Available online at www.sciencedirect.com
SCIENCE DIRECT®
ELSEVIER
Deep-Sea Research I 53 (2006) 321–332
DEEP-SEA RESEARCH PART I
www.elsevier.com/locate/dsr

Effects of mesoscale phytoplankton variability on the copepods *Neocalanus flemingeri* and *N. plumchrus* in the coastal Gulf of Alaska

M.J. Dagg[a,*], H. Liu[a,1], A.C. Thomas[b]

[a]*Louisiana Universities Marine Consortium, 8124 Highway 56, Chauvin, LA 70344, USA*
[b]*School of Marine Sciences, University of Maine, 5741 Libby Hall, Orono, ME 04469-5741, USA*

Received 25 January 2005; received in revised form 16 June 2005; accepted 26 September 2005
Available online 28 November 2005

Abstract

The copepods *Neocalanus flemingeri* and *N. plumchrus* are major components of the mesozooplankton on the shelf of the Gulf of Alaska, where they feed, grow and develop during April–June, the period encompassing the spring phytoplankton bloom. Satellite imagery indicates high mesoscale variability in phytoplankton concentration during this time. Because copepod ingestion is related to food concentration, we hypothesized that phytoplankton ingestion by *N. flemingeri* and *N. plumchrus* would vary in response to mesoscale variability of phytoplankton. We proposed that copepods on the inner shelf, where the phytoplankton bloom is most pronounced, would be larger and have more lipid stores than animals collected from the outer shelf, where phytoplankton concentrations are typically low. Shipboard feeding experiments with both copepods were done in spring of 2001 and 2003 using natural water as food medium. Chlorophyll concentration ranged widely, between 0.32 and 11.44 $\mu g l^{-1}$ and ingestion rates varied accordingly, between 6.0 and 627.0 $ng\,chl\,cop^{-1}\,d^{-1}$. At chlorophyll concentrations $<0.50\,\mu g l^{-1}$, ingestion is always low, $<40\,ng\,cop^{-1}\,d^{-1}$. Intermediate ingestion rates were observed at chlorophyll concentrations between 0.5 and 1.5 $\mu g l^{-1}$, and maximum rates at chlorophyll concentrations $>1.5\,\mu g l^{-1}$. Application of these feeding rates to the phytoplankton distribution on the shelf allowed locations and time periods of low, intermediate and high daily feeding to be calculated for 2001 and 2003. A detailed cross-shelf survey of body size and lipid store in these copepods, however, indicated they were indistinguishable regardless of collection site. Although the daily ingestion of phytoplankton by *N. flemingeri* and *N. plumchrus* varied widely because of mesoscale variability in phytoplankton, these daily differences did not result in differences in final body size or lipid storage of these copepods. These copepods efficiently dealt with small and mesoscale variations in their food environment such that mesoscale structure in phytoplankton did not affect their final body size.

Keywords: *Neocalanus*; Grazing; Mesoscale; Phytoplankton; Gulf of Alaska

1. Introduction

Three species of large calanoid copepods, *Neocalanus flemingeri*, *N. plumchrus* and *N. cristatus*, dominate mesozooplankton biomass throughout the entire subarctic Pacific Ocean, including the

*Corresponding author. Tel.: +1 985 851 2856; fax: +1 985 851 2874.
E-mail address: mdagg@lumcon.edu (M.J. Dagg).
[1]Current address: Department of Biology, Atmospheric, Marine and Coastal Environment, Hong Kong University of Science and Technology, Clear Water Bay, Kowloon, Hong Kong.

0967-0637/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.dsr.2005.09.013

marginal seas. They have annual life cycles except for a portion of the *N. flemingeri* population in the western Pacific, which is biennial (Mackas and Tsuda, 1999; Miller and Terazaki, 1989; Tsuda et al., 1999). All three *Neocalanus* spp. mate and spawn at depth (500–2000 m) in autumn to early winter. Their egg production is dependent on their lipid reserves and body tissues, and adults die after spawning in deep water. Development through the naupliar (N1–N6) stages occurs while they ascend to the surface. After ascending to the upper ocean, *Neocalanus* spp. complete their annual feeding, growth and development above the permanent pycnocline (0–150 m) in spring and summer. Diel vertical migration is weak or absent. *N. flemingeri* and *N. plumchrus* partition the upper layer temporally. In the open Gulf of Alaska, *N. plumchrus* lags *N. flemingeri* by about 1–2 developmental stages (25–30 days) (Miller and Clemons, 1988). In the western gyre, seasonal segregation between *N. flemingeri* and *N. plumchrus* is also clear (Tsuda et al., 1999). On completion of their upper ocean growing season and accumulation of large lipid stores, *Neocalanus* spp. descend from the upper layer to spend the late summer, autumn and early winter at 500–2000 m. The life cycle of each species then repeats.

Neocalanus spp. cannot overwinter on the continental shelf, although there are small populations in some of the deep coastal fjords of western North America (Fulton, 1973; Evanson et al., 2000; Cooney et al., 2001). Nevertheless, as a result of onshore transport of oceanic surface water in the late winter and early spring, oceanic *Neocalanus* spp. typically dominate the biomass of mesozooplankton in shelf waters of the Gulf of Alaska during spring and early summer (Coyle and Pinchuk, 2005). The fate of these populations in the fall is unclear.

Neocalanus spp. are particle grazers, feeding on suspended particulate materials in seawater. To a large degree, their diet reflects the composition of the particulate materials surrounding them and their nutritional state reflects the concentrations of available food. High nutrient, low chlorophyll (HNLC) conditions prevail in oceanic subarctic regions but spring blooms of chain forming diatoms occur in the marginal seas and in the gyre margins (Miller et al., 1992; Banse and English, 1999). Consequently, *Neocalanus* spp. occupy rather different ecological niches in marginal seas compared to the oceanic gyres. Phytoplankton appears to be less important to their diet in the Alaskan Gyre because the phytoplankton community consists mostly of cells too small to be ingested, and because concentrations are routinely very low in these HNLC environments (Dagg, 1993a; Tsuda and Sugisaki, 1994). Microzooplankton, especially ciliates and heterotrophic flagellates, are important diet items for *N. flemingeri* and *N. plumchrus* in the gyres (Gifford and Dagg, 1991; Gifford, 1993). In contrast, in coastal regions during periods of high phytoplankton concentration, these copepods appear to be predominantly herbivorous. For example, ingestion rate of phytoplankton by *Neocalanus* spp. in the Bering Sea during the spring bloom (Dagg et al., 1982; Dagg and Wyman, 1983) was much higher than in the open subarctic Pacific Ocean (Dagg, 1993a).

Phytoplankton concentration, however, is not uniformly high during the spring bloom in the coastal Gulf of Alaska but is spatially and temporally variable, with significant mesoscale variability superimposed on a general pattern of high inshore and low offshore concentrations (Brickley and Thomas, 2004; Fig. 1). Consequently, *N. plumchrus* and *N. flemingeri* in coastal regions encounter a wide range of feeding conditions during their major period of growth and development on the shelf. In this paper, we examine the effects of the mesoscale structure of phytoplankton on the feeding of these two copepods in the coastal Gulf of Alaska, and compare feeding variability with variability in body size and lipid storage across the shelf.

2. Methods and Materials

2.1. Ingestion rates

Feeding experiments were conducted on shipboard during spring of 2001 and 2003 (Fig. 1). For each experiment, copepods were collected by vertically hauling a plankton net with mesh size of 202 μm and a 20 l aquarium cod-end from 50 m to the surface. Cod-end contents were gently poured into an insulated container. In the laboratory, healthy individuals were sorted with ladles or large-bore pipettes and transferred into small jars containing surface seawater. These animals were kept cool for about 30–90 min before being transferred to experimental bottles.

For food medium, seawater was collected from the 50% light depth by Niskin bottles

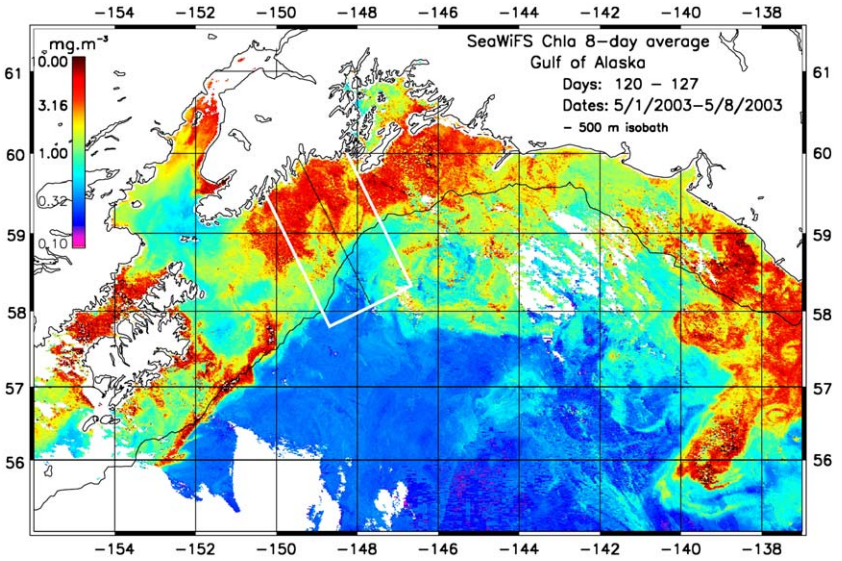

Fig. 1. Our study region including a sample image showing mesoscale structure of surface chlorophyll. For this image, chlorophyll concentration was derived from an 8 day average of SeaWiFS images between 5/1/2003 and 5/8/2003. All feeding experiments in this paper were done on the Seward line, indicated by the black line perpendicular to the coast, or in Prince William Sound. A region encompassing 30 km on each side of the Seward line is indicated by the white box.

mounted to a CTD rosette. Seawater from several Niskin bottles was gently drained into a polycarbonate carboy and then screened through a 202 μm mesh during the filling of 2.3 l polycarbonate bottles. All carboys, bottles, tubing and other labware used in the experimental set-up were acid cleaned and rinsed with milli-Q water before use.

N. flemingeri and *N. plumchrus* C5s were placed into experimental bottles and incubated on deck for 24 h. In most experiments, three different concentrations of copepods were incubated with 2–4 replicate bottles for each treatment. Two or three bottles with no copepods were incubated as controls. All experimental bottles were tightly capped after filling and one layer of neutral screen was applied to each bottle to reduce light by about 50%. During incubation, temperature was controlled by running surface seawater through the incubator. Except for ship motion, bottles were not mixed. Chlorophyll *a* concentration in three size classes (>20, 5–20 and <5 μm) was determined at the beginning and end of the incubation. For chlorophyll analysis, filters were placed in 90% acetone for 24 h at $-20\,^{\circ}C$ and the extract was measured with a Turner Designs fluorometer (Strickland and Parsons, 1972).

Clearance rate, F (ml cop^{-1} d^{-1}), on each size category of phytoplankton was calculated according to the formula of Frost (1972):

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

where V is the volume of the incubation bottle, Z is the number of copepods 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

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

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, ng chl cop^{-1} d^{-1}) is calculated by

$$I = CF,$$

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

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

To assess mesoscale structure of phytoplankton, satellite-measured chlorophyll concentrations were calculated from SeaWiFS imagery for 2001 and

2003. Daily 1 km resolution LAC data for each year from the study region were acquired from the NASA Distributed Active Archive Center, re-mapped to a standard projection, cloud masked, and processed to chlorophyll by the current global SeaWiFS chlorophyll algorithm, OC4v4 (O'Reilly et al., 2000). Daily scenes were formed into 8-day composites, beginning January 1 of each year, to reduce data volume and reduce data gaps caused by clouds. Cross-shelf chlorophyll profiles along the Seward line were subsampled from the 8-day composite time series by extracting chlorophyll concentration at each 1 km location along the line, and forming a spatial mean of all valid returns within a 30 km direction perpendicular to each side of the Seward line. This extracted a 60 km wide mean chlorophyll transect, centered on the Seward line, with 1 km cross-shelf resolution (e.g. Fig. 1), as an 8-day time series in each study year.

Between May 3 and 8, 2004, samples of C5 *N. flemingeri* and *N. plumchrus* were collected by MOCNESS net at locations along the Seward line from the inner shelf to outer shelf. A subsample of copepods collected at each station was taken and immediately frozen in seawater for later determination of dry weight and lipid content. In the laboratory, frozen samples were thawed under a dissecting microscope. C5 *N. flemingeri* and *N. plumchrus* were identified (Miller, 1988) and sorted. Prosome length of each animal was recorded. At stations with plentiful animals, 15 replicates of each species were analyzed for dry weight and lipid content. Fewer replicates were used at some stations. Once sorted and measured, copepods were rinsed in distilled water and placed in pre-weighed aluminum pans. Samples were dried for >24 h at 55 °C and weighed on a Cahn microbalance to determine dry weight. After weighing, samples were immersed in 2 ml of methylene chloride in capped vials to extract body lipids (Miller, 1993). The solvent was changed after 6 and 24 h with disposable glass pipettes. After 30 h, the final volume was removed and the samples were dried again for >24 h and weighed to determine lipid-free dry weight. Lipid content was determined as the difference between total dry weight and lipid-free dry weight.

3. Results

Seventeen feeding experiments were done with *N. flemingeri* C5 and 13 with *N. plumchrus* C5. Chlorophyll concentration ranged widely, between 0.32 and 11.44 $\mu g\,l^{-1}$, and ingestion rates varied accordingly, between 6.0 and 627.0 ng chl $cop^{-1}\,d^{-1}$ (Table 1).

An example of the feeding behavior observed at high phytoplankton concentration is shown in Fig. 2. In this experiment with *N. flemingeri* C5 (Experiment 2, Table 1), total chlorophyll concentration at the beginning of the experiment was 3.75 $\mu g\,l^{-1}$ and the community was dominated by large cells, with 82% of the total in the >20 μm fraction, 10% in the 5–20 μm fraction and only 8% in the <5 μm fraction (Table 1). The apparent growth rate of cells in the >20 μm size fraction declined as the concentration of grazing copepods increased (Fig. 2a), indicating direct consumption of these cells. In contrast, the apparent growth rate of cells in the two smaller size categories increased with increasing copepod concentration (Fig. 2a). We attribute this to a cascade effect whereby the protozoan grazers of these smaller cells are consumed by the copepods, reducing the mortality rate of small cells (Liu et al., 2005). The ingestion rate measured in this experiment was high (mean-292 ng chl $cop^{-1}\,d^{-1}$, $n=6$, stdev $=71$), and ingested phytoplankton consisted almost entirely of cells in the >20 μm size fraction (Fig. 2b, Table 1).

An example of feeding behavior observed at low phytoplankton concentration is shown in Fig. 3. In this experiment with *N. flemingeri* C5 (Experiment 5, Table 1), total chlorophyll concentration was 0.77 $\mu g\,l^{-1}$ and the community was dominated by small cells, with 75% of the total in the <5 μm size fraction and only 6% in the >20 μm category (Table 1). In common with the experiment at high food concentration (Fig. 2), there was a strong decrease in the net growth of phytoplankton in the >20 μm size fraction with increasing copepod concentration, indicative of increased grazing with increased number of grazers (Fig. 3a). In this experiment however, there was also some measurable grazing in the 5–20 μm size category. No measurable grazing was seen in the <5 μm size fraction and, as was typically observed, there was an apparent cascade effect in this size category (Fig. 3a). Total ingestion rate of phytoplankton was low (mean $=24.2$ ng chl $cop^{-1}\,d^{-1}$, $n=6$, stdev $=5.3$), less than 10% of the ingestion observed at high chlorophyll concentration in Fig. 2. In spite of their scarcity, large cells dominated the diet with 50% of the ingested phytoplankton derived from this size category. Most of the remainder (47%) came from

Table 1
The average ingestion rate of phytoplankton, by size category, in each shipboard experiment with *Neocalanus flemingeri* and *N. plumchrus* during 2001 and 2003

Exp. no.	Species	Date	Location	Initial chlorophyll ($\mu g\,l^{-1}$)				Ingestion (ng chl or $cop^{-1}\,d^{-1}$)			
				$<5\,\mu m$	5–20 μm	$>20\,\mu m$	Total	$<5\,\mu m$	5–20 μm	$>20\,\mu m$	Total
1	*flemingeri*	4/20/2001	MS	0.300	0.060	0.030	0.393	0.00	2.00	3.99	5.99
2	*flemingeri*	4/25/2001	IS	0.302	0.362	3.087	3.751	0.00	6.06	286.21	292.27
3	*flemingeri*	4/27/2001	PWS	0.112	0.112	0.538	0.762	1.67	8.39	112.14	122.19
4	*flemingeri*	4/28/2001	PWS	0.071	0.175	1.202	1.448	0.00	0.42	127.14	127.56
5	*flemingeri*	5/18/2001	OS	0.577	0.143	0.051	0.772	0.85	11.31	12.06	24.23
6	*plumchrus*	5/18/2001	OS	0.577	0.143	0.051	0.772	0.00	1.85	9.57	11.41
7	*flemingeri*	5/24/2001	MS	0.272	0.048	0.054	0.374	0.00	0.04	7.06	7.10
8	*plumchrus*	5/24/2001	MS	0.272	0.048	0.054	0.374	0.00	6.20	10.42	16.62
9	*flemingeri*	5/27/2001	MS	0.184	0.131	3.413	3.728	1.33	1.46	158.70	161.49
10	*plumchrus*	5/27/2001	MS	0.184	0.131	3.413	3.728	0.81	2.04	239.88	242.73
11	*plumchrus*	5/29/2001	IS	0.228	0.199	4.766	5.192	5.29	0.57	84.36	90.22
12	*flemingeri*	5/29/2001	IS	0.228	0.199	4.766	5.192	0.00	1.11	205.35	206.45
13	*plumchrus*	5/22/2001	PWS	0.231	0.315	0.741	1.287	0.00	2.42	101.83	104.25
14	*plumchrus*	5/23/2001	PWS	0.170	0.102	0.183	0.455	0.00	0.00	23.28	23.28
15	*plumchrus*	7/12/2001	IS	0.174	0.234	0.914	1.323	25.38	0.00	141.24	166.62
16	*plumchrus*	7/15/2001	MS	0.773	0.176	0.060	1.008	67.37	31.30	10.92	109.59
17	*plumchrus*	7/17/2001	MS	0.716	0.151	0.075	0.942	21.71	14.66	3.77	40.14
18	*plumchrus*	7/18/2001	OS	0.790	0.245	0.068	1.103	10.81	40.16	7.16	58.13
19	*plumchrus*	7/20/2001	OS	0.905	0.215	0.108	1.227	33.69	27.65	10.81	72.16
20	*plumchrus*	4/27/2003	OS	0.320	0.096	0.065	0.481	12.40	2.50	6.60	21.50
21	*flemingeri*	4/28/2003	OS	0.199	0.075	0.050	0.324	0.00	1.60	8.30	9.90
22	*flemingeri*	4/30/2003	PWS	0.165	0.201	1.317	1.684	0.00	0.00	187.20	187.20
23	*flemingeri*	5/2/2003	PWS	0.291	0.147	0.610	1.048	0.00	0.00	89.60	89.60
24	*flemingeri*	5/3/2003	PWS	0.041	0.081	1.151	1.273	0.00	0.00	192.20	192.20
25	*flemingeri*	5/6/2003	IS	0.281	0.458	2.050	2.789	0.00	0.00	127.80	127.80
26	*flemingeri*	5/7/2003	IS	0.248	0.599	2.476	3.333	0.00	0.00	328.10	328.10
27	*flemingeri*	5/11/2003	PWS	0.552	0.829	9.103	10.484	0.00	0.00	109.10	109.10
28	*flemingeri*	5/12/2003	PWS	0.456	0.457	10.526	11.438	0.00	0.00	627.00	627.00
29	*flemingeri*	5/13/2003	MS	0.999	0.244	0.058	1.301	0.00	0.00	136.60	136.60
30	*plumchrus*	5/13/2003	MS	0.999	0.244	0.058	1.301	0.00	0.00	144.20	144.20

IS = inner shelf, MS = mid-shelf, OS = outer shelf, PWS = Prince William Sound.

the intermediate size class and only a few percent came from the smallest size category (Fig. 3b, Table 1).

With only a few exceptions (see below) large cells dominated the diet of both copepods under all conditions. Generally, when large cells were abundant, chlorophyll concentration was high and high ingestion rates resulted. When large cells were rare and chlorophyll concentration was low, ingestion rate was low but large cells still dominated the diet.

Simultaneous experiments with *N. flemingeri* and *N. plumchrus* during periods when their populations overlapped did not show any consistent differences in their feeding behavior (paired experiments 5 and 6, 7 and 8, 9 and 10, 11 and 12, 29 and 30 in Table 1) but in all 30 experiments, only *N. plumchrus* consumed significant amounts of phytoplankton in the $<5\,\mu m$ size fraction (experiments 15–20, Table 1). As an example, results from experiment 20 (Table 1) are shown in Fig. 4. Total chlorophyll concentration at the beginning of this experiment was $0.48\,\mu g\,l^{-1}$ and the community was dominated by small cells, with 66% in the $<5\,\mu m$ category and only 14% in the $>20\,\mu m$ category. Total ingestion was low, averaging only $21.5\,ng\,chl\,cop^{-1}\,d^{-1}$ ($n = 4$, stdev = 11.8) but cells in the $<5\,\mu m$ category comprised 58% of this (Fig. 4). As observed in almost all experiments, large cells were ingested in greater proportion than their abundance (30% vs. 14%) but only in these experiments with *N. plumchrus* was there a significant contribution by small cells to the diet, between 15 and 61% of the

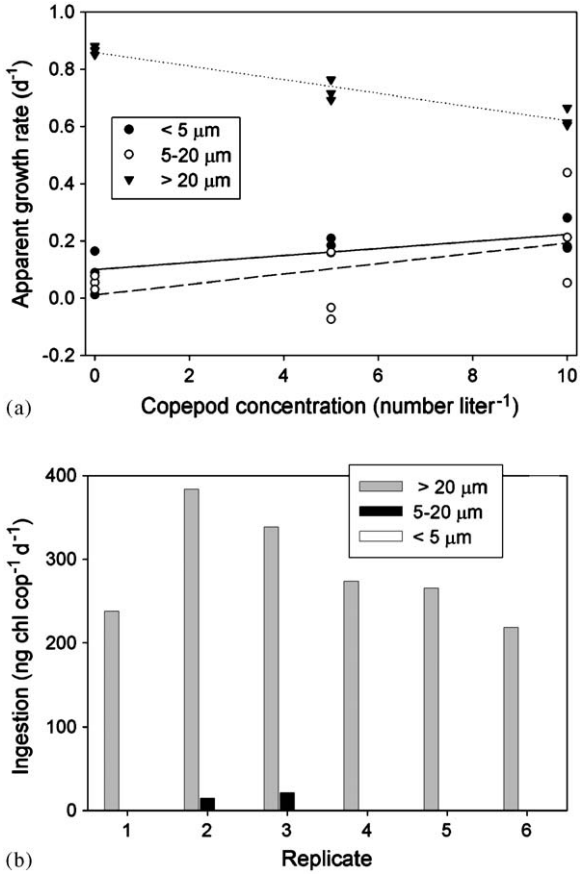

Fig. 2. Results from feeding experiment 2, with *N. flemingeri* C5 on April 25, 2001, using water collected from the inner shelf containing a high concentration of phytoplankton. (a) The apparent growth rate of each size category of phytoplankton. Slopes are significantly different from each other (ANCOVA, $p<0.005$) and significantly different from 0 for the $>20\,\mu m$ ($p<0.001$) and $<5\,\mu m$ ($p<0.05$) lines. (b) Phytoplankton ingested in each size category.

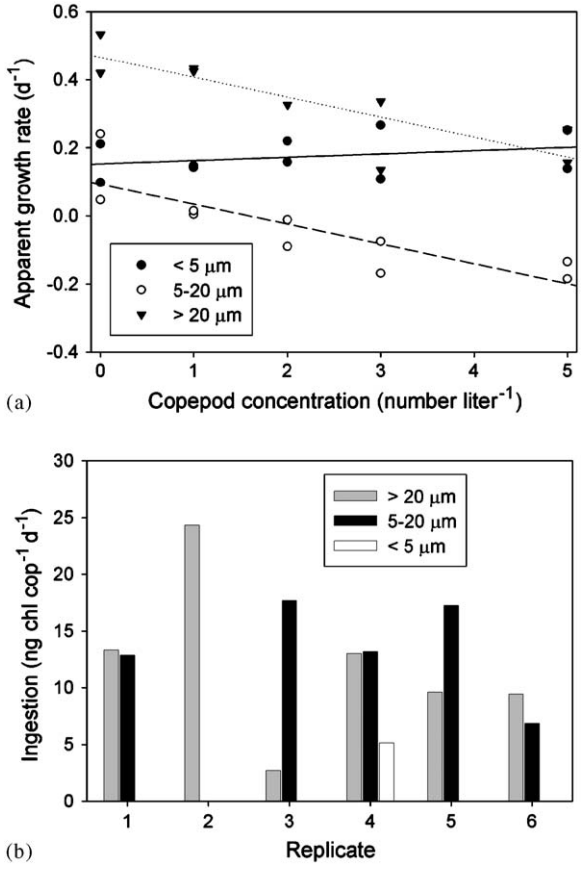

Fig. 3. Results from feeding experiment 5, with *N. flemingeri* C5 on May 18, 2001, using water collected from the outer shelf containing a low concentration of phytoplankton. (a) The apparent growth rate of each size category of phytoplankton. Slopes are significantly different from each other (ANCOVA, $p<0.001$) and significantly different from 0 for the $>20\,\mu m$ ($p<0.001$) and 5–20 μm ($p<0.001$) lines. (b) Phytoplankton ingested in each size category.

total ingested phytoplankton. Collectively, these 6 experiments suggest that *N. plumchrus* C5 may be more capable of feeding on small cells than *N. flemingeri* C5.

Although feeding behavior of these two copepods is yet not fully understood, there is sufficient information to allow an initial estimate of the effect of mesoscale or small-scale variation in phytoplankton on their feeding in the Gulf of Alaska shelf region. Data from all feeding experiments combined ($n=132$) show there is a general tendency for higher ingestion rates at higher phytoplankton concentrations (Fig. 5). There is a lot of variability but we can use this relationship to characterize shelf waters as supportive of low, intermediate

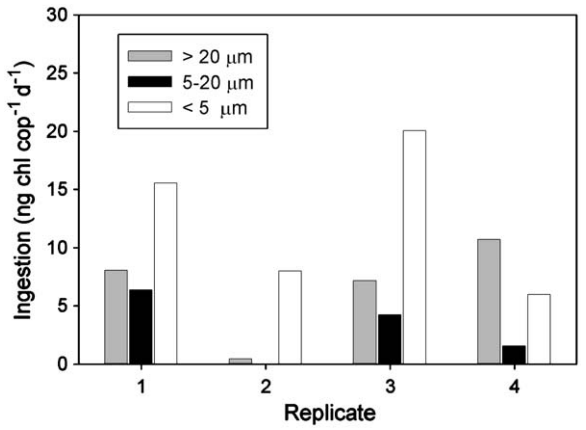

Fig. 4. Results from feeding experiment 20, with *N. plumchrus* C5 on April 27, 2003, using water collected from outer shelf containing a low concentration of phytoplankton.

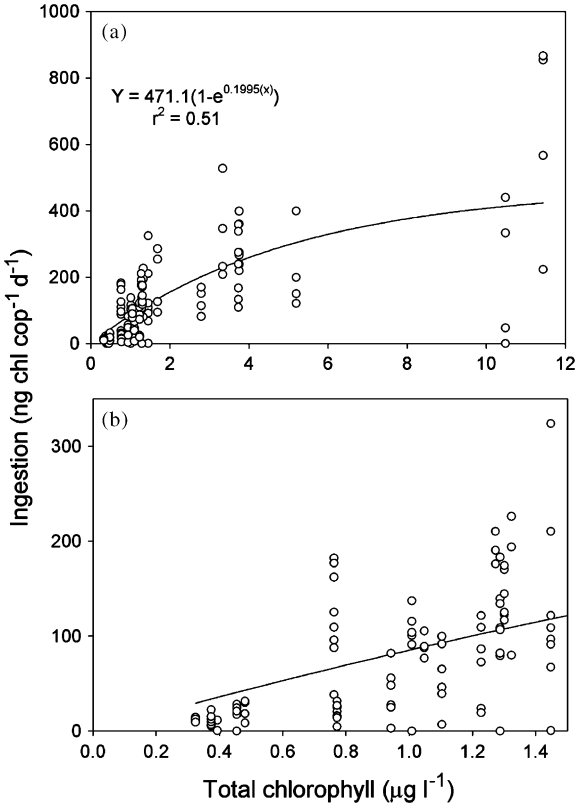

Fig. 5. The relationship between ingestion rate and total chlorophyll concentration derived by combining all feeding experiments: (a) all data for both *N. flemingeri* C5 and *N. plumchrus* C5; (b) expanded scale showing ingestion rates at chlorophyll concentrations $<1.5\,\mu g\,chl\,l^{-1}$. The curvilinear relationship plotted in both panels is the same.

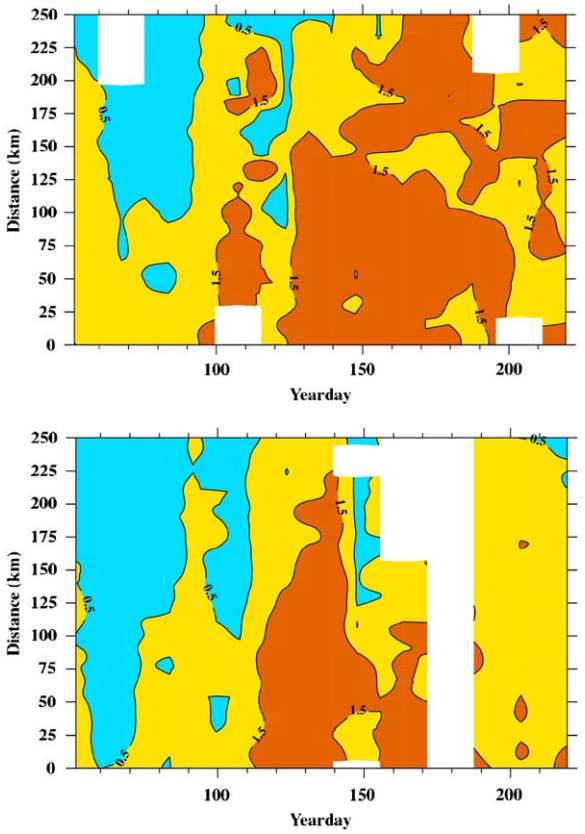

Fig. 6. Chlorophyll concentration within the area 30 km each side of the Seward line (the white line in Fig. 1). Blue indicates concentrations $<0.5\,\mu g\,l^{-1}$ which support low feeding rates, yellow indicates concentrations between 0.5 and $1.5\,\mu g\,l^{-1}$ which support intermediate feeding rates, and orange indicates concentrations $>1.5\,\mu g\,l^{-1}$ which support high feeding rates. (top panel) 2001, (bottom panel) 2003.

or high ingestion rate. At chlorophyll concentrations $<0.50\,\mu g\,l^{-1}$, ingestion is always low, $<40\,ng\,cop^{-1}\,d^{-1}$ (Fig. 5). Ingestion rate calculated from the derived equation for a chlorophyll concentration of $0.50\,\mu g\,l^{-1}$ is $44.7\,ng\,chl\,cop^{-1}\,d^{-1}$. At chlorophyll concentrations between 0.5 and $1.5\,\mu g\,l^{-1}$, ingestion increases rapidly and can be $>300\,ng\,cop^{-1}\,d^{-1}$ (Fig. 5). Ingestion rate calculated from the derived equation for a chlorophyll concentration of $1.00\,\mu g\,l^{-1}$ is $85.2\,ng\,chl\,cop^{-1}\,d^{-1}$, and at $1.50\,\mu g\,l^{-1}$ is $121.8\,ng\,chl\,cop^{-1}\,d^{-1}$. At chlorophyll concentrations $>1.5\,\mu g\,l^{-1}$, ingestion can be even higher, $>500\,ng\,cop^{-1}\,d^{-1}$ (Fig. 5). Ingestion rate calculated from the derived equation for a chlorophyll concentration of $5.00\,\mu g\,l^{-1}$ is $297.4\,ng\,chl\,cop^{-1}\,d^{-1}$.

The spatial and temporal distribution of chlorophyll in these three concentration ranges is shown in Fig. 6. This represents the mesoscale structure of phytoplankton on the shelf from the perspective of C5 *N. flemgeri* and *N. plumchrus* feeding. Conditions that identify periods and locations of low feeding rate are represented by the portions of Fig. 6 in blue, intermediate feeding rate is represented by yellow, and high feeding rate by orange. The spring bloom is readily apparent in both years between approximately day 120 and 180. During this time, there is a tendency for higher concentrations of phytoplankton to occur in the inner shelf compared to the outer shelf but mesoscale structure is evident in both years and there is some interannual variability apparent. At all times some portion of the study region is supportive of at least two levels of feeding. The fractions of our imaged region that support low, intermediate and high ingestion rates of phytoplankton directly reflect this phytoplankton distribution (Fig. 7). A seasonal integration of these

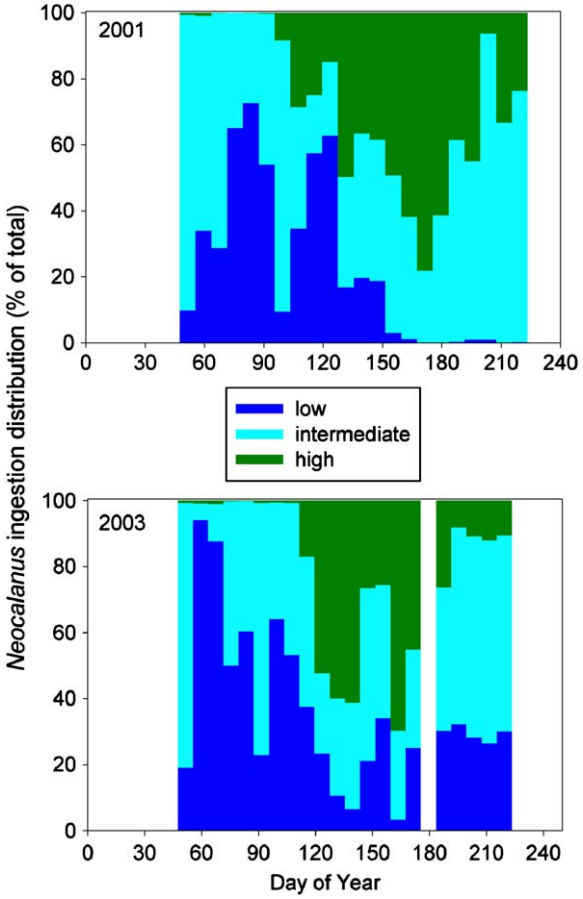

Fig. 7. The fraction (%) of the 60 km wide cross-shelf swath supporting low, medium and high feeding rates of *N. flemingeri* and *N. plumchrus* C5 during 2001 (top) and 2003 (bottom).

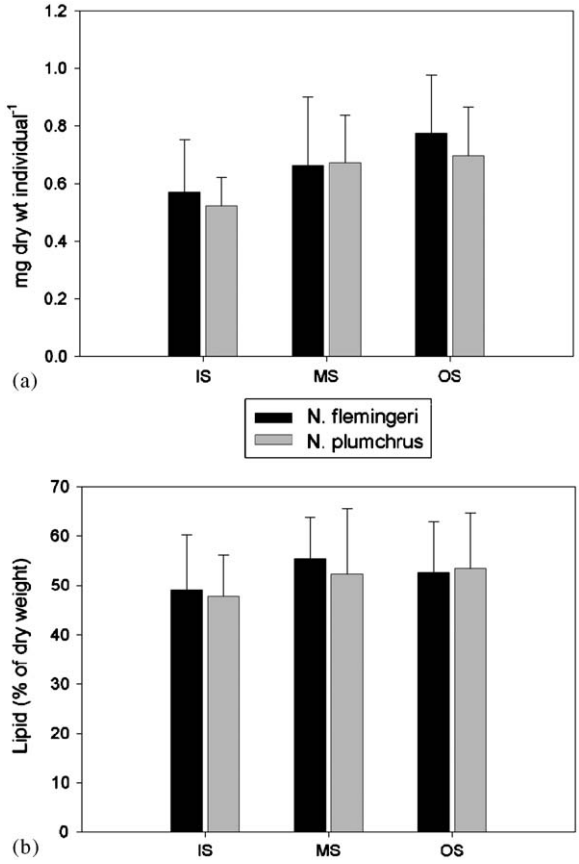

Fig. 8. The dry weight (a) and lipid store (b) of individual *N. flemingeri* C5 and *N. plumchrus* C5 collected May 3–10, 2004. Samples from three stations are pooled from the inner shelf (IS), from four stations for the middle shelf (MS) and from six stations for the outer shelf (OS). The number of samples used for each plot are: *N. flemingeri* IS 24, MS 22, OS 35; *N. plumchrus* IS 27, MS 30, OS 36. Bars indicate 95% C.I.

patterns over the April, May and June period when *N. flemingeri* and *N. plumchrus* do most of their feeding and growing on the shelf indicates, in 2001, a copepod would have encountered low feeding conditions 18% of the time, intermediate feeding conditions 41% of the time and high feeding conditions 41% of the time. In 2003, the fractions are 29%, 42%, and 29% for low, intermediate and high feeding rates, respectively, for the AMJ time period. Throughout the growing season for *N. flemingeri* and *N. plumchrus*, there is always some mesoscale phytoplankton structure on the shelf and this structure affects the daily ingestion rate of C5s of both copepods. However, variability in the daily ingestion rate of phytoplankton, induced as a response to mesoscale structure in the phytoplankton, was not reflected in the body size or lipid content of individual copepods (Fig. 8). In May 2004, the individual body weight (Fig. 8a) and the % body weight consisting of lipid (Fig. 8b) were identical over all parts of the shelf in C5s of both species. Day to day variation in the ingestion of phytoplankton did not affect the total amount of growth and food storage that occurred over the 60–90 day period these copepods spent feeding and growing in surface water.

4. Discussion

Our feeding experiments indicated that total chlorophyll was a reasonable indicator of daily phytoplankton ingestion, although there is a lot of variability in the data used to derive this relationship. Ingestion was always low at low phytoplankton concentrations and higher but variable at high concentrations. This pattern has also been

observed in other studies with these copepods (e.g. Dagg et al., 1982; Dagg and Walser, 1987). In all feeding experiments at chlorophyll concentrations $>1.50\,\mu g\,chl\,l^{-1}$ ingestion of phytoplankton was heavily dominated by cells $>20\,\mu m$. In some of these experiments, ingestion of intermediate sized cells was measurable but made only a minor contribution to the total diet. Ingestion of cells from the small size category, $<5\,\mu m$, was typically not measurable. At low chlorophyll concentrations, ingestion rates were much lower and small and intermediate sized cells often made up a greater proportion of the diet than large cells. Even under low chlorophyll conditions however, large cells were always a greater fraction of the diet than they were in the phytoplankton community. Small cells were a significant portion of the total ingestion only for *N. plumchrus*, perhaps indicating that *N. plumchrus* is more capable of feeding on smaller food sizes than *N. flemingeri*. This needs to be further examined in detailed, direct comparative experiments. In the five direct comparisons made in this study, there were no consistent differences in the feeding behavior of *N. flemingeri* and *N. plumchrus*, but size fractionated chlorophyll is a coarse index of feeding behavior.

The satellite data clearly indicate strong mesoscale structure of chlorophyll on the shelf during our study years (2001 and 2003), even during the spring bloom, consistent with earlier analyses for the 1997–2001 time period (Brickley and Thomas, 2004). The imagery measures surface chlorophyll as a weighted integral of radiance over the first optical depth. However, based on vertical profiles of chlorophyll made at stations used for collecting water for feeding experiments, subsurface chlorophyll maxima were typically not present and community composition was similar at all depths. The exceptions were late in the season during the post-bloom period on the mid- and outer-shelf, when a subsurface chlorophyll maximum sometimes developed. *Neocalanus* spp. do not undergo diel migrations in this region (Napp unpublished) and are most heavily concentrated in the surface layer. We believe that surface chlorophyll represents the phytoplankton environment encountered by *N. flemingeri* and *N. plumchrus*.

An accurate assessment of the validity of the NASA global chlorophyll algorithm for these waters requires optical sampling protocols, instruments and effort beyond the scope of our study. The in situ surface chlorophyll data we do have available is formed into cross-shelf transects representative of two time periods, and compared to satellite-derived transects subsampled from monthly composite imagery approximately concurrent with the field operations. Comparisons of these transects (Fig. 9) further suggests that, within the strong temporal and spatial variability present on the shelf, the satellite data provide a reasonable assessment of chlorophyll structure.

Another potential difficulty with the satellite derived chlorophyll calculations is that the size composition of the phytoplankton community cannot be resolved. Because both *N. flemingeri* and *N. plumchrus* fed more efficiently on large

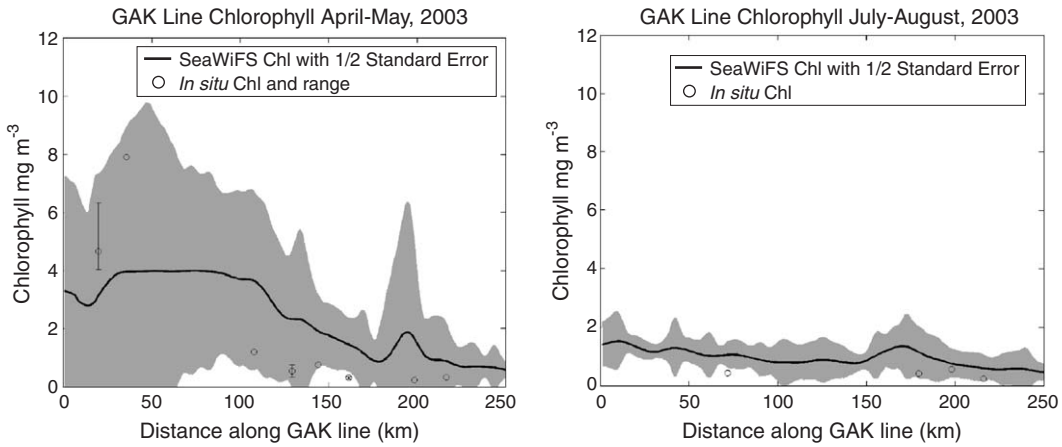

Fig. 9. Comparisons of cross-shelf chlorophyll structure in the vicinity of the Seward line using satellite-derived chlorophyll and available surface in situ data from two periods in 2003. Although strong time and space differences coupled with strong variability do not allow direct comparison of the two data sets, overall structure and magnitudes are similar.

particles, the ingestion per unit of chlorophyll was higher when the phytoplankton community was dominated by large cells. The same amount of chlorophyll detected by imagery might support different amounts of ingestion if the size composition of that chlorophyll was different. This would introduce an error in our use of imagery to map the feeding environment. However, with few exceptions, the size composition of the phytoplankton community changed in a systematic manner (Fig. 10), being dominated by large cells ($>20\,\mu m$) whenever total chlorophyll concentration was higher than about $0.5\,\mu g\,chl\,l^{-1}$ and by small cells otherwise. This might introduce a small systematic error but would not be significant given the broad variability around our shipboard derived relationship between ingestion and chlorophyll concentration. We concluded that, for the purposes of this paper, surface chlorophyll measured by satellite imagery is a reasonable representation of the phytoplankton food environment for C5 *N. flemingeri* and *N. plumchrus*.

Imagery indicated that mesoscale variability in phytoplankton concentration existed on the Gulf of Alaska shelf at all times that *N. flemingeri* and *N. plumchrus* were present during 2001 and 2003. Our shipboard experiments indicated this variability affected the daily feeding of C5 *N. flemingeri* and *N. plumchrus* on phytoplankton although it did not explain all the variability in phytoplankton ingestion that we observed. This mesoscale effect will not be equally important over the entire 60–90 day period

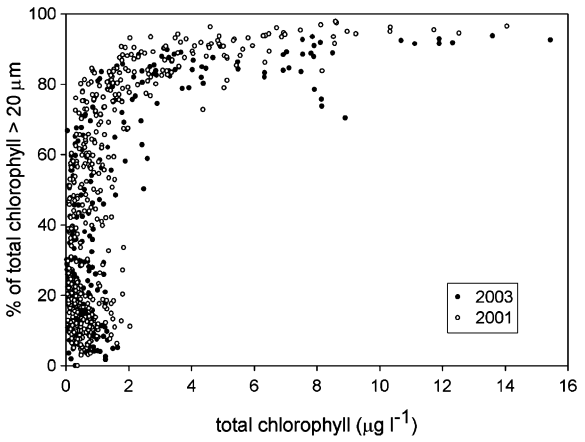

Fig. 10. The relationship between the large cell component of the phytoplankton community and the total chlorophyll concentration, indicating the phytoplankton community is always dominated by large cells when chlorophyll concentration is high, and typically dominated by small cells when the chlorophyll concentration is low.

of *N. flemingeri* and *N. plumchrus* development and growth on the shelf. Relationships between phytoplankton concentration and ingestion rate are not known for younger copepodid stages of *N. flemingeri* and *N. plumchrus* but, in general, smaller copepods reach feeding saturation at lower food concentrations than larger copepods. It is reasonable to assume that effects of mesoscale phytoplankton variability on the daily ingestion by younger (smaller) copepodid stages are less than we indicate for the C5s. Ingestion of phytoplankton by the earliest (smallest) copepodid stages may even be maximum over all conditions observed on the shelf. As development and growth proceed, however, the food concentration required for maximum ingestion increases and variation in available phytoplankton will induce wider variations in daily ingestion. In spite of this, variations in daily ingestion did not result in differences in final body size or food storage (% lipid), which were statistically similar for all individuals collected on the shelf. Copepodid stage C5s collected from anywhere on the shelf during early May 2004 were indistinguishable in terms of body weight and food lipid store. *N. flemingeri* and *N. plumchrus* were able to average out mesoscale-induced fluctuations in daily feeding during their 60–90 day period of growth and development. There are several possible mechanisms for this, including alternative food sources, physiological adaptations, and environmental displacement.

Additional food sources such as microzooplankton and other particulate matter may smooth out variability in the phytoplankton environment if they are not distibutionally or temporally correlated with phytoplankton. These foods could provide nutrition in areas or times of scarce phytoplankton food, resulting in approximately similar daily ingestion rates in terms of carbon. Microzooplankton, however, are not sufficiently abundant to support high carbon ingestion rates during the months of the spring bloom (Liu et al., 2005). Microzooplankton concentrations increase dramatically during the post-bloom period (Lessard et al., 2003), but *N. flemingeri* and *N. plumchrus* have completed their growth and development by this time. The role of detrital aggregates as food for *N. flemingeri* and *N. plumchrus* is not well understood but aggregates appear to be an important source of nutrition for *N. cristatus* (Dagg, 1993b).

Most copepods are able to smooth out some of the variability in their food environment as long as they encounter conditions supporting a high feeding

rate at a physiologically appropriate frequency (Dagg, 1977; Bochdansky and Bollens, 2004). Such behavior, sometimes called a 'hunger response' (Runge, 1980), involves bursts or short periods of very high feeding activity when a patch or region of high food concentration is encountered. This might explain how *N. flemingeri* and *N. plumchrus* in our study are able to accommodate mesoscale variability in their food environment without affecting their final body size. This behavior might also explain some of the variability observed in our shipboard experiments, assuming individuals in different bottles had different feeding histories.

For individual copepods to encounter a range of phytoplankton concentrations over periods of days, either the phytoplankton within the water containing both phytoplankton and copepods must change or the copepods must somehow be displaced or moved to a different parcel of water containing a different concentration of phytoplankton. Both are probable for large copepods like *N. flemingeri* and *N. plumchrus*.

In conclusion, the daily ingestion of phytoplankton by *N. flemingeri* and *N. plumchrus* varies with phytoplankton concentration, but mesoscale variability in phytoplankton on the shelf of the Gulf of Alaska does not result in differences in final body size or lipid storage of these copepods. These copepods efficiently deal with small and mesoscale variations in their food environment such that mesoscale structure in phytoplankton does not affect their final body size.

Acknowledgements

This field work would not have been possible without close collaborations with S. Strom and J. Napp and their assistants. We thank the Captain and crew of the R.V. Alpha Helix for shipboard assistance. This research was supported by the Biological Oceanography program of the National Science Foundation under grant number OCE-0102381 to MJD/HL and OCE-0000899 to ACT as part of the US GLOBEC program, and by NASA grant number NAG5-6604 to ACT.

References

Banse, K., English, D.C., 1999. Comparing phytoplankton seasonality in the eastern and western subarctic Pacific and the western Bering Sea. Progress in Oceanography 43, 235–288.

Bochdansky, A.B., Bollens, S.M., 2004. Relevant scales in zooplankton ecology: distribution, feeding, and reproduction of the copepod *Acartia hudsonica* in response to thin layers of the diatom *Skeletonema costatum*. Limnology and Oceanography 49, 625–636.

Brickley, P.J., Thomas, A.C., 2004. Satellite-measured seasonal and interannual chlorophyll variability in the Northeast Pacific and coastal Gulf of Alaska. Deep-Sea Research II 51, 229–245.

Cooney, R.T., Coyle, K.O., Stockmar, E., Stark, C., 2001. Seasonality in surface-layer net zooplankton communities in Prince William Sound, Alaska. Fisheries Oceanography 10 (Supplement 1), 97–109.

Coyle, K.O., 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., 1977. Some effects of patchy food environments on copepods. Limnology and Oceanography 22, 99–107.

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 calanoid copepod *Neocalanus cristatus* in the subarctic Pacific Ocean. Deep-Sea Research I 40, 1431–1445.

Dagg, M.J., Walser Jr., W.E., 1987. Ingestion, gut passage, and egestion by the copepod *Neocalanus plumchrus*, in the laboratory and in the subarctic Pacific Ocean. Limnology and Oceanography 32, 178–188.

Dagg, M.J., Wyman, K.D., 1983. Natural ingestion rates of the copepods *Neocalanus plumchrus* and *N. cristatus*, calculated from gut contents. Marine Ecology Progress Series 13, 37–46.

Dagg, M.J., Vidal, J., Whitledge, T.E., Iverson, R.L., Goering, J.J., 1982. The feeding respiration, and excretion of zooplankton in the Bering Sea during the spring bloom. Deep-Sea Research 29, 45–63.

Evanson, M., Bornhold, E.A., Goldblatt, R.H., Harrison, P.J., Lewis, A.G., 2000. Temporal variation in body composition and lipid storage of the overwintering, subarctic copepod *Neocalanus plumchrus* in the Strait of Georgia, British Columbia (Canada). Marine Ecology Progress Series 192, 239–247.

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.

Fulton, J.D., 1973. Some aspects of the life history of *Calanus plumchrus* in the Strait of Georgia. Journal of the Fisheries Research Board of Canada 30, 811–815.

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

Gifford, D.J., Dagg, M.J., 1991. The microzooplankton-mesozooplankton link: consumption of planktonic Protozoa by the calanoid copepods *Acartia tonsa* Dana and *Neocalanus plumchrus* Marukawa. Marine Microbial Food Webs 5, 161–177.

Lessard, E.J., Foy, M.S., Bernhardt, M., Opatkiewicz, A., 2003. Seasonal, interannual and spatial patterns in phytoplankton and microzooplankton community composition and size

structure in the coastal Gulf of Alaska. EOS Transactions, American Geophysical Union 84, 62.

Liu, H., Dagg, M.J., Strom, S., 2005. Grazing by the calanoid copepod Neocalanus cristatus on the microbial food web in the coastal Gulf of Alaska. Journal of Plankton Research 27, 647–662.

Mackas, D.L., 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., 1988. *Neocalanus flemingeri*, a new species of Calanidae (Copepoda: Calanoida) from the subarctic Pacific Ocean, with a comparative rediscription of *Neocalanus plumchrus* (Marukawa) 1921. Progress in Oceanography 20, 223–273.

Miller, C.B., 1993. Development of large copepods during spring in the Gulf of Alaska. Progress in Oceanography 32, 295–317.

Miller, C.B., Clemons, M.J., 1988. Revised life history analysis for large grazing copepods in the subarctic Pacific Ocean. Progress in Oceanography 20, 293–313.

Miller, C.B., Terazaki, M., 1989. The life histories of *Neocalanus flemingeri* and *Neocalanus plumchrus* in the Sea of Japan. Bulletin of Plankton Society of Japan 36, 27–41.

Miller, C.B., Fulton, J., Frost, B.W., 1992. Size variation of *Neocalanus plumchrus* and *Neocalanus flemingeri* in a 20-yr sample series from the Gulf of Alaska. Canadian Journal of Fisheries and Aquatic Science 49, 389–399.

O'Reilly, J.E., et al., 2000. Ocean color chlorophyll algorithms for SeaWiFS, OC2 and OC4: Version 4. In: Hooker, S.B., Firestone, E.R. (Eds.), SeaWiFS Postlaunch Technical report Series, Part 3. NASA Tech. Memo. 2000-206892, vol. 11, October, 2000, NASA Goddard Space Flight Center, Greenbelt, MD.

Runge, J.A., 1980. Effects of hunger and season on the feeding behavior of *Calanus pacificus*. Limnology and Oceanography 25, 134–145.

Strickland, J.D.H., Parsons, T.R., 1972. A practical handbook of seawater analysis. second ed. Bulletin of the Fisheries Research Board of Canada, vol. 167, pp. 201–203.

Tsuda, A., Sugisaki, H., 1994. In situ grazing rate of the copepod population in the western subarctic North Pacific during spring. Marine Biology 120, 203–210.

Tsuda, A., Saito, H., Kasai, H., 1999. Life history of *Neocalanus flemingeri* and *Neocalanus plumchrus* (Calanoida: Copepoda) in the western subarctic Pacific. Marine Biology 135, 533–544.