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

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


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 μm, and phytoplankton in the smaller size-fractions (<20 μm) 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 ~10% of daily growth of phytoplankton >20 μm in the outer-shelf region, where chlorophyll a concentrations were <0.5 mg m⁻³, and in PWS. Mesozooplankton consumed a smaller percentage of the >20 μm daily phytoplankton production in the inner- and mid-shelf regions where chlorophyll a concentrations were typically >5 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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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; Shiromoto 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.

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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 μm 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 μm 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 neutral screen was applied to each bottle to decrease light by 35%. Incubation temperature was controlled by running seawater neutral screen was applied to each bottle to decrease light by 35%. Incubation temperature was controlled by running seawater neutral screen was applied to each bottle to decrease light by 35%. Incubation temperature was controlled by running seawater neutral screen was applied to each bottle to decrease light by 35%.

Figure 1. Northern Gulf of Alaska experimental sites.

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

<table>
<thead>
<tr>
<th>Region</th>
<th>Dates</th>
<th>Number of experiments</th>
<th>Clearance rates measured for</th>
</tr>
</thead>
<tbody>
<tr>
<td>OS</td>
<td>25–28 April, 13 May</td>
<td>6</td>
<td>Neocalanus flemingeri CV, N. plumchrus CV, N. cristatus CV</td>
</tr>
<tr>
<td>MS</td>
<td>11–12 May</td>
<td>3</td>
<td>Neocalanus flemingeri CV, N. cristatus CV, MESO</td>
</tr>
<tr>
<td>IS</td>
<td>5–8 May</td>
<td>4</td>
<td>N. flemingeri CV, N. cristatus CV, MESO</td>
</tr>
<tr>
<td>PWS</td>
<td>30 April–3 May</td>
<td>4*</td>
<td>Neocalanus flemingeri CV, N. cristatus CV, MESO</td>
</tr>
</tbody>
</table>

*Two experiments using water from the deep chlorophyll maximum (16 m, ~3% of surface irradiance) were excluded.

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

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-m² MOCNESS with 500 μm 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.
Mesozooplankton grazing in the coastal Gulf of Alaska

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, \( F \) (ml animal\(^{-1}\) d\(^{-1}\) for Neocalanus spp. and ml mg dry wt\(^{-1}\) 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

\[
k(d^{-1}) = \ln \left( \frac{C_0}{C_f} \right)
\]

for 24 h incubation, where \( C_0 \) is the concentration of phytoplankton at time 0, and \( C_f \) is the concentration in the control and treatment bottles at the end of the incubation.

Ingestion rate (\( I, \) ng Chl animal\(^{-1}\) d\(^{-1}\) for Neocalanus spp. and ng Chl mg dry wt\(^{-1}\) 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

\[
C = \frac{C_0(e^{k_c} - 1)}{k_t}
\]

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 mg m\(^{-3}\) with 62% and 78% of that in <5 \( \mu \)m fraction, respectively. Average clearance rate was 182.6 ml copepod(s)\(^{-1}\) d\(^{-1}\) (\( n = 10, \) s.d. = 125.5). Experiments with \( N. \) flemingeri CIV were conducted at the IS station on 25 April 2001 (chlorophyll a concentration = 3.75 mg m\(^{-3}\) with 82% in >20 \( \mu \)m size fraction), with measured average clearance rate of 62.5 ml copepod(s)\(^{-1}\) d\(^{-1}\) (\( n = 6, \) 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 \( \mu \)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 mg m\(^{-3}\), and small phytoplankton (<20 \( \mu \)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 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 CV 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 mg dry wt m\(^{-2}\) at OS. In contrast, the biomass of other mesozooplankton was only 2.5 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 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 its abundance (Figure 4b, Table 2).

All three species of Neocalanus fed mostly on phytoplankton cells >20 \( \mu \)m; only at the OS stations, where chlorophyll a concentration was low and dominated by small cells, were positive clearance rates on chlorophyll <20 \( \mu \)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...
from *Neocalanus* were applied to *Pseudocalanus* to estimate total ingestion at stations where the clearance of the latter was not measured.

As with *Neocalanus*, we measured positive filtration rates for other mesozooplankton, mainly on cells >20 μm (Table 5). The clearance rates of *Neocalanus* spp. and other mesozooplankton on >20 μm 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 *a* 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 *a* 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 ~7% of the >20 μm 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 μm 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 μm size class that was consumed by mesozooplankton in spring was highest (12.4%) in PWS, followed by OS (9.2%), 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 μm fraction and about half the production of >20 μm 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⁻¹).

<table>
<thead>
<tr>
<th>Region</th>
<th>Date</th>
<th><em>Neocalanus flemingeri</em></th>
<th><em>Neocalanus plumchrus</em></th>
<th><em>Neocalanus cristatus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>CV</td>
<td>CIV</td>
<td>CV</td>
</tr>
<tr>
<td>OS</td>
<td>27 April</td>
<td>0.355 (51)</td>
<td>0.050 (33)</td>
<td>0.121 (25)</td>
</tr>
<tr>
<td>OS</td>
<td>13 May</td>
<td>0.553 (19)</td>
<td>-</td>
<td>0.510 (21)</td>
</tr>
<tr>
<td>MS</td>
<td>11 – 12 May</td>
<td>0.407 (15)</td>
<td>0.125 (15)</td>
<td>0.190 (10)</td>
</tr>
<tr>
<td>IS</td>
<td>5 – 6 May</td>
<td>0.283 (33)</td>
<td>0.139 (12)</td>
<td>0.122 (15)</td>
</tr>
<tr>
<td>PWS</td>
<td>30 April, 13 May</td>
<td>0.636 (40)</td>
<td>0.107 (15)</td>
<td>0.324 (12)</td>
</tr>
</tbody>
</table>

Numbers in parentheses are number of specimens measured.
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 copepod(s)\(^{-1}\) 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 experiment 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 of more than 100 ind. m\(^{-3}\) at all sites except OS in spring, and 10–40 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 \(\mu\)m (Alldredge 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. pacifica. 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

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**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.

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

<table>
<thead>
<tr>
<th>Region</th>
<th>Neocalanus flemingeri</th>
<th>Neocalanus plumchrus</th>
<th>Neocalanus cristatus</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>&lt;5 (\mu)m</td>
<td>5–20 (\mu)m</td>
<td>&gt;20 (\mu)m</td>
</tr>
<tr>
<td>OS</td>
<td>–44.4 (23.4)</td>
<td>–37.9 (18.2)</td>
<td>235.2 (94.8)</td>
</tr>
<tr>
<td>MS</td>
<td>–40.9 (11.1)</td>
<td>–214.5 (82.5)</td>
<td>32.8 (31.4)</td>
</tr>
<tr>
<td>IS</td>
<td>–68.8 (33.0)</td>
<td>–176.4 (48.9)</td>
<td>54.7 (62.0)</td>
</tr>
<tr>
<td>PWS</td>
<td>–40.3 (5.6)</td>
<td>–138.1 (18.4)</td>
<td>159.7 (42.5)</td>
</tr>
</tbody>
</table>

Data show the mean value of several experiments at each site, and the standard deviations are given in parentheses.
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 cyclopoids. Our few data are in general agreement with these patterns (Table 2, Figure 4).

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

<table>
<thead>
<tr>
<th>Region</th>
<th>April/May</th>
<th>July/August</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>&lt;5 μm</td>
<td>5–20 μm</td>
</tr>
<tr>
<td>OS</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>MS</td>
<td>−164.0 (21.2)</td>
<td>−305.3 (114.2)</td>
</tr>
<tr>
<td>IS</td>
<td>−147.0 (130.2)</td>
<td>−422.5 (236.1)</td>
</tr>
<tr>
<td>PWS</td>
<td>189.2 (135.0)</td>
<td>−890 (0)</td>
</tr>
</tbody>
</table>

Values in parentheses are the standard deviations of the means.

**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.
In our study, the abundance of total mesozooplankton (including \textit{Neocalanus} spp.) in the oceanic OS region decreased slightly during summer (Table 2), but biomass decreased 20-fold from 62.6 to 3.2 mg dry wt m$^{-3}$ (Figure 4). In the shelf waters, where \textit{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 $\mu$m) of the net we used to collect mesozooplankton was not adequate to retain smaller organisms such as \textit{Oithona} and \textit{Oncaea} (Gallienne and Robins, 2001).

\textit{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 $>5\mu$m (Frost et al., 1983) or $>2\mu$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 mortality in pico- and nanophytoplankton than in microphytoplankton (Strom et al., 2007).

Besides \textit{Neocalanus} spp., \textit{Metridia} spp., \textit{Pseudocalanus} spp., and \textit{Oithona} spp. are the predominant mesozooplankton taxa in both seasons. \textit{Metridia pacifica} is carnivorous in summer in the Alaskan gyre, feeding on dinoflagellates and heterotrophic flagellates $>25\mu$m, but the abundance of \textit{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 $<1$ mm total length (e.g. \textit{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 copepodes 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**


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