485.3	17.0	330.2	6.1	149.5	73.2
<i>Pseudocalanus</i> spp.	105.1	22.7	1 416.4	1 717.4	764.6	1 547	309.9	2 072.5
<i>Calanus marshallae</i>	0.4	–	26.7	15.0	148.2	22.3	5.7	1.2
<i>Calanus pacificus</i>	–	8.2	–	2.7	–	0.6	–	15.1
<i>Acartia longiremis</i>	3.3	1.1	115.8	173.1	92.4	69.5	25.3	75.4
<i>Eucalanus bungii</i>	–	3.1	15.5	–	4.6	2.1	–	1.2
Small calanoid copepodites	–	5.4	877.2	708.1	329.4	320.1	237.2	443.0
<i>Oithona</i> spp.	94.3	363.6	1 287.5	743.8	844.4	341.2	1 370.2	674.3
<i>Oncaea</i> sp.	–	3.3	80.9	19.7	36.4	–	164.9	–
Other copepods ( $m^{-3}$ )	–	0.5	13.9	29.2	20.6	10.4	22.8	10.5
Total copepods	402	424	4 380	3 426	2 873	2 320	2 570	3 367
Total mesozooplankton	471	602	6 837	3 951	3 839	2 600	3 663	3 448

Data presented were from 50 to 0 m ringnet tows (202  $\mu$ m mesh size), except for *Neocalanus* CIII–CV, which were the average abundance of the upper 40 m from MOCNESS samples (500  $\mu$ m mesh size).

<sup>a</sup>Only the data from 27 April are provided.

from *N. flemingeri* were applied to *N. plumchrus* to estimate total ingestion at stations where the clearance of the latter was not measured.

As with *Neocalanus* spp., we measured positive filtration rates for other mesozooplankton, mainly on cells  $>20 \mu$ m (Table 5). The clearance rates of *Neocalanus* spp. and other mesozooplankton on  $>20 \mu$ m phytoplankton revealed a negative relationship with chlorophyll *a* concentration in both spring and summer (Figure 5).

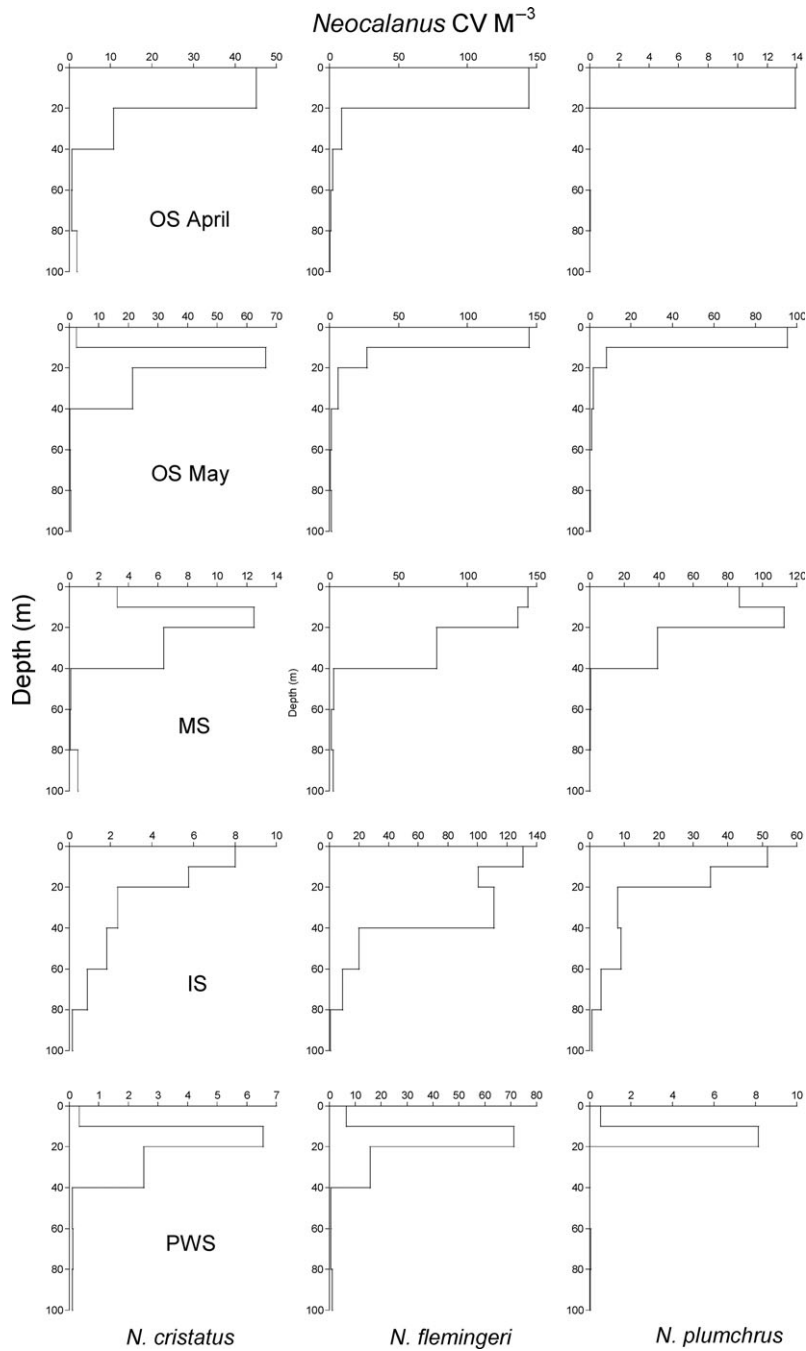
*Neocalanus* spp. accounted for most zooplankton herbivory in the shelf-break region in April/May, although low total ingestion was caused by low chlorophyll concentration (Figure 6). The *Neocalanus* spp. contribution to total mesozooplankton herbivory was lower in the IS region and PWS than in the OS, although high total ingestion was the result of high chlorophyll concentrations. Mesozooplankton ingestion of chlorophyll *a* was extremely low during July/August.

Overall, only a small fraction of total chlorophyll *a* was consumed by mesozooplankton during both seasons. On the basis of zooplankton biomass derived from net tows of the upper 50 m (upper 40 m for *Neocalanus* spp. CIV and CV), mesozooplankton consumed  $\sim 7\%$  of the  $>20 \mu$ m chlorophyll *a* during 24 h in the OS station, with *Neocalanus* spp. CIV and CV responsible for  $>96\%$  of this ingestion (Figure 7a). Mesozooplankton ingested 2–3%  $d^{-1}$  of  $>20 \mu$ m chlorophyll *a* at the MS and IS

stations and in PWS. During summer when *Neocalanus* spp. were absent, mesozooplankton (mostly small copepods) consumed less than 1%  $d^{-1}$  of phytoplankton standing stock throughout the coastal and shelf regions. Using phytoplankton growth rates measured by the dilution method on the same cruises (data provided by S. Strom), the percentage of the daily growth (i.e. production) of phytoplankton in  $>20 \mu$ m size class that was consumed by mesozooplankton in spring was highest (12.4%) in PWS, followed by OS (9.7%), IS (4.2%), and MS (3.3%; Figure 7b). Mesozooplankton daily consumption of large phytoplankton production in summer was below 1% at all sites, ranging from 0.1% to 0.7%.

## Discussion

It has been demonstrated that grazing by the copepod community is not able to control phytoplankton production in the Subarctic Pacific Ocean (Dagg, 1993a). It is also well demonstrated that microzooplankton is capable of consuming all phytoplankton production in the  $<20 \mu$ m fraction and about half the production of  $>20 \mu$ m phytoplankton in the coastal water of the Gulf of Alaska (Strom *et al.*, 2007). We know that *Neocalanus* spp. and other copepods do not feed on small cells (Frost *et al.*, 1983; Landry and Lehner-Fournier, 1988; Liu *et al.*, 2005). One objective of this study was to determine if mesozooplankton dominated by *Neocalanus* spp. are able to consume most large phytoplankton

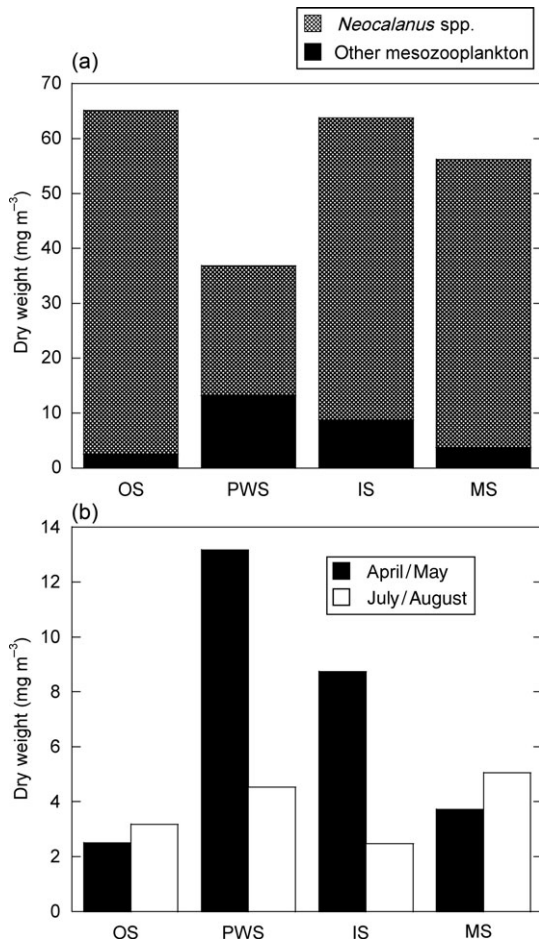


**Figure 3.** Vertical distribution of *Neocalanus* spp. CV in the upper 100 m water column of each experimental site during the April/May cruise.

**Table 3.** Dry weight of *Neocalanus* spp. CV and CIV (mg cop<sup>-1</sup>).

Region	Date	<i>Neocalanus flemingeri</i>		<i>Neocalanus plumchrus</i>		<i>Neocalanus cristatus</i>	
		CV	CIV	CV	CIV	CV	CIV
OS	27 April	0.355 (51)	0.050 (33)	0.121 (25)	0.049 (26)	1.325 (28)	0.189 (16)
OS	13 May	0.553 (19)	–	0.510 (21)	–	2.231 (13)	–
MS	11–12 May	0.407 (15)	0.125 (15)	0.190 (10)	0.061 (11)	1.450 (2)	0.203 (3)
IS	5–6 May	0.283 (33)	0.139 (12)	0.122 (15)	0.094 (11)	0.850 (22)	0.178 (45)
PWS	30 April, 13 May	0.636 (40)	0.107 (15)	0.324 (12)	0.162 (7)	1.600 (27)	0.236 (4)

Numbers in parentheses are number of specimens measured.



**Figure 4.** (a) Dry weight of the CIV and CV of *Neocalanus* spp. in the upper 40 m and other mesozooplankton in the upper 50 m water column of each experimental site during the April/May cruise. (b) Dry weight of mesozooplankton excluding *Neocalanus* spp. in the upper 50 m during April/May and July/August.

that escape microzooplankton grazing in the Subarctic Pacific. On the basis of our results, mesozooplankton grazing is largely ineffective at controlling phytoplankton biomass, because mesozooplankton removed at most 12% of the  $>20\ \mu\text{m}$  phytoplankton production (Figure 7b). Estimating mesozooplankton removal of phytoplankton using *Neocalanus* spp. abundance in the upper 20 m instead of 40 m yielded estimates that do not change our conclusions; consumption of daily phytoplankton growth at OS increased to  $\sim 16\%$  from 10%. However, our estimates of the impact of mesozooplankton grazing on phytoplankton biomass are likely an underestimate for two reasons. First, ingestion rates of *Neocalanus* spp. and the remaining mesozooplankton were

probably underestimated, mainly because the abundance of large particles in the incubation bottles was greatly reduced before the end of the 24 h incubation. Clearance rates obtained for *Neocalanus* spp. CV in this study were somewhat lower than those observed in a similar study conducted in the same area in 2001, in which the clearance rate of *N. cristatus* CV was estimated to be as high as  $>1\ \text{l copepod(s)}^{-1}\ \text{d}^{-1}$  in low chlorophyll OS waters (Liu *et al.*, 2005). Because we typically added two *N. cristatus* CV in a 2.3 l bottle, the water inside the bottle would be completely filtered once during the incubation period, thus severely reducing the concentration of large prey particles and underestimating the *in situ* clearance rates. Second, our calculation used average mesozooplankton abundance in the upper 50 m (upper 40 m for *Neocalanus* spp. CIV and CV) and chlorophyll concentration in the surface (50% surface irradiance) layer. Because the euphotic layer was much shallower than 50 m at all study sites, except at OS which was close to 50 m, average chlorophyll concentrations in the upper 50 m would be much lower, which could translate to a greater mesozooplankton grazing impact. On the other hand, *Neocalanus* spp. were concentrated in the upper 20 m or between 10 and 20 m (Figure 3; Mackas *et al.*, 1993; Goldblatt *et al.*, 1999), resulting in a much higher grazing impact on phytoplankton in that particular layer.

Grazing by gelatinous mesozooplankton was largely excluded in our estimate because our experimental design was not able to handle their fragile bodies. Appendicularians were the most abundant gelatinous mesozooplankton in the study area with average abundance in the upper 50 m of more than  $100\ \text{ind. m}^{-3}$  at all sites except OS in spring, and  $10\text{--}40\ \text{ind. m}^{-3}$  during summer at all stations. In contrast to copepods, appendicularians have very high ingestion rates (up to 100–1000% of body carbon per day; e.g. Deibel, 1988; Vargas and González, 2004) and feed mostly on cells  $<20\ \mu\text{m}$  (Allredge and Madin, 1982; Bedo *et al.*, 1993). Separate experiments conducted during the summer cruise revealed that appendicularians consumed up to 8% of total chlorophyll *a* in the water layer above the thermocline in the IS and MS regions (RS, unpublished data).

Diel vertical migration of copepod species was not considered in this study. No significant diel vertical migration has been observed for all three *Neocalanus* species in the open Subarctic Pacific (Mackas *et al.*, 1993) or in the coastal Gulf of Alaska (Napp *et al.*, 1996), but many other copepods are known to migrate to the surface during the night and stay at depth during the day. Goldblatt *et al.* (1999) reported significant diel difference in biomass in summer in the oceanic Gulf of Alaska, probably because of diel vertical migration by copepods such as *Metridia pacifica* and *C. pacificus*. Our experiments were all conducted during daylight from net tows conducted in the morning. Net tows conducted at noon and midnight during the spring cruise at IS (50–0 m) and PWS (100–0 m) did not reveal any difference

**Table 4.** Measured clearance rates ( $\text{ml copepod(s)}^{-1}\ \text{d}^{-1}$ ) of the copepodite stage V of three *Neocalanus* species.

Region	<i>Neocalanus flemingeri</i>			<i>Neocalanus plumchrus</i>			<i>Neocalanus cristatus</i>		
	$<5\ \mu\text{m}$	5–20 $\mu\text{m}$	$>20\ \mu\text{m}$	$<5\ \mu\text{m}$	5–20 $\mu\text{m}$	$>20\ \mu\text{m}$	$<5\ \mu\text{m}$	5–20 $\mu\text{m}$	$>20\ \mu\text{m}$
OS	–44.4 (23.4)	–37.9 (18.2)	235.2 (94.8)	7.3 (39.4)	–6.6 (45.7)	240 (217)	–45.7 (20.3)	–46.2 (35.5.0)	380.6 (96.1)
MS	–40.9 (11.1)	–214.5 (82.5)	32.8 (31.4)	–	–	–	–161.8 (46.9)	–693.7 (144.7)	–6.2 (36.2)
IS	–68.8 (33.0)	–176.4 (48.9)	54.7 (62.0)	–	–	–	–179.7 (161.5)	–378.0 (39.6)	45.4 (58.5)
PWS	–40.3 (5.6)	–138.1 (18.4)	159.7 (42.5)	–	–	–	–227.2 (4.5)	–392.0 (87.3)	317.2 (88.1)

Data show the mean value of several experiments at each site, and the standard deviations are given in parentheses.

**Table 5.** The average clearance rate (ml mg dry wt<sup>-1</sup> d<sup>-1</sup>) of phytoplankton, by size category, in each shipboard experiment with mesozooplankton excluding *Neocalanus* spp. CV and CIV during April/May and July/August 2003.

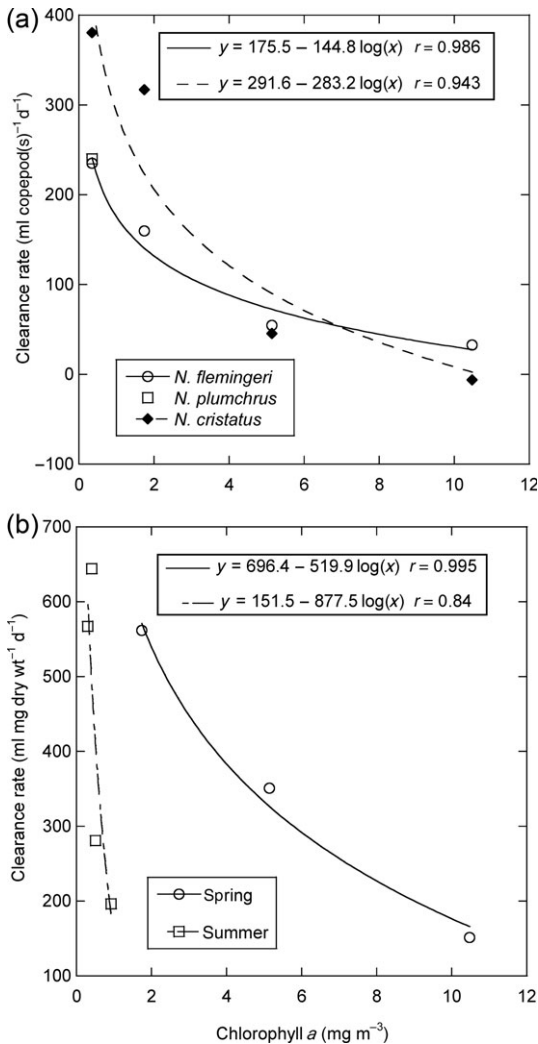
Region	April/May			July/August		
	<5 μm	5–20 μm	>20 μm	<5 μm	5–20 μm	>20 μm
OS	N/A	N/A	N/A	–237.6 (67.0)	48.7 (211.3)	644.3 (204.2)
MS	–164.0 (21.2)	–305.3 (114.2)	151.3 (69.8)	–2 578 (425.8)	–1 719.7 (272.8)	567.0 (305.9)
IS	–147.0 (130.2)	–442.5 (236.1)	350.9 (66.7)	–1 243.8 (38.7)	–1 335.8 (98.5)	196.5 (143.4)
PWS	189.2 (135.0)	–890 (0)	561.7 (87.9)	–956.9 (66.4)	–203.6 (674.8)	281.0 (757.2)

Values in parentheses are the standard deviations of the means.

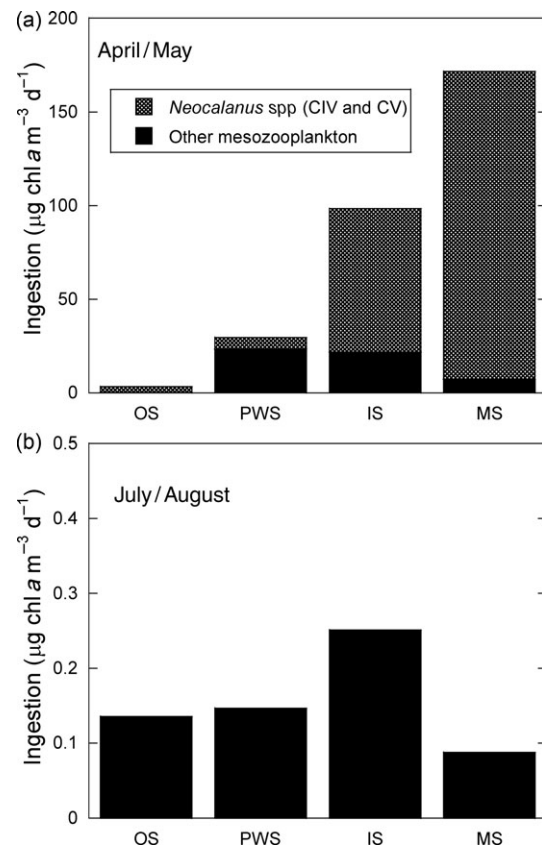
in zooplankton abundance and composition (data not shown). However, this does not completely rule out diel vertical migration as an important phenomenon to be included in estimating mesozooplankton herbivory.

Our results also indicate that some of the small copepods increased in the offshore waters in summer after the descent of *Neocalanus* spp. from the surface layer, but the total grazing impact was still small. Previous studies of the annual cycle of

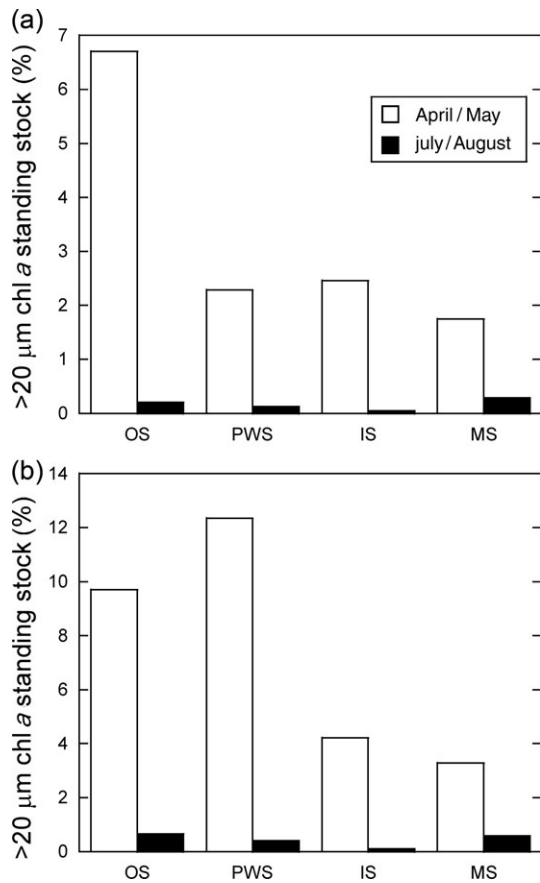
mesozooplankton biomass in the coastal Gulf of Alaska demonstrate the same pattern with a spring peak coinciding with the occurrence of *Neocalanus* spp. (Coyle and Pinchuk, 2003, 2005). Monthly sampling conducted along the Seward Line and in PWS, 1997–2000 (Coyle and Pinchuk, 2003), revealed a sharp decrease in the abundance of large calanoid copepods from May to July, because of the absence of *Neocalanus* spp. from shelf waters. At the same time, the total abundance of copepods was greater in July, mostly as a result of greater abundances of small species such as *Pseudocalanus* spp. and *Oithona similis*. Nevertheless, biomass was lower in July because populations are dominated by smaller calanoids and cyclopooids. Our few data are in general agreement with these patterns (Table 2, Figure 4).



**Figure 5.** Mean clearance rates of (a) *Neocalanus* spp. in spring, and (b) other mesozooplankton in spring and summer on >20 μm phytoplankton plotted as a function of total chlorophyll *a* concentrations.



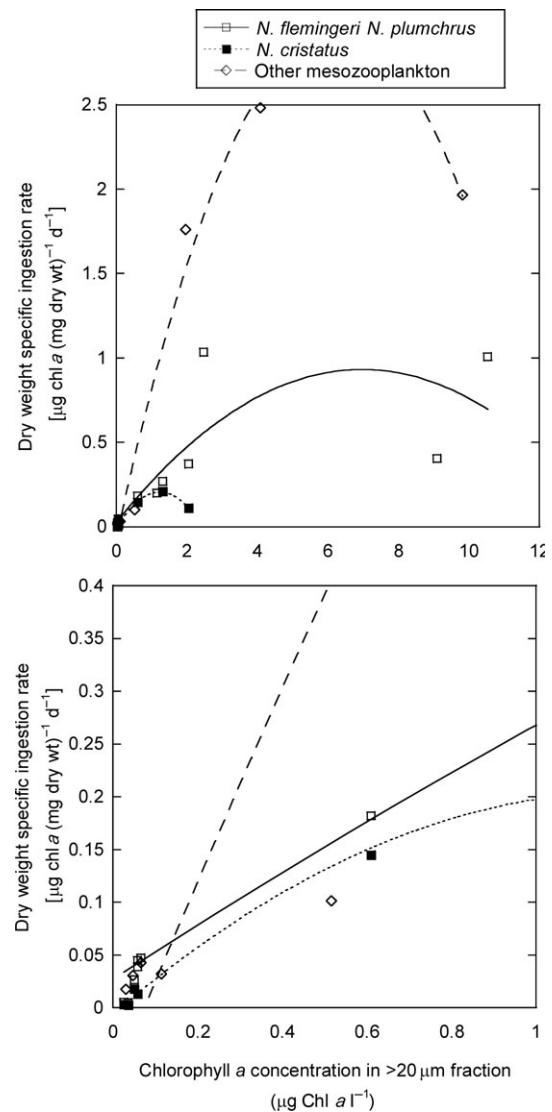
**Figure 6.** Ingestion rates for *Neocalanus* spp. CIV and CV and “other mesozooplankton” during spring and summer. Ingestion of “other mesozooplankton” at OS in spring is estimated using the clearance rate from the summer cruise. Ingestion rates for *Neocalanus* CIV were calculated from clearance rates measured at approximately the same time in 2001. Note the difference in scales between the two plots.



**Figure 7.** Percentage of (a)  $>20 \mu\text{m}$  chlorophyll *a* standing stock, and (b) growth that was ingested daily by the mesozooplankton community, including *Neocalanus* spp.

In our study, the abundance of total mesozooplankton (including *Neocalanus* spp.) in the oceanic OS region decreased slightly during summer (Table 2), but biomass decreased  $\sim 20$ -fold from 62.6 to 3.2 mg dry wt  $\text{m}^{-3}$  (Figure 4). In the shelf waters, where *Neocalanus* spp. biomass was not as high during spring, the summer decrease in biomass was not great (Figure 4). One reason we did not observe a significant increase in total copepod abundance in summer is probably that the mesh size (202  $\mu\text{m}$ ) of the net we used to collect mesozooplankton was not adequate to retain smaller organisms such as *Oithona* and *Oncaea* (Gallienne and Robins, 2001).

*Neocalanus* spp. are suspension-feeders that rely on the establishment of a feeding current to collect food particles. They are efficient at taking in particles  $>5 \mu\text{m}$  (Frost *et al.*, 1983) or  $>2 \mu\text{m}$  (Landry and Lehner-Fournier, 1988) and have been reported feeding on phytoplankton, microzooplankton, and detrital particles (Greene and Landry, 1988; Dagg, 1993b; Gifford, 1993; Liu *et al.*, 2005). Because microheterotrophs are the major grazers of phytoplankton in the Subarctic Pacific (Landry *et al.*, 1993b; Rivkin *et al.*, 1999; Liu *et al.*, 2002; Strom *et al.*, 2007), mesozooplankton may exert an indirect effect on phytoplankton production as predators of microzooplankton (Landry *et al.*, 1993a; Liu *et al.*, 2005). The overall effect of mesozooplankton grazing is to shift phytoplankton community structure towards dominance by small cells, a mechanism that counterbalances the microzooplankton grazing pressure, which usually causes greater



**Figure 8.** Dry-weight-specific ingestion rates of *Neocalanus cristatus*, *N. flemingeri*, and *N. plumchrus* and other mesozooplankton plotted vs. *in situ* chlorophyll *a*  $>200 \mu\text{m}$  phytoplankton. Bottom plot shows the ingestion rates at chlorophyll *a* concentration  $<1 \mu\text{g Chl a l}^{-1}$ . Curve fittings in the plots are second order polynomial with  $r^2 = 0.64, 0.996,$  and  $0.98$  for *N. flemingeri* and *N. plumchrus*, *N. cristatus*, and other mesozooplankton, respectively.

mortality in pico- and nanophytoplankton than in microphytoplankton (Strom *et al.*, 2007).

Besides *Neocalanus* spp., *Metridia* spp., *Pseudocalanus* spp., and *Oithona* spp. are the predominant mesozooplankton taxa in both seasons. *Metridia pacifica* is carnivorous in summer in the Alaskan gyre, feeding on dinoflagellates and heterotrophic flagellates  $>25 \mu\text{m}$ , but the abundance of *Metridia* is low enough that only  $\sim 1\%$  of daily production and standing stock of their prey is ingested (Goldblatt *et al.*, 1999). Goldblatt *et al.* (1999) suggest that predation by small mesozooplankton may be an important source of phytoplankton mortality. Copepods  $<1 \text{ mm}$  total length (e.g. *Oithona* spp.) are always the most abundant type of mesozooplankton in the Gulf of Alaska, and their weight-specific ingestion rate is higher than that of the large



copepods (Peters, 1983; Moloney and Field, 1991). In our study, *Pseudocalanus* spp. and *Oithona* spp. are the most abundant copepods (Table 2), and the weight-specific clearance rate for mesozooplankton other than *Neocalanus* was higher than those measured for *Neocalanus* spp. CV (Figure 8). However, despite their great abundance, the overall grazing impact of mesozooplankton other than *Neocalanus* spp. remained insignificant in both spring and summer (Figure 7).

In our study, *Neocalanus* spp. CI–CIII stages were mixed within other mesozooplankton. On the basis of the abundance of these copepodites and the dry weight data reported by Kobari *et al.* (2003), they accounted for a maximum of 28.5% of the other mesozooplankton dry weight biomass in OS, but were virtually non-existent in IS. Therefore, their contribution of both biomass and ingestion (assuming they have the same dry-weight-specific ingestion rate as the other mesozooplankton) is very small compared with that of *Neocalanus* spp. CIV and CV.

## Conclusions

*Neocalanus* spp. CIV and CV accounted for most mesozooplankton biomass and herbivory throughout the Gulf of Alaska and in PWS during April/May. Composition of other mesozooplankton (mostly small copepods) varied between spring and summer, although the net effect was that total mesozooplankton biomass did not increase in summer after the descent of *Neocalanus* spp. from the surface layer.

In spring, grazing by *Neocalanus* spp. and other crustacean mesozooplankton consumed a minimum of ~10% of daily growth of phytoplankton >20 µm in the OS region of the Gulf of Alaska and in PWS, and less than that in the MS and IS region. As these rates are most likely underestimated, the real impact of mesozooplankton on phytoplankton biomass in spring could be higher. In contrast, because of the disappearance of *Neocalanus* spp. in the surface layer and the constant low biomass, copepod herbivory has very little impact on phytoplankton during summer. Gelatinous mesozooplankton, such as appendicularians, which have a dry-weight-specific clearance rate more than one order of magnitude higher than copepods, may be responsible for significant grazing on phytoplankton in both seasons.

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## References

Allredge, A. L., and Madin, L. P. 1982. Pelagic tunicates: unique herbivores in the marine plankton. *BioScience*, 32: 655–663.

Bedo, A. W., Acuna, J. L., Robins, D., and Harris, R. P. 1993. Grazing in the micron and sub-micron particle size range: the case of *Oikopleura dioica* (Appendicularia). *Bulletin of Marine Science*, 53: 2–14.

Beklemishev, K. V. 1957. The spatial relationships of marine zoo- and phytoplankton. *Trudy Instituta Okeanologii, Akademiya Nauk SSSR*, 10: 253–378.

Boyd, P. W., Goldblatt, R. H., and Harrison, P. J. 1999. Mesozooplankton grazing manipulations during *in vitro* iron enrichment studies in the NE Subarctic Pacific. *Deep-Sea Research II*, 46: 2645–2668.

Cooney, R. T. 1986. The seasonal occurrence of *Neocalanus cristatus*, *Neocalanus plumchrus* and *Eucalanus bungii* over the northern Gulf of Alaska. *Continental Shelf Research*, 5: 541–553.

Coyle, K. O., and Pinchuk, A. I. 2003. Annual cycle of zooplankton abundance, biomass and production on the northern Gulf of Alaska Shelf, October 1997 through October 2000. *Fisheries Oceanography*, 12: 327–338.

Coyle, K. O., and Pinchuk, A. I. 2005. Seasonal cross-shelf distribution of major zooplankton taxa on the northern Gulf of Alaska shelf relative to water mass properties, species depth preferences and vertical migration behavior. *Deep-Sea Research II*, 52: 217–245.

Dagg, M. J. 1993a. Grazing by the copepod community does not control phytoplankton production in the Subarctic Pacific Ocean. *Progress in Oceanography*, 32: 163–183.

Dagg, M. J. 1993b. Sinking particles as a possible source of nutrition for the large calanoid copepod *Neocalanus cristatus* in the Subarctic Pacific Ocean. *Deep-Sea Research I*, 40: 1431–1445.

Dagg, M., Liu, H., and Thomas, A. 2006. Effects of mesoscale phytoplankton variability on the copepods *Neocalanus flemingeri* and *N. plumchrus* in the coastal Gulf of Alaska. *Deep-Sea Research I*, 53: 321–332.

Deibel, D. 1988. Filter feeding by *Oikopleura vanhoeffeni*: grazing impact on suspended particles in cold ocean waters. *Marine Biology*, 99: 177–186.

Frost, B. W. 1972. Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. *Limnology and Oceanography*, 17: 805–815.

Frost, B. W. 1987. Grazing control of phytoplankton stock in the open Subarctic Pacific Ocean: a model assessing the role of mesozooplankton, particularly the large calanoid copepods *Neocalanus* spp. *Marine Ecology Progress Series*, 39: 49–68.

Frost, B. W. 1993. A modeling study of processes regulating plankton standing stock and production in the open Subarctic Pacific Ocean. *Progress in Oceanography*, 32: 17–56.

Frost, B. W., Landry, M. R., and Hassett, R. P. 1983. Feeding behavior of large calanoid copepods *Neocalanus cristatus* and *N. plumchrus* from the Subarctic Pacific Ocean. *Deep-Sea Research*, 30: 1–13.

Gallienne, G. P., and Robins, D. B. 2001. Is *Oithona* the most important copepod in the world's oceans? *Journal of Plankton Research*, 12: 1421–1432.

Gifford, D. J. 1993. Protozoa in the diets of *Neocalanus* spp. in the oceanic Subarctic Pacific Ocean. *Progress in Oceanography*, 32: 223–237.

Goldblatt, R. H., Mackas, D. L., and Lewis, A. G. 1999. Mesozooplankton community characteristics in the NE Subarctic Pacific. *Deep-Sea Research II*, 46: 2619–2644.

Greene, C. H., and Landry, M. R. 1988. Carnivorous suspension feeding by the Subarctic calanoid copepod *Neocalanus cristatus*. *Canadian Journal of Fisheries and Aquatic Sciences*, 45: 1069–1074.

Heinrich, A. K. 1962. The life histories of plankton animals and seasonal cycles of plankton communities in the oceans. *Journal du Conseil Permanent International pour l'Exploration de la Mer*, 27: 15–24.

Incze, L. S., Siefert, D. W., and Napp, J. M. 1997. Mesozooplankton of Shelikof Strait, Alaska: abundance and community composition. *Continental Shelf Research*, 17: 287–305.

Kobari, T., Shinada, A., and Tsuda, A. 2003. Functional roles of interzonal migrating mesozooplankton in the western Subarctic Pacific. *Progress in Oceanography*, 57: 279–298.

Landry, M. R., Gifford, D. J., Kirchman, D. L., Wheeler, P. A., and Monger, B. C. 1993a. Direct and indirect effects of grazing by *Neocalanus plumchrus* on plankton community dynamics in the Subarctic Pacific. *Progress in Oceanography*, 32: 239–258.

Landry, M. R., and Lehner-Fournier, J. M. 1988. Grazing rates and behaviors of *Neocalanus plumchrus*: implications for phytoplankton control in the Subarctic Pacific. *Hydrobiologia*, 167/168: 9–19.

- Landry, M. R., Monger, B. C., and Selph, K. E. 1993b. Time dependency of microzooplankton grazing and phytoplankton growth in the Subarctic Pacific. *Progress in Oceanography*, 32: 205–222.
- Liu, H., and Dagg, M. J. 2003. Interactions between nutrients, phytoplankton growth, and micro- and mesozooplankton grazing in the plume of the Mississippi River. *Marine Ecology Progress Series*, 258: 31–42.
- Liu, H., Dagg, M. J., and Strom, S. 2005. Grazing by the calanoid copepod *Neocalanus cristatus* on the microbial foodweb in the coastal Gulf of Alaska. *Journal of Plankton Research*, 27: 647–662.
- Liu, H., Suzuki, K., and Saino, T. 2002. Phytoplankton growth and microzooplankton grazing in the Subarctic North Pacific Ocean and Bering Sea during summer 1999. *Deep-Sea Research I*, 49: 363–375.
- Mackas, D. L., Sefton, H., Miller, C. B., and Raich, A. 1993. Vertical habitat partitioning by large calanoid copepods in the oceanic Subarctic Pacific during spring. *Progress in Oceanography*, 32: 259–294.
- Mackas, D. L., and Tsuda, A. 1999. Mesozooplankton in the eastern and western Subarctic Pacific: community structure, seasonal life histories, and interannual variability. *Progress in Oceanography*, 43: 335–363.
- Miller, C. B. 1993. Development of large copepods during spring in the Gulf of Alaska. *Progress in Oceanography*, 32: 295–317.
- Miller, C. B., and Clemons, M. 1988. Revised life history analysis for large grazing copepods in the Subarctic Pacific Ocean. *Progress in Oceanography*, 20: 293–313.
- Miller, C. B., and Terazaki, M. 1989. The life histories of *Neocalanus flemingeri* and *Neocalanus plumchrus* in the Sea of Japan. *Bulletin of the Plankton Society of Japan*, 36: 27–41.
- Moloney, C. L., and Field, J. G. 1991. The size-based dynamics of plankton food webs. I. A simulation model of carbon and nitrogen flows. *Journal of Plankton Research*, 13: 1003–1038.
- Napp, J. M., Incze, L. S., Ortner, P. B., Siefert, D. L. W., and Britt, L. 1996. The plankton of Shelikof Strait, Alaska: standing stock, production, mesoscale variability and their relevance to larval fish survival. *Fisheries Oceanography*, 5: 19–38.
- Parsons, T. R., and Lalli, C. M. 1988. Comparative oceanic ecology of the plankton communities of the Subarctic Atlantic and Pacific Oceans. *Oceanography and Marine Biology Annual Review*, 26: 317–359.
- Parsons, T. R., Maita, Y., and Lalli, C. M. 1984. *A Manual of Chemical and Biological Methods for Seawater Analysis*. Pergamon Press, Oxford. 173 pp.
- Peters, R. H. 1983. *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge.
- Reeve, M. R. 1981. Large cod-end reservoirs as an aid to the live collection of delicate zooplankton. *Limnology and Oceanography*, 26: 577–580.
- Rivkin, R. B., Putland, J. N., Anderson, M. R., and Deibel, D. 1999. Microzooplankton bacterivory and herbivory in the NE Subarctic Pacific. *Deep-Sea Research II*, 46: 2579–2618.
- Shiomoto, A., and Asami, H. 1999. High-west and low-east distribution patterns of chlorophyll *a*, primary productivity and diatoms in the Subarctic North Pacific surface waters, midwinter 1996. *Journal of Oceanography*, 55: 493–503.
- Strom, S. L., Macri, E. L., and Olson, M. B. 2007. Microzooplankton grazing in the coastal Gulf of Alaska: variations in top-down control of phytoplankton. *Limnology and Oceanography*, 52: 1480–1494.
- Tsuda, A., Saito, H., and Kasai, H. 1999. Life history of *Neocalanus flemingeri* and *Neocalanus plumchrus* (Calanoida: Copepoda) in the western Subarctic Pacific. *Marine Biology*, 135: 533–544.
- Tsuda, A., and Sugisaki, H. 1994. *In situ* grazing rate of the copepod population in the western Subarctic North Pacific during spring. *Marine Biology*, 120: 203–210.
- Vargas, C. A., and González, H. E. 2004. Plankton community structure and carbon cycling in a coastal upwelling system. I. Bacteria, microprotozoans and phytoplankton in the diet of copepods and appendicularians. *Aquatic Microbial Ecology*, 34: 151–161.

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