ABUNDANCE, DISTRIBUTION, AND FEEDING ASPECTS OF SELECTED
ZOOPLANKTON SPECIES IN THE SUBARCTIC PACIFIC

by

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to the required standard

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Abstract

Changes in the abundance of zooplankton species from the North American west coast to the open northeastern subarctic Pacific are not well documented. This study examines the abundance and distribution of important zooplankton species in the subarctic Pacific from the continental slope region to the open ocean in relation to physical, chemical, and biological parameters. Zooplankton samples were collected to a depth of at least 100 m using a modified SCOR (WP-2) net along the Line P transect (about 49°N, 127°W to 50°N, 145°W), during March and May 1993, and February and May 1994.

Despite recent efforts to quantify the grazing pressures imposed on phytoplankton by the predominant copepods species of the subarctic Pacific, there is little detailed information on the diets of the predominant copepod species in this region. A shipboard experiment was conducted at Station P in May 1994, to examine the feeding behaviour of a predominant subarctic copepod species, *Neocalanus flemingeri* (Miller), grazing on a natural assemblage of prey items. Single copepods were incubated in 1 L bottles for 24 h with controls, and laboratory enumeration of autotrophic and heterotrophic prey items was made using inverted transmission microscopy and epifluorescence microscopy.

Zooplankton biomass (0–500 m) was generally predominated by copepods of the genus *Neocalanus*, although other zooplankton genera made significant contributions during all cruises. The development of some species of *Neocalanus* appears to occur progressively later seaward of the continental slope which may be the result of a coupling mechanism between copepod spawning and small blooms of large diatoms in the eastern subarctic Pacific. Zooplankton biomass was greatest during May cruises, but was also more variable between the two late spring cruises than between the two winter cruises.
biomass (excluding salps) was more variable east of 134°40'W in late spring (< 100 m) and was generally lower when salps were present, except at Station P16 in May 1993, when salp numbers and zooplankton biomass were both at their highest during this cruise. Salps were observed only during the 1993 cruises and were never present at Station P. Although their presence along Line P in 1993 may be due to the encroachment of southern waters, their numbers do not appear to be directly associated with changes in sea surface temperature.

*Neocalanus flemingeri* did not clear all size fractions of prey items at equal rates, and a calculated selectivity index indicates a feeding preference on autotrophic cells over heterotrophic cells. In addition, the selectivity index shows that cells < 10 µm were generally predated on preferentially to larger cells. *N. flemingeri* obtained about 69% of its metabolic requirements from ciliates alone. However, a comparison of ciliate growth rate and copepod clearance rate on ciliates suggests that *N. flemingeri* and *Neocalanus plumchrus* (Marukawa) cannot control the ciliate population. *N. flemingeri* consumed < 5 µm autotrophic cells at double the rate previously reported for *N. flemingeri* or *N. plumchrus*. Total ingested carbon was enough to allow substantial daily body growth. Despite this fact, estimates of community ingestion support the notion that copepods in the subarctic Pacific do not control the phytoplankton stock. *N. flemingeri* and *N. plumchrus* do not appear to contribute substantially to ammonium recycling in the mixed-layer, suggesting there exist other mechanisms for this process. Estimated biomass of fecal pellets produced by these species was approximately 61% of the downward vertical carbon flux at 100 m and may account for up to 28% of the metabolic requirements of *N. cristatus* residing at the bottom of the mixed-layer. Other sources of sinking particles are likely important for *N. cristatus* nutrition, and probably come from other major zooplankton species.
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pour Yvonne De Jong
Chapter 1

Distribution and Abundance of Mesozooplankton

1.1 Introduction

1.1.1 General Background

Mesozooplankton (hereafter called zooplankton), by definition, include species that range in size from 0.2 to 20 mm (Sieburth et al., 1978), and rely primarily on water currents for horizontal movement. Within neritic and oceanic marine food webs, they are phytoplankton grazers, secondary consumers of other mesozooplankton and microzooplankton, and are prey for fish, whales and other planktivores (see review by Parsons et al., 1984b). Of zooplankton waste products, nitrogen is assimilated by phytoplankton (Goering et al., 1970; Syrett, 1981), organics are remineralized by heterotrophic bacteria (Turner, 1979; Turner & Ferrante, 1979), and some sink out of the mixed-layer, contributing to the flux of carbon into deep waters (Knauer et al., 1979; Angel, 1989) (Fig. 1.1).

Marine zooplankton include, among other taxa, chaetognaths, euphausiids, amphipods, jellyfish, salps, and larvaceans, but the class Copepoda is by far the most ubiquitous and abundant, often comprising at least 70% of the biomass of planktonic fauna (Raymont, 1983). In some areas, such as the northeastern subarctic Pacific, only a small number of copepod species are predominant in the spring zooplankton biomass (LeBrasseur, 1965a; Vinogradov, 1968; Fulton, 1978; Fulton, 1983). With the exception of often numerically important cyclopoid copepods, species of the order Calanoida tend to predominate this and other oceanic regions (Brodsky, 1950).
Figure 1.1: Schematic diagram summarizing the various functions of mesozooplankton in the marine food web.
Calanoid copepods generally have a fused head and first thoracic segment. Free living filter feeding species have setose maxillae coupled with antennae and mandibular palps to produce water currents that enable the filtration of water (Raymont, 1983). However, not all copepods are filter-feeding. For example, some cyclopoid species are raptorial, with modified antennae and maxillipeds aiding in the capture of prey or in tearing off prey tissue (Raymont, 1983).

1.1.2 Copepod Life History Strategies

Copepod development generally includes an embryonic stage and a series of 6 naupliar (N1–N6) and 6 copepodite (C1–C6) stages, where C6 is the final, sexually mature, adult stage (Raymont, 1983). Despite the constancy of developmental stages, copepod life cycles are extremely variable among species or even intraspecifically. For example, the seasonality of the *Neocalanus plumchrus* (Marukawa) life cycle is different in the open ocean compared to that of coastal populations (Fulton, 1973; Miller et al., 1984). Furthermore, the life cycles of copepods endemic to the North Pacific and North Atlantic are distinct. The absence of a spring bloom in the subarctic Pacific, despite the presence of ample macronutrients (> 5 μm NO₃⁻) and strong thermal stratification during summer months (Parsons & Lalli, 1988), is in contrast to the subarctic Atlantic where nutrient levels are seasonally high but where the chlorophyll standing stock is typically an order of magnitude greater than in the North Pacific (Parsons & Lalli, 1988). The long-standing paradigm used to explain the low phytoplankton stock in the subarctic Pacific is that copepod grazing is closely coupled with primary production and prevents bloom formation (Heinrich, 1962).

According to Heinrich (1962; 1968), in the subarctic Pacific, young copepodites of the major grazer, *Neocalanus plumchrus*, are in the mixed-layer before the onset of the main period of phytoplankton growth in May, meaning that there is little delay in the grazing
activity of these copepods. The intense grazing in the spring maintains a low phytoplankton stock and relatively high macronutrient levels. Heinrich (1962) viewed this cycle as balanced, where the biomass of zooplankton exceeds the biomass of phytoplankton year round. In the subarctic Atlantic, the grazing copepods, principally *Calanus finmarchicus* (Gunnerus), overwinter at depth and do not arrive at the surface to spawn until the onset of the spring bloom (Heinrich, 1962). By the time the newly hatched copepods are in their late copepodite stage, the phytoplankton stock already exceeds that of the zooplankton. Because of this lag in copepod development, zooplankton grazing and phytoplankton production are out of phase, allowing the phytoplankton stock to escape intense grazing pressures and to exceed zooplankton in biomass. In contrast to the subarctic Pacific, this seasonal cycle of the plankton community is unbalanced, resulting in a seasonally high and low phytoplankton stock (Heinrich, 1962). The underlying idea in this hypothesis is that the zooplankton life history characteristics determine in large part the plankton trophodynamics in the oceans (Heinrich, 1962).

### 1.1.3 A New Synthesis—The SUPER Group Contribution

Work done in the 1980s by the SUbartic Pacific Ecosystem Research (SUPER) group (Miller et al., 1991; Miller, 1993a and references therein) has only recently been synthesized to give a new view of the ecological relations in the subarctic Pacific. Early work by the SUPER group focused on defining more precisely the life histories of the most abundant copepod species of the subarctic Pacific (Miller et al., 1984), and will be discussed in the next section. The majority of the field work was conducted in the vicinity of Ocean Station PAPA (Station P), located at 50°N, 145°W. The SUPER work in this area was preceded by three decades of hydrographic and plankton data collection from Canadian weather ships patrolling the area, making this locale ripe for a detailed study of plankton dynamics.
From the start, the working hypothesis of the SUPER group was the Major Grazer Hypothesis (Miller et al., 1991), more or less as Heinrich (1962) had previously proposed with copepods of the genera *Neocalanus* and *Eucalanus* as the important grazers in this region. However, based on *in vitro* iron fertilization experiments conducted by Martin & Fitzwater (1988) and Martin et al. (1989), independent of the SUPER program, Martin (1990) suggested that the persistence of macronutrients and low chlorophyll standing stock in this and other high nitrate, low chlorophyll (HNLC) regions is not due to grazing by copepods, but to limitation of phytoplankton production by low iron availability. This finding led the SUPER group to re-evaluate some of their earlier data, and to consider Fe limitation as a possible explanation for the high nutrients and low chlorophyll levels of the subarctic Pacific (Miller et al., 1991).

It is generally accepted that small cells (2–10 \( \mu \text{m} \)) are predominant in the subarctic Pacific because they are able to grow at maximum rates (Booth et al., 1988) under low iron conditions (Boyd et al., *In review*). Bottle incubation results show that growth of large diatoms is severely limited by the lack of iron, explaining their paucity in the water column (Martin & Fitzwater, 1988; Banse, 1990; Martin et al., 1990). Additionally, Dagg (1993a) refuted the Major Grazer Hypothesis by showing that the large subarctic copepods do not graze sufficiently in the spring and early summer to maintain the low phytoplankton stocks observed in this region.

These results disproved the importance of copepods as major grazers and led the SUPER group to consider microzooplankton as the principal grazers (Miller et al., 1991). In this scheme, heterotrophic protozoans comprising ciliates, dinoflagellates and other flagellates (Booth et al., 1993; Strom et al., 1993) are the most important grazers in the subarctic Pacific (Welschmeyer & Lorenzen, 1985; Frost, 1987; Frost, 1993; Landry et al., 1993a). Protozoans are capable of growing much faster than phytoplankton (Banse,
1982), potentially allowing them to keep the stock of small photoautotrophs under control during the more productive summer months. In addition, these micrograzers are effective at recycling nutrients via their easily degradable, slow-sinking excreta. These nitrogen-rich waste products are recycled as ammonium (NH$_4^+$), contributing to the input of NH$_4^+$ to the system. The uptake of even low concentrations of NH$_4^+$ by phytoplankton is favoured over that of nitrate (NO$_3^-$) although the mechanism for this is not yet understood (Dortch, 1990; Wheeler & Kokkinakis, 1990; Price et al., 1991). Thus, over the long term, a relatively constant residual stock of NO$_3^-$ remains in the mixed-layer. An ecosystem process model developed by Frost (1991; 1993) supports the idea that low chlorophyll and high NO$_3^-$ stocks can be accounted for by grazing control of phytoplankton by microzooplankton and the pattern of nitrogen utilization during the summer.

Although the model developed by Frost (1991; 1993) duplicates typical seasonal conditions in this region, he acknowledges the lack of information on the control of microzooplankton populations. Further, if microzooplankton are the major grazers in this new synthesis of the subarctic Pacific food web, what is the role of copepods? Major subarctic copepods may be responsible for controlling microzooplankton in this region since their consumption of protozoan prey has been documented (Gifford & Dagg, 1991; Gifford, 1993a). Using a series of bottle incubation experiments, Gifford (1993a) showed that the feeding activity of *Neocalanus* C5 is sufficient to control protozoan stocks in the subarctic Pacific at least during spring and early summer, when these copepods are abundant in the mixed-layer. Thus, copepods of the subarctic Pacific are not primary consumers of phytoplankton, but instead are secondary consumers of microzooplankton. The maintenance of high microzooplankton stocks during winter (Boyd et al., *in press* a), necessary to prevent the spring phytoplankton bloom, may be in part due to the absence of large C5 calanoid copepods from the mixed-layer in winter (Boyd et al., *in press* b).
1.1.4 The Life Histories of the Major Subarctic Pacific Copepods

Knowledge of the ecology of the predominant copepod species is vital to understanding the context of research efforts concerning the subarctic Pacific ecosystem. For this reason, the life history of the predominant copepod species from this region, *Neocalanus plumchrus* (Marukawa), *Neocalanus flemingeri* (Miller), *Neocalanus cristatus* (Krøyer), *Eucalanus bungii* (Giesbrecht), and *Metridia pacifica* (Brodsky), are summarized in more detail. LeBrasseur (1965a,b) examines long term zooplankton abundance from the continental shelf to the central Alaskan Gyre, and gives an account of the life history of major copepod species of the subarctic Pacific. For the current study, more recent work by Miller et al. (1984) will serve as the primary reference for life history patterns of endemic subarctic copepods.

In the spring and early summer in the subarctic Pacific, *Neocalanus* feeds in surface waters before it ceases feeding and migrates below a depth of 250 m where its activity is less intense (Miller et al., 1984). Maturation and reproduction of *N. plumchrus* begins almost immediately, and continues until January (Miller et al., 1984). Development of the oil-rich eggs through the sixth naupliar stage occurs within three months during and shortly after the ascent to the surface (Fig. 1.2). The first copepodite stages appear at the surface near the end of October and continue to arrive for three months thereafter (Miller et al., 1984). Surface development from the first through to the fifth copepodite occurs within five months, and virtually all C5s have left the surface by mid August after having spent two or three months grazing in the mixed-layer (Fig. 1.2).

The life history of *N. plumchrus* in the subarctic is in contrast to that in the Strait of Georgia (Fig. 1.2), adjacent to mainland British Columbia, where an apparent\(^1\) diapause

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\(^1\)As French (1988) notes, *N. plumchrus* from the Strait of Georgia do not enter diapause *per se*, but do enter a state of reduced activity. Thus the use of the word diapause is used hereafter to mean such a state.
Figure 1.2: Schematic diagram of *N. plumchrus* life history showing the distribution of stages with respect month and depth. The top panel is for the Strait of Georgia (redrawn from Fulton, 1973) and the bottom panel is for Station P (adapted from Miller *et al.*, 1984).
state is long (July to January), followed by maturation from January to February (Fulton, 1973; French, 1988). Unlike the seven-month reproductive period in the *N. plumchrus* subarctic population, the Strait of Georgia population reproduces in two months, from February to March (Fulton, 1973). Miller *et al.* (1984) postulate that this dissimilarity between regions is due to either a specific or subspecific difference in the two populations or a difference in environmental conditions between the two regions affecting the onset of maturation. Thus, reasons for the development of *N. plumchrus* in the open subarctic Pacific occurring out of phase with *N. plumchrus* near the continental margin (Fulton, 1973; Miller *et al.*, 1984; Miller & Clemons, 1988) are not fully understood.

The recent distinction made between *N. plumchrus* and its congener, *N. flemingeri* (Miller, 1988) does not significantly alter the original interpretation of the life history of *N. plumchrus* in the subarctic Pacific (Miller & Clemons, 1988). Both species follow the same life cycle, but the developmental schedule of *N. flemingeri* is one month ahead of *N. plumchrus*. The development of *N. cristatus* in the subarctic Pacific parallels that of *N. plumchrus* with the exception of the persistence of C5s at the surface until late August (Miller *et al.*, 1984).

Unlike *Neocalanus*, it takes more than a year for *E. bungii* copepodites to develop into mature adults in the subarctic Pacific (Miller *et al.*, 1984). The development includes a few diapause phases and is generally spread out over three years, with maturation of C5s typically occurring at the beginning of the third year. Reproduction occurs in the mixed-layer twice during spring and summer: once in early May, and again in early July. The abundance of late-stage copepodites of this species in the mixed-layer generally does not exceed 20% that of *Neocalanus* (Miller *et al.*, 1984).

In addition to having varied life history strategies, *Neocalanus* and *Eucalanus* do not have the same vertical distribution within the upper water column (Mackas *et al.*, 1993). From a fine-scale vertical distribution study, Mackas *et al.* (1993) showed that *Neocalanus*
and *Eucalanus* form species pairs at different depths, possibly due to food preferences or varying responses to turbulence. *N. plumchrus* and *N. flemingeri* form a near surface pairing while *N. cristatus* and *E. bungii* form a subsurface pairing. Demarcation between these two species pairs is coincident with a weak and transient thermocline, and their distinctive vertical distributions may be set by a response to different intensities in turbulent mixing in the mixed-layer (Mackas *et al.*, 1993). From analyses of gut content, Dagg (1993b) showed that *N. cristatus* may be feeding on aggregated particulate material, and that this copepod's abundance is greatest just beneath the surface mixed-layer, where the flux of particulate material is greatest. The *plumchrus-flemingeri* pair, however, feed on the protozoan and phytoplankton populations in the mixed-layer (Gifford, 1993a; Mackas *et al.*, 1993). Thus there appears to be some niche partitioning between these two species pairs.

A one year study of the life history of *M. pacifica* at Station P (Batchelder, 1985; Batchelder & Miller, 1989) revealed that the copepod is a strong vertical migrator, except in the winter when trips to the surface are less frequent. Batchelder (1985) concluded that this winter migration behaviour is akin to 'diapausing' *Neocalanus*. Further, he found that three cohorts were completed over the course of his one year study, suggesting that *Metridia* spawns three times annually in this region. However, the patterns of vertical distribution and the interannual variability in the three overlapping winter months from his study suggests that the life cycle of *Metridia* may be even more complex.

### 1.1.5 Study Objectives

While major zooplankton species of the subarctic Pacific (copepods of the genera *Neocalanus*, *Eucalanus* and *Metridia*) have been studied in oceanic waters, little is known about the transition in species abundance and composition from the North American west coast to the open ocean (Line P, Fig. 1.3), other than the work by LeBrasseur
Figure 1.3: Map of the eastern subarctic Pacific Ocean showing the location of Station P and zooplankton sampling stations along Line P. For the location of all stations along Line P consult Table B.10.
Chapter 1. Distribution and Abundance of Mesozooplankton

(1965a, b). The principal goal of this thesis (Chapter 1) was to investigate the abundance and distribution of the major mesozooplankton species in the subarctic Pacific, as part of the Canadian contribution to the Joint Global Ocean Flux Study (JGOFS) (Calvert et al., 1990).

The second objective of this study (Chapter 2) was to examine and reevaluate the link between nanoplankton, microzooplankton, and mesozooplankton. Previous studies (e.g., Gifford & Dagg, 1991; Gifford, 1993a) have not examined, simultaneously, the grazing by copepods on the various size fractions of autotrophic and heterotrophic nanoplankton in the subarctic Pacific. The goal was thus to quantify these interactions and to characterize the diet of these copepods and their impact on the phytoplankton community.

The third objective was to make an estimate of the amount of fecal material produced by *N. plumchrus* and *N. flemingeri* in the subarctic Pacific (Chapter 2). These estimates are important since sinking fecal pellets can be an important flux of carbon out of the mixed-layer (Honjo & Roman, 1978; Turner & Ferrante, 1979; Urrère & Knauer, 1981; Angel, 1984) and can serve as a source of food for other copepod species living below the mixed-layer (Dagg, 1993b). As such, this estimate will be compared to the amount of organic carbon typically collected in sediment traps at 100 m and to the metabolic requirements of possibly coprophagous copepods.

1.1.6 Study Area

The distribution of zooplankton in the subarctic Pacific is often associated with characteristics of the physical oceanography of the region (Beklemishev, 1957; Wickett, 1967; Marlowe & Miller, 1975; Frost, 1983; Brodeur & Ware, 1992). Thus, it is important to outline the characteristics of the oceanographic domains and basic physical oceanographic features of the region.
Figure 1.4: Map of the subarctic Pacific Ocean showing the extent of domains and current systems at a depth of 125 m (from Favorite et al., 1976). The location of Station P is marked with a star.

The subarctic Pacific region is composed of a number of distinct domains and gyres (Fig. 1.4). Its southern boundary is defined by where the 34 isohaline comes to the surface (Dodimead et al., 1963), however, the latitude of the boundary varies within the Transition Domain (Favorite et al., 1976). Net precipitation over evaporation in the Gulf of Alaska results not only in a salinity less than 34, but also in a permanent halocline between 100–200 m that limits winter mixing to a depth of about 100 m (Dodimead et al., 1963). North of the Transition Domain, the eastward flowing Subarctic Current System bifurcates into north- and south-flowing branches somewhere in the region east of Station P (50°N, 145°W) (Fig. 1.4). The north branch, called the Alaska Current, eventually flows west seaward of the Alaska Peninsula, forming the boundary intensified Alaskan Stream. These flow regimes complete the northern branch of the Alaska Current System and the Alaskan Gyre (Fig. 1.4). The south-flowing branch, called the California
Current is part of the California Current System. Station P is located at the southern limit of the Gulf of Alaska near the bifurcation region, on the edge of the Dilute Domain (Fig. 1.4). This dilute domain extends east to the continental slope region where there is a summer upwelling regime (Fig. 1.4). Because the current systems vary with season and year (Tabata, 1965; 1989), the position of Station P varies relative to flow patterns.

1.2 Materials and Methods

Zooplankton samples were collected on four cruises (March 1993, May 1993, February 1994, and May 1994) at six stations (P4, P12, P16, P18, P23 and P26) along a 1500 km transect (Line P) from southern Vancouver Island to Ocean Station P (Fig. 1.3). Only three of these stations were sampled for zooplankton on each cruise. Nutrient samples were generally taken at five stations along Line P and CTD profiles were usually made at all Line P stations (Table B.10) on each cruise. On the February 1994 cruise, inclement weather prevented the ship from tracking further west than station P23 (Fig. 1.3). Thus station P23 will be referred to as Station P for the February 1994 data. When scheduling of winch use permitted, samples were taken along Line P at night, when the most abundant subarctic zooplankton species were known to be near the surface (Mackas et al., 1993). On the March 1993 cruise, samples were collected during both day and night at Station P to evaluate the extent of diel vertical migration.

1.2.1 Zooplankton Sampling and Preservation

Triplicate samples were taken by vertically hauling a 57 cm (diameter) Scientific Committee on Oceanic Research (SCOR), Working Party No. 2 (WP–2) net (Tranter, 1968) equipped with 293–296 μm mesh and modified (mSCOR) to close when triggered with a messenger (French, 1988) (Fig. 1.5). The net was lowered backwards to a predetermined
Figure 1.5: Schematic of the modified SCOR (WP-2) net used in the present study. The mouth opening of the net is 0.25 m$^{-2}$, the net mesh is 296 μm, and the cod-end mesh is 200 μm.
depth then retrieved vertically at a rate of 1 m·s⁻¹ to the surface or closed at another predetermined depth while still in motion to provide discrete sampling. The net was weighted with a 23 kg pig iron weight to ensure that the wire angle remained as close to the vertical as possible. Although the angle occasionally deviated from 90° due to excessive winds, a best effort was made to maneuver the ship so that the wire angle was maintained at or near the vertical.

The mSCOR net diameter (57 cm) is such that once the thickness of the collar attached to the opening of the net is considered, the mouth of the net has an area of 0.25 m² (Fig. 1.5). Thus the total volume filtered on each cast depends on the depth of the vertical haul and the net filtration efficiency, assuming there is no deviation in wire angle from the vertical and no change in volume flow due to heave on the net. Tranter & Smith (1968) suggest that unencased nets made from modern gauze have an initial filtration efficiency > 85%. Tranter & Heron (1968) note that the probable filtration efficiency of the SCOR net equipped with 200 μm mesh is between 93–94.5%. Because these efficiency estimates are based on test tank experiments, and presumably in the absence of phytoplankton, they do not take into account the effects of clogging. French (1988) estimated the efficiency of the same mSCOR net used in the present study by hauling the net vertically to the surface from a depth of 50 m with a calibrated flowmeter placed midway from the rim to the centre of the net opening. The flowmeter revolutions were compared to identical hauls of the flowmeter without the net assembly. Although French’s (1988) efficiency estimate is 45%, her measurements were made in coastal waters where clogging by phytoplankton is usually more severe than in offshore waters (pers. obs.). For these reasons, an arbitrary filtration efficiency of 85% was chosen for the present study to reflect the high efficiency of the SCOR net but with some consideration to minimal
clogging effects. The volume filtered was thus estimated from the change in depth, using the formula:

\[
\text{Volume filtered (m}^3\text{)} = \Delta \text{depth (m)} \times 0.25 \text{ (m}^2\text{)} \times 0.85. \tag{1.1}
\]

A note should be made on the use of the mSCOR net over other possible zooplankton sampling devices. Severe winter conditions generally precluded the use of multiple net systems such as the MOCNESS (Wiebe et al., 1976), the Tucker trawl (Tucker, 1951; Frost & McCrone, 1974), and the BIONESS (Sameoto et al., 1977). In contrast, the deployment of the smaller mSCOR net was possible even in the most inclement weather. The mSCOR net was utilized throughout this study, including in calm late spring weather, in order to have a consistent method of sample collection. A serious effort was made to test a newly constructed modified Tucker trawl, which proved unsatisfactory even in calm weather.

The time and location of various samples taken with the mSCOR net are given in Table 1.1. Sampling depths indicated in Table 1.1 for Station P were chosen to include the mixed-layer and the deepest depth possible, given weather conditions, time constraints, and wire-length limitations. Strata below the mixed-layer were divided so that each was filtered in approximately equal proportions. Sampling depth along Line P was arbitrarily set at 100 m to include late spring and winter mixed-layer zooplankton. Samples from Station P were categorized as day samples when they were taken at least half an hour after dawn or half an hour before dusk. Samples were considered ‘night samples’ when they were taken at least half an hour after dusk or half an hour before dawn.

1.2.2 Zooplankton Enumeration and Abundance Calculations

Immediately after being collected, specimens were preserved in 1 L glass jars, with a 3–5% formalin-seawater solution buffered with sodium-tetra-borate (Parsons et al., 1984a).
Table 1.1: The time, location and depth of mesozooplankton sampling. Each depth stratum was sampled in triplicate using a 296 μm mesh modified SCOR net (see text for details). The upper stratum sampled at Station P was always from the surface to about the top of the mixed-layer. Note that in the text, Station P refers to station P23 and P26.

<table>
<thead>
<tr>
<th>Date</th>
<th>Pacific Standard Time</th>
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</tr>
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</tr>
<tr>
<td>10 March 1993</td>
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<td>16</td>
<td>0–100</td>
</tr>
<tr>
<td>14 March 1993</td>
<td>01:00–03:26</td>
<td>26</td>
<td>0–100</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>100–200</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>200–500</td>
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<tr>
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<td>26</td>
<td>0–100</td>
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<td></td>
<td>100–200</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>200–500</td>
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<tr>
<td>15 May 1993</td>
<td>20:50–21:20</td>
<td>4</td>
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<tr>
<td>17 May 1993</td>
<td>06:30–06:50</td>
<td>12</td>
<td>0–100</td>
</tr>
<tr>
<td>18 May 1993</td>
<td>05:10–05:30</td>
<td>16</td>
<td>0–100</td>
</tr>
<tr>
<td>21 May 1993</td>
<td>20:30–22:15</td>
<td>26</td>
<td>0–50</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>50–150</td>
</tr>
<tr>
<td></td>
<td></td>
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<td>23 May 1993</td>
<td>23:40–00:48</td>
<td>26</td>
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</tr>
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<td></td>
<td></td>
<td></td>
<td>150–300</td>
</tr>
<tr>
<td>08 February 1994</td>
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<td>4</td>
<td>0–100</td>
</tr>
<tr>
<td>15 February 1994</td>
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<td>0–100</td>
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<td>75–240</td>
</tr>
</tbody>
</table>
Preserved specimens were enumerated within six months of their collection using a stereo microscope. Individual species were enumerated separately, as were a number of copepod life stages. Because the length of the diagonal in the 296 μm mesh of the mSCOR net was greater than the maximum cephalosome width of many early life stages, small and young copepods may have been extruded from the sampling gear (Smith et al., 1968). Miller et al. (1984) found that a 333 μm (471 μm diagonal) mesh net could underestimate early copepodite stages of *N. plumchrus*, compared to a 73 μm (103 μm diagonal) mesh net. To minimize bias due to extrusion in this study, most copepod species were separated into groups consisting of partially extrusible copepodite stages C1 to C4, non-extrusible C5s and adults. These group divisions varied according to copepodite size classes.

Copepods were keyed according to descriptions in Gardner & Szabo (1982) and Brodsky (1950); *Neocalanus plumchrus* and *Neocalanus flemingeri* were distinguished using descriptions given by Miller (1988). Chaetognaths and amphipods were keyed to species using descriptions from Fraser (1957), Bowman (1960), and Bowman & Gruner (1973), however no life stage distinctions were made. The genus *Metridia* was not identified to species because, although the majority of *Metridia* in the subarctic Pacific are *M. pacifica* (Raymont, 1983), there are several similar species of *Metridia* in this region (Brodsky, 1950). Salps were identified from drawings by Fraser (1947). When the abundance of individual zooplankton species was greater than 100 per sample, subsamples were made using a modified Motoda plankton splitting box (model 20) (Motoda, 1959). When adult abundance was less than 100 per sample, no subsampling was done and all individuals in the sample were counted. The scarcity of some species precluded any attempts at estimating abundance and were therefore not enumerated.

Volumetric abundance was calculated for each species by dividing the filtered volume (m³) into the zooplankton net count. The distance traveled by the net in each stratum and the respective volumetric abundance for the stratum were multiplied to give integrated
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abundance. The integrated abundance of all strata for a profile was weighted according to the vertical distance sampled and summed to give a single integrated abundance value.

1.2.3 Mesozooplankton Carbon Conversions

The carbon content of copepods was estimated from the percentage of dry weight of preserved specimens \( n > 3 \) corrected for the effects of formalin preservation using the empirical relationship (Giguère et al., 1989):

\[
\ln(\% \text{ Dry weight loss}) = 4.149 - 0.576 \times \text{Length}^{0.333},
\]

where length is in millimeters. Because the size range for the regression equation (Eq. 1.2) is only from 200 \( \mu \text{m} \) to 18.5 mm (Giguère et al., 1989), it could not be applied to smaller copepod life stages. Thus, the appropriateness of the relationship was first determined by measuring the length of randomly selected copepods (Neocalanus spp., Eucalanus bungii, and Metridia spp.) using an in-house (UBC) electronic measuring device.

Estimates of copepod carbon from corrected dry weight were made using conversion factors after Omori (1969) and Miller (1993b). Carbon content of small cyclopoid Oithona spp., was assumed to be 0.2 \( \mu \text{g C-ind}^{-1} \) (González & Smetacek, 1994). Total zooplankton carbon biomass, excluding salps, was estimated from wet weight measurements converted to carbon using the conversion factor (8.3 mg wet weight = 1 mg C) given by Raymont (1983) for mixed zooplankton. The proportional contribution of selected species to the total zooplankton biomass in the shallowest strata sampled (Table 1.1) was calculated by comparing the individual contributions of each species to the total zooplankton carbon biomass. The biomass of Oithona spp. was not determined since it was not enumerated in all samples. The unaccounted biomass was categorized as ‘other.’
1.2.4 Physical and Chemical Data

Physical data were provided by the Institute of Ocean Sciences (Sidney, B.C.). Vertical profiles of conductivity, temperature and depth (CTD) were obtained using shipboard-data Guildline digital CTDs (models 8737 and 8705). A CTD failure occurred on the May 1993 cruise, and a Sea Bird CTD with a transmissometer was used. Temperature and salinity were used to derive $\sigma_t$ from an in-house BASIC computer program (UBC). Mixed-layer depth was identified as the depth where a 0.125 decrease in $\sigma_t$ first occurred, relative to a surface reference value (after Levitus, 1982).

Ammonium and nitrate data for the upper water column were provided by D. Varela (UBC). Water samples were collected by means of a clean 30 L Go-Flo bottle on a Kevlar wire and a shipboard Technicon AutoAnalyzer was used to measure $\text{NH}_4^+$ (Slawyk & Macisaac, 1972) and $\text{NO}_3^-$ (Wood et al., 1967).

1.2.5 Statistical Analyses

The effects of sampling year were examined using a one factor (cruise) ANOVA with standardized counts of zooplankton in the mixed-layer as the dependent variable (Zar, 1984). An a posteriori Tukey test was used to determine where the differences in mean abundance were located among the four cruises. When abundance of individuals was equal to zero during winter cruises, Student’s $t$-tests were used to compare mean abundance estimates between late spring cruises. Mean and variability are reported in the text as $\bar{X} \pm \text{SE}$.

The vertical profiles made at night and during the day on the March 1993 cruise at Station P were used to evaluate vertical migration out of the mixed-layer. Two-way ANOVAs on abundance, with depth and time (day or night) as factors, were used to assess possible effects of time on the vertical distribution of zooplankton species.
The vertical plankton hauls taken on two consecutive nights during the May 1993 cruise at Station P were used to evaluate the reproducibility of zooplankton abundance estimates. Effects of sampling night, depth and species on zooplankton abundance were examined using a three factor (depth, night and species) ANOVA with standardized counts as the dependent variable.

Spearman rank correlations were used to determine the co-occurrence of mesozooplankton species on all cruises and at all stations and depths. The experiment-wise error rate for all correlations was maintained at $\alpha = 0.05$ by using the sequential Bonferroni method (Rice, 1989; Chandler, 1995). Stepwise multiple linear regression analysis was done using total zooplankton biomass as the dependent variable regressed with environmental parameters. The purpose of this analysis was to determine which factors were associated with changes in biomass of zooplankton, including: salinity, NO$_3^-$ and NH$_4^+$ concentrations. Where other statistical analyses were performed, they are specified in the text. It is important to acknowledge the fact that the relatively low sample size used in most analyses resulted in low statistical power (usually $\beta > 0.50$), especially when tests failed to reject the null hypothesis.

The analyses of the data were made using SAS (SAS Institute Inc., 1985) and SigmaStat (Jandell Scientific, 1992) statistical software, as well as with programs written in BASIC.

1.3 Results

1.3.1 Physical Data

The depth of the mixed-layer deepened from the coast seaward to Station P during the March 1993 (Figs. 1.6a, b, c, 1.9a) and February 1994 (Figs. 1.7a, b, c, 1.9b) cruises. In
May 1994, the mixed-layer was shallow from stations P1 to P9 (10–40 m) then deepened to an average depth of 65 m from Stations P10 to P26 (1.8a, b, c, 1.9c).

On all cruises, the average mixed-layer temperature was greatest between stations P1 and P4, and lowest at Station P. The mean temperature in the mixed-layer at Station P was, 5.71°C, 7.29°C, and 7.61°C during the March 1993, February 1994 (station P23) and May 1994 cruises, respectively (Fig. 1.10). Because of the CTD failure during the May 1993 cruise, only surface temperature determined from a Sea Bird profiler could be compared to CTD-measured surface temperatures from the other cruises. Surface temperature was lower from station P4 to P16 in May 1993 compared to mean mixed-layer temperature in May 1994. From station P20 to Station P, the surface temperature in May 1993 was greater than or equal to the mean mixed-layer temperature in May 1994 surface temperature. The surface temperature at Station P during the May 1993 cruise was 7.8°C, compared to mean mixed-layer temperatures of 5.79°C, 7.3°C, and 7.61°C for March 1993, February 1994, and May 1994, respectively. The May 1993, and 1994, temperatures were typical for late May, before intensification of the thermocline and usual shoaling of the mixed-layer to a depth of 25–50 m starting in July (Miller et al., 1984).

Average mixed-layer salinity was always at a minimum between stations P1 and P4. A slight surface discontinuity in salinity appeared between station P16 and P17 in March 1993 (Fig. 1.6b). This was accompanied with a discontinuity in $\sigma_t$ at station P19 (Fig. 1.6c). A similar discontinuity in salinity was observed in February 1994, but further shoreward, at station P14 (Fig. 1.7b). In May 1994, a distinct freshwater layer appeared to extend from the coast seaward to station P8 (Figs. 1.8b, c, 1.10). This feature was also reflected in the shallow mixed-layer depth between these stations ($\bar{Z} = 18$ m). A similar feature was not detected in the May 1993 surface salinity data obtained from the Sea Bird profiler. However, only a single data point exists between stations P1 and P11.
1.3.2 Nutrients

At Station P, the average mixed-layer NH$_4^+$ concentration was greatest during the two winter cruises (0.30 and 0.56 mg-atoms·m$^{-3}$ for March and February cruises, respectively). May 1993 and 1994 concentrations were 0.28 and 0.22 mg-atoms·m$^{-3}$ respectively. Mixed-layer concentrations along Line P ranged from 0.21 to 0.66 mg-atoms·m$^{-3}$ with no discernible trend seaward from the coast.

Nitrate concentrations generally increased from the coast (station P4) (0.22–0.41 mg-atoms·m$^{-3}$) seaward to Station P (0.92–1.20 mg-atoms·m$^{-3}$) on all cruises.

1.3.3 Mesozooplankton Distribution

The results of mesozooplankton counts are described in a series of graphs summarizing the changes in mean abundance ($\bar{X}±SE$) in the upper water column at the different stations sampled along Line P during the four cruises (see Table 1.1 for detailed sampling depths and locations). The bar graphs presented for selected species at Station P are meant to illustrate depth distributions, day and night differences in abundance (for March 1993 cruise only) and nightly variability (for May 1993 cruise only). The lengths of bars are means ($\bar{X}$) and error bars are one standard error of the mean ($±SE$). Graphs for the 1993 data include three depth strata, whereas graphs for February 1994 have only one stratum and those of May 1994 have two strata. Note that graphs that are without bars are included for consistency, but represent the absence of zooplankton (e.g., Fig. 1.11: *N. plumchrus* and *N. flemingeri* C5 in March 1993, and February 1994). Although not central to this thesis, data on the depth distribution of other species examined are presented in a series of graphs in Appendix A. All species examined in this study are listed in Table 1.2.
Figure 1.6: A) temperature (°C), B) salinity and C) $\sigma_t$ contour plots for stations along Line P during March 1993. The black silhouette on the left of each graph represents the coastline.
Figure 1.7: A) temperature (°C), B) salinity and C) $\sigma_t$ contour plots for stations along Line P during February 1994. Blank spaces in the graphs indicate no data for those stations. The black silhouette on the left of each graph represents the coastline.
Figure 1.8: A) temperature (°C), B) salinity and C) $\sigma_t$ contour plots for stations along Line P during May 1994. The black silhouette on the left of each graph represents the coastline.
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Figure 1.9: Calculated mixed-layer depth at all stations along Line P during the A) March 1993, B) February 1994, and C) May 1994 cruises.
Figure 1.10: Average temperature and salinity in the mixed-layer along Line P. May 1993 data are near surface values.
Table 1.2: List of all species enumerated in this study.

<table>
<thead>
<tr>
<th>Group</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Copepods</td>
<td><em>Neocalanus plumchrus</em> Marukawa</td>
</tr>
<tr>
<td></td>
<td><em>Neocalanus flemingeri</em> Miller</td>
</tr>
<tr>
<td></td>
<td><em>Neocalanus cristatus</em> Krøyer</td>
</tr>
<tr>
<td></td>
<td><em>Eucalanus bungii</em> Giesbrecht</td>
</tr>
<tr>
<td></td>
<td><em>Metridia</em> spp.</td>
</tr>
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<td></td>
<td>mostly <em>M. pacifica</em> Brodsky and <em>M. lucens</em> Boeck</td>
</tr>
<tr>
<td></td>
<td><em>Pleuromamma scutullata</em> Brodsky</td>
</tr>
<tr>
<td></td>
<td><em>Oithona</em> spp.</td>
</tr>
<tr>
<td></td>
<td>mostly <em>O. spinirostris</em> Claus and <em>O. similis</em> Claus</td>
</tr>
<tr>
<td>Chaetognaths</td>
<td><em>Eukronia hamata</em> Möbias</td>
</tr>
<tr>
<td></td>
<td><em>Sagitta elegans</em> Verrill</td>
</tr>
<tr>
<td></td>
<td><em>Sagitta scrippsaе</em> Alvariño</td>
</tr>
<tr>
<td></td>
<td><em>Sagitta zetesios</em> Fowler</td>
</tr>
<tr>
<td>Amphipods</td>
<td><em>Parathemisto pacifica</em> Boeck</td>
</tr>
<tr>
<td>Salps</td>
<td><em>Salpa</em> spp.</td>
</tr>
<tr>
<td></td>
<td>mostly <em>S. fusiformis</em> Cuvier and <em>S. maxima</em> Forskal</td>
</tr>
</tbody>
</table>
Copepods

*Neocalanus* spp.

Although *Neocalanus* spp. C1–4 were always present in the water column, *Neocalanus* spp. C5 stages were usually absent from net samples at Station P during the winter cruises (March 1993: 0–500 m, Feb. 1994: 0–100 m). Late spring abundance of *Neocalanus* spp. was typical for this time of year (Dagg, 1993a; Miller, 1993b), and agrees with the general understanding of the life history strategies of these species (Miller *et al.*, 1984; Miller & Clemons, 1988). Whenever multiple strata were sampled, copepodites of *Neocalanus* spp. were always the most abundant in the mixed-layer (Figs. 1.11, 1.12, 1.13). Mixed-layer abundance was greater for both *N. plumchrus* C5 (*t*-test: $P < 0.01$) and *N. flemingeri* C5 (*t*-test: $P < 0.01$) (see Table 1.3) in May 1994 compared to May 1993 (Table 1.4).

The integrated (0–250 m) abundance at Station P during late spring cruises was higher in 1994 for all *Neocalanus* spp. C5, and lower for *Neocalanus* spp. C1–4 compared to 1993 (Table 1.4). The areal abundance of all copepodites was roughly two-fold greater in May, 1994, compared to May, 1993. Despite considerable variability in *Neocalanus* spp. abundance among stations during the late spring cruises (Fig. 1.14), this trend was also apparent along Line P. The average combined abundance of *N. plumchrus* and *N. flemingeri* C5 was consistently greater along Line P in May 1994 compared to May 1993. The within-station variability along Line P was also consistently greater in May 1994 compared to May 1993 (Fig. 1.14). In contrast, the within-station variability on winter cruises was low because few individuals of *N. plumchrus*, *N. flemingeri* and *N. cristatus* were observed in the 0–100 m samples along Line P (Fig. 1.14).
Figure 1.11: Abundance estimates ($\bar{X} \pm SE$, $n = 3$) of *Neocalanus* spp. C1-4, and the combined abundance of *N. plumchrus* and *N. flemingeri* C5 at Station P during the two winter and summer cruises. The shallowest depth strata was the depth of the mixed layer at the time of sampling. Open bars are day samples, filled bars are night samples, and empty graphs signify abundance estimates of 0. Graphs with two night plots represent samples taken on consecutive nights. See Section 1.3.3 for more details. Note different scales.
Figure 1.12: Abundance estimates ($\bar{X} \pm SE, n = 3$) of *N. plumchrus* and *N. flemingeri* C5 at Station P during the two winter and summer cruises. Filled bars as in Fig. 1.11. Note different scales.
Figure 1.13: Abundance estimates ($\bar{X} \pm SE, n = 3$) of *Neocalanus cristatus* C5 at Station P during the two winter and summer cruises. Filled bars as in Fig. 1.11.
Table 1.3: Average \((n = 3)\) mixed-layer abundance of selected zooplankton species at Station P on all cruises. Mixed layer depth: March 1993 = 100 m, May 1993 = 50 m, February 1994 = 100 m, and May 1994 = 75 m. All units are \(\text{ind}\cdot\text{m}^{-3}\).

<table>
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<tr>
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<td></td>
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<td>May 93</td>
<td>Feb. 94</td>
<td>May 94</td>
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</tr>
<tr>
<td>Neocalanus spp.</td>
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<td></td>
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</tr>
<tr>
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</tr>
<tr>
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<td>18.2</td>
<td>0</td>
<td>41.7</td>
<td></td>
</tr>
<tr>
<td>Neocalanus plumchrus &amp; N. flemingeri</td>
<td>C5</td>
<td>0</td>
<td>44.6</td>
<td>0</td>
<td>120.7</td>
<td></td>
</tr>
<tr>
<td>N. cristatus</td>
<td>C5</td>
<td>0.2</td>
<td>11.9</td>
<td>0</td>
<td>11.9</td>
<td></td>
</tr>
<tr>
<td>Neocalanus spp.</td>
<td>C4</td>
<td>0.3</td>
<td>39.2</td>
<td>0.4</td>
<td>12.1</td>
<td></td>
</tr>
<tr>
<td>E. bungii</td>
<td>FC5-6</td>
<td>0</td>
<td>5.7</td>
<td>0.3</td>
<td>0.1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>MC5-6</td>
<td>0</td>
<td>3.5</td>
<td>0.1</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>C1-4</td>
<td>0.1</td>
<td>0.8</td>
<td>0.6</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Metridia spp.</td>
<td>FC5-6</td>
<td>5.2</td>
<td>23.3</td>
<td>9.2</td>
<td>27.7</td>
<td></td>
</tr>
<tr>
<td></td>
<td>MC5-6</td>
<td>1.9</td>
<td>7.9</td>
<td>34.3</td>
<td>8.9</td>
<td></td>
</tr>
<tr>
<td>Oithona spp.</td>
<td>FC6</td>
<td>62.8</td>
<td>146.2</td>
<td>30.9</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Other zooplankton</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P. pacifica</td>
<td>All</td>
<td>0.4</td>
<td>5.8</td>
<td>0.5</td>
<td>6.7</td>
<td></td>
</tr>
<tr>
<td>E. hamata</td>
<td>All</td>
<td>1.5</td>
<td>19.6</td>
<td>1.1</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>
Table 1.4: Integrated (0–250 m) abundance estimates at Station P for both late spring cruises. Night samples only. The 1993 integration required extrapolation of the 75–240 m sample to 75–250 m, and the 1994 integration required interpolation of the 150–300 m sample to 150–250 m.

<table>
<thead>
<tr>
<th></th>
<th>Number·m$^{-2}$</th>
<th>May 21, 1993</th>
<th>May 20, 1994</th>
</tr>
</thead>
<tbody>
<tr>
<td>N. plumchrus C5</td>
<td>1323</td>
<td>7179</td>
<td></td>
</tr>
<tr>
<td>N. flemingeri C5</td>
<td>919</td>
<td>3162</td>
<td></td>
</tr>
<tr>
<td>N. cristatus C5</td>
<td>665</td>
<td>1004</td>
<td></td>
</tr>
<tr>
<td>Neocalanus spp. C1–4</td>
<td>4365</td>
<td>3576</td>
<td></td>
</tr>
<tr>
<td>Total copepodites</td>
<td>7272</td>
<td>14 921</td>
<td></td>
</tr>
</tbody>
</table>

On both May cruises, the ratio of N. plumchrus to N. flemingeri C5 abundance generally decreased from station P4 to Station P (Table 1.5), indicating that, relative to N. flemingeri, there were more N. plumchrus C5 inshore than at Station P. For all stations, there were consistently more N. plumchrus than N. flemingeri, except at station P16 in May, 1993, where the ratio was about one-to-one (Table 1.5). The ratio could not be calculated for the winter cruises due to the paucity of Neocalanus spp. during March 1993 and February 1994.

The mean weight ($\bar{X}$±SE) of N. plumchrus C5 was 125 ± 7 μg C ($n = 22$) in May 1994 compared to 113 ± 0.4 μg C ($n = 106$) in May 1993. This trend was reversed for N. flemingeri C5, with a weight of 184 ± 4 μg C ($n = 50$) measured in May 1993 compared to 129 ± 9 μg C ($n = 10$) in May 1994. N. cristatus C5 weight was 1080 ± 96 μg C ($n = 10$) in May 1994 compared to 698 ± 43 μg C ($n = 21$) in May 1993. Although these data indicated some interannual variability in copepod weight at Station P, for respective years, individual weight generally increased towards the continental slope for Neocalanus species. For example, in May 1994, N. plumchrus C5 weight increased from Station P (125 ± 7 μg C, $n = 22$) to stations P12–P16 (130 ± 8 μg C, $n = 7$), to a
Figure 1.14: Net abundance estimates (X±SE, n = 3) of *Neocalanus* spp. C1–4, *N. cristatus* C5, and the combined abundance of *N. plumchrus* and *N. flemingeri* C5 in the upper 100 m along Line P during all cruises. May estimates for Station P (P26) represent weighted averages of two strata in the upper 100 m.
Table 1.5: Ratio of *N. plumchrus* (*N.p.*) to *N. flemingeri* (*N.f.*) C5 along Line P during the two late spring cruises.

<table>
<thead>
<tr>
<th>Cruise</th>
<th>Depth (m)</th>
<th>Station</th>
<th><em>N.p./N.f.</em> Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>May 1993</td>
<td>0–100</td>
<td>4</td>
<td>4.3</td>
</tr>
<tr>
<td></td>
<td>0–100</td>
<td>12</td>
<td>2.9</td>
</tr>
<tr>
<td></td>
<td>0–100</td>
<td>16</td>
<td>0.9</td>
</tr>
<tr>
<td></td>
<td>0–50</td>
<td>26</td>
<td>1.4</td>
</tr>
<tr>
<td>May 1994</td>
<td>0–100</td>
<td>4</td>
<td>273.8</td>
</tr>
<tr>
<td></td>
<td>0–100</td>
<td>12</td>
<td>54.5</td>
</tr>
<tr>
<td></td>
<td>0–75</td>
<td>26</td>
<td>1.9</td>
</tr>
</tbody>
</table>

maximum weight of 193 ± 24 μg C (*n = 6*) at station P4 that was significantly different than the weight at Station P (*t*-test: *P* < 0.01).

The low winter abundance of *N. cristatus* C5 was also in contrast with relatively high late spring abundance, although their numbers were often one order of magnitude less than that of the combined *N. plumchrus* and *N. flemingeri* C5 abundance (Fig. 1.14). Unlike *N. plumchrus* and *N. flemingeri* however, there was no detectable difference in average mixed-layer abundance of *N. cristatus* C5 at Station P between May 1993 and May 1994 cruises (*t*-test: *P* > 0.05) (Fig. 1.13). The mean *N. cristatus* C5 abundance in the upper water column along Line P was similar among May cruises, and low (*X < 14 ind·m⁻³*) in comparison to *N. plumchrus* and *N. flemingeri* (Table 1.3).

*Eucalanus bungii*

At Station P, *E. bungii* C1–4 were always present in the upper 500 m of the water column, however, their abundance never exceeded 3 ind·m⁻³ and their average mixed-layer abundance (Table 1.3) did not differ significantly among cruises (ANOVA: *P* > 0.05). Although C5 and adult males and females of *E. bungii* were also present at Station
P during all cruises (Table 1.3), their mixed-layer abundance was significantly greater during the May 1993 cruise (ANOVAs: $P < 0.05$, Tukey tests: $P < 0.05$). Although this significant difference was detected, neither the mean abundance of males nor females ever exceeded 9 ind.m$^{-3}$.

Although the pattern of low abundance of C1–4 was generally repeated along Line P, there was an increase in abundance to about 9 ind.m$^{-3}$ at station P12 in May 1994 (Fig. 1.15). Adult male and female, and C5 stage abundance remained low ($\bar{X} < 2$ ind.m$^{-3}$) at all stations along Line P during all cruises, with the exception of a small increase at Station P in May 1993 (Fig. 1.15). This low abundance of *E. bungii*, especially in winter, is similar to that observed in the upper 250 m by Miller *et al.* (1984) during their study of the life history of this species.

Metridia spp.

Unlike *Neocalanus* and *Eucalanus*, *Metridia* spp. were relatively abundant at Station P and along Line P during both winter and late spring cruises (Fig. 1.16).

Stages C1–4 of *Metridia* spp. were not always concentrated in the mixed-layer at Station P, and the maximum mean abundance occurred during the May 1993 cruise at the depth stratum (50–150 m) immediately below the thermocline ($55.2 \pm 16.5$ ind.m$^{-3}$) (Appendix A). In contrast to young copepodites, the greatest number of C5 and adult females always occurred in the mixed-layer at Station P (Table 1.1). Although the lowest observed number of C5 and adults in the mixed-layer was during the March 1993 cruise (ANOVA: $P < 0.01$, Tukey test: $P < 0.05$), the number of C5 and adult females was fairly constant during the two late spring, and two winter cruises, respectively (Table 1.3). The ratio of females-to-males (C5 and adult) in the mixed-layer was close to 3:1 for both May cruises, but varied between 0.3 and 2.7 for the February and March cruises, respectively. Batchelder (1985) also found a female to male ratio close to 3:1 during the
Figure 1.15: Net abundance estimates ($\bar{X} \pm \text{SE}, n = 3$) of *Eucalanus bungii* in the upper 100 m along Line P during all cruises. May estimates for Station P (P26) represent weighted averages of two strata in the upper 100 m.
month of May, although his February and March ratios are both closer to 6:1. These differences in ratios, as well as highly variable winter male abundance could be due in part to the mis-identification of C4 and C5 stages in the present study.

Along Line P, the mean number of *Metridia* spp. C1–4 was below 5 ind·m$^{-3}$, except at station P23 during the February 1994 cruise, where mean abundance increased to 21 ind·m$^{-3}$ (Fig. 1.16). This increase was matched by an even greater number of C5 and adult males (Fig. 1.16). Moreover, combined C5 and adult male abundance matched more closely the abundance of C1–4 stages along Line P during all four cruises than did the combined C5 and female *Metridia* abundance. Again, these similar trends in male and C1–4 stage abundances could be due, in part, to the possible misidentification of C4s as C5s.

*Oithona* spp.

Because the absolute abundance of the small cyclopoid copepod, *Oithona*, was probably seriously underestimated due to extrusion from the net, only counts at Station P were made. Extrusion from nets has been reported to occur when the maximum cephalosome dimension is smaller than the diagonal of the mesh opening (Miller *et al.*, 1984), as is the case for *Oithona* sampled with a 296 μm mesh net. A single day and night profile from March, 1993, is included (Fig. 1.17) to show the depth distribution of the species at that time. *Oithona* abundance was low in samples deeper than 200 m, and its abundance was greatest in the mixed-layer during both day and night profiles.

Mixed-layer abundance of *Oithona* spp. was among the most variable of all copepod species (Table 1.3). The average abundance in the mixed-layer was 63 ind·m$^{-3}$ in March, 1993 (Fig. 1.17), and half that in February, 1994. Late spring abundance was even more variable. May 1993 had the highest average mixed-layer abundance of *Oithona* spp.,
Figure 1.16: Net abundance estimates ($\bar{X} \pm SE, n = 3$) of *Metridia* spp. in the upper 100 m along Line P during all cruises. May estimates for Station P (P26) represent weighted averages of two strata in the upper 100 m.
Figure 1.17: Abundance estimates ($\bar{X} \pm SE, n = 3$) of *Oithona* spp. C1–6 at Station P during the March 1993 cruise. Filled bars as in Fig. 1.11.

whereas the May 1994 abundance was negligible (Table 1.3). The numerical abundance of *Oithona* spp. was generally lower in samples taken at station P4 compared to Station P (pers. obs.).

Non-Copepod Species

*Eukronia hamata* and *Sagitta elegans*

The predominant chaetognath species in most net samples was *E. hamata*. Samples from the mixed-layer at Station P (0–50 m) during the May 1993 cruise had the greatest mean abundance of *Eukronia hamata*, whereas the lowest mean abundance occurred during the May 1994 cruise (Table 1.3). However, *E. hamata* abundance was not always greater in the mixed-layer. For example, although mixed-layer abundance was low in May 1994, *E. hamata* appeared to be distributed below the mixed-layer on the day of sampling. Thus, it is difficult to evaluate the abundance of this species since it may be distributed well below the strata considered in this study (per Sullivan, 1980).
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The greatest abundance of *Sagitta elegans* also occurred in the mixed-layer during the May 1993 cruise. Although the abundance of this species at Station P was usually an order of magnitude less than that of *E. hamata*, its abundance was always greatest in the shallowest strata of water sampled (Appendix A). Along Line P, a similar trend was observed; when *E. hamata* was present in the upper water column (0–100 m) its abundance was generally greater than that of *S. elegans* (Fig. 1.18).

One of the most striking characteristics of chaetognath abundance, particularly *E. hamata*, was strong association with its prey, the small cyclopoid *Oithona*, at Station P. A Pearson correlation analysis detected a strong association between these species in the mixed-layer at Station P \((r = 0.81, P < 0.005)\). Sullivan (1980) showed by gut content analysis of chaetognaths from Station P, that their dietary intake comprises between 31% and 86% *Oithona* and another small cyclopoid, *Oncaea*. She suggests that the development of larval chaetognaths is tied to the abundance of these small copepod species.

In addition to the two predominant chaetognath species, a few individuals of *S. scrippsae* and *S. zetesios* were counted in deep (150–500 m) Station P samples from May 1993. Because of their low abundance in the samples, the distribution of these species will not be discussed further.

*Parathemisto pacifica*

Where multiple strata were sampled at Station P, mean abundance of this amphipod was always greatest in the mixed-layer (Appendix A). Here, mean abundance was significantly different among the four cruises (Kruskal-Wallis test: \(P < 0.05\)). Samples from the two May cruises generally contained greater numbers of *P. pacifica* compared to winter samples, however, mean abundance never exceeded 7 ind·m\(^{-3}\) in the mixed-layer (Table 1.3).
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Figure 1.18: Net abundance estimates ($\bar{X} \pm SE, n = 3$) of *Eukronia hamata* and *Sagitta elegans* (all stages) in the upper 100 m along Line P during all cruises. May estimates for Station P (P26) represent weighted averages of two strata in the upper 100 m.
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Parathemisto pacifica all stages

Figure 1.19: Net abundance estimates (X±SE, n = 3) of Parathemisto pacifica in the upper 100 m along Line P during all cruises. May estimates for Station P (P26) represent weighted averages of two strata in the upper 100 m.

This trend of higher late spring abundance compared to February and March abundance at Station P, was similar at all stations along Line P (Fig. 1.19). Maximum abundance occurred at station P4 in May 1994 (17.1 ± 7.7 ind·m⁻³). Although March 1993 and February 1994 samples had few individuals of P. pacifica, these were always present in low absolute numbers in the upper water column (z < 100 m) (Fig. 1.19).

Salps

Salps were absent in net samples from both 1994 cruises. In March 1993, salp abundance was relatively low, with the maximum at station P4 (3.0±2.3 ind·m⁻³), and an abundance of 1.5 ± 1.5 ind·m⁻³ at station P20, the last station where salps were observed in the upper 100 m (Fig. 1.20). In May 1993, salp numbers increased seaward from station P4 (1.2 ± 0.6 ind·m⁻³) to station P16 (32.1 ± 7.4 ind·m⁻³) (Fig. 1.20), but were rarely seen beyond station P16 (Fig. 1.20). Although the last stations sampled were P16 and P12...
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Figure 1.20: Net abundance estimates ($\bar{X}$±SE, $n = 3$) of salps (solitary and colonial forms) in the upper 100 m along Line P during all cruises. May estimates for Station P (P26) represent weighted averages of two strata in the upper 100 m.

(in May 1993 and 1994, respectively), few salps were sighted at the surface past station P20 on either of these cruises. All collected salps were members of the genus Salpa.

1.3.4 Diel Vertical Migration and Nightly Variability

Diel vertical migration into and out of the mixed-layer was not detected amongst any species present in net samples from Station P during the March 1993 cruise (ANOVAs: $P > 0.05$). In some cases however, the absence of individuals from surface and slightly deeper waters in the day may be an indication of diel vertical migration into and out of the mixed-layer, albeit not statistically detectable ($E. bungii$ FC5–6, $Metridia$ spp. FC5–6, and $S. elegans$ see Appendix A for depth distributions).

No significant effect of night sampled (first or second night) was detected (ANOVA: $P > 0.05$), suggesting that night-to-night variability was low. Although the estimates of zooplankton abundance may be fairly precise, this does not imply that the estimates were
accurate. Using a computer simulation, Wiebe & Holland (1970) showed that high precision can be achieved without high accuracy. However, the precision in abundance estimates made from night samples taken at Station P during the May 1993 cruise does imply sampling consistency.

1.3.5 Co-occurrence of Species

Within the net samples, certain species were associated with other taxa during all cruises and at all depths. The following correlations were significant at the table-wide significance level of $\alpha = 0.05$. Table-wide refers to the correlation matrix of the abundance of all species and stages considered in this study.

The *N. plumchrus* and *N. flemingeri* C5 group was correlated with *N. cristatus* C5 ($r_s = 0.85$). The presence of the *Neocalanus* spp. C1–4 in the mixed-layer during all cruises associated it with the chaetognath *S. elegans* ($r_s = 0.65$).

The abundance of the *Metridia* spp. C5 and adult male group was correlated with its younger life history stages ($r_s = 0.68$). Similarly, C1–4 of the copepod *Pleuromamma scutullata* were associated with adult female *P. scutullata* ($r_s = 0.80$), and to *Oithona* spp. ($r_s = 0.83$), although the abundance of *P. scutullata* was extremely low and is thus not reported or discussed elsewhere in this study. Males (C5–6) of *E. bungii* were associated with females (C5–6) of *E. bungii* ($r_s = 0.91$).

1.3.6 Zooplankton Biomass

**Station P**

There was a marked decrease in zooplankton biomass in the mixed-layer during the winter cruises compared to late spring estimates (Fig. 1.21). On both late spring cruises, zooplankton biomass was about 50 mg C·m$^{-3}$ in the mixed-layer, or five-fold the winter
biomass. When strata below the thermocline were sampled, zooplankton biomass was about the same during both winter and late spring cruises (Fig. 1.21). For all profiles taken, zooplankton biomass decreased from the mixed-layer down to deeper depths.

**Line P**

Consistent with biomass estimates for Station P, late spring zooplankton biomass along Line P (0–100 m) was greater than winter estimates (Fig. 1.22). May 1994 zooplankton biomass was consistently greater than May 1993 biomass at all stations along Line P
(Fig. 1.22), and paralleled the abundance of *N. plumchrus* and *N. flemingeri* C5 (Fig 1.14). Although Station P biomass was always greater than the most landward station, for respective years this difference was on occasion only slight. In May 1993, the most predominant feature of the Line P biomass distribution was the sudden increase in biomass at station P16. Here, it increased from about 20 to 50 mg C·m$^{-3}$. This increase was not caused by greater numbers of *N. plumchrus* or *N. flemingeri* C5 (Fig. 1.14), and was not associated with a sudden change in salinity or temperature (Fig. 1.10).

The proportional contribution of selected species to the total zooplankton biomass is given for 3 stations for both 1993 (Fig. 1.23) and 1994 (Fig. 1.24) cruises. The zooplankton species considered in this study contributed, on average, 28% and 44% of the total zooplankton carbon biomass, on winter and late spring cruises, respectively (Figs. 1.23, 1.24). *Neocalanus* spp. were consistently important contributors, especially during May cruises, when their contribution reached a maximum of 56% of the total zooplankton biomass at Station P (Fig. 1.24). During February and March cruises, the zooplankton biomass at Station P was predominated by species other than those considered in this study (Figs. 1.23, 1.24).

1.4 Discussion

This chapter documents interannual, seasonal and spatial variability in zooplankton abundance and biomass in the subarctic Pacific Ocean at about 50°N, along a transect from 126°W to Ocean Station P at 145°W. Changes in zooplankton abundance and biomass and the occasional presence of species from southern transition waters may result from ENSO (El Niño/Southern Oscillation) events at the equator and north-south shifts in oceanic boundaries in the subarctic Pacific. However, seasonal coverage of zooplankton data is insufficient to make firm conclusions.
Figure 1.22: Zooplankton biomass along Line P calculated from wet weight measurements. Estimates were made from 0–100 m hauls along Line P and to the thermocline at Station P. 8.3 mg wet weight were assumed to be equivalent to 1 mg C (Raymont, 1983).

1.4.1 Zooplankton Variability at Station P and on Line P

Zooplankton biomass estimates made here reflect in large part the abundance of *Neo-calanus* species, although a number of other zooplankton species (possibly *Calanus* spp.) also appear to be important. The fraction of ‘other’ zooplankton, however, may have been overestimated since the total zooplankton biomass and its components were calculated independently. The total zooplankton biomass was calculated from wet weight measurements of whole samples, whereas the components of the total biomass were calculated from numerical abundance and estimates of specific biomass. The component biomass values were recalculated as a percentage of the total. Thus if the specific biomass estimates are conservative the ‘other’ fraction will be inflated. For these reasons, Fig. 1.23 and Fig. 1.24 should not be interpreted as absolute values of the total zooplankton biomass, but as relative values among cruises.
Figure 1.23: Proportional contribution of selected species to the total zooplankton carbon biomass (excluding salps) in the upper 100 m during 1993 cruises.
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Figure 1.24: Proportional contribution of selected species to the total zooplankton carbon biomass (excluding salps) in the upper 100 m during 1994 cruises. Note station differences.
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The low mixed-layer winter biomass reflects the known overwintering phase of *Neocalanus* species at depth (> 600 m), whereas the higher late spring mixed-layer biomass reflects the spring and summer development of these copepods at the surface (Fig. 1.2) (Miller et al., 1984; Miller & Clemons, 1988). Since the bulk of zooplankton biomass is located in the mixed-layer, as observed in previous studies (McAllister, 1961; Marlowe & Miller, 1975), the seasonal increase in zooplankton biomass is greatest in the mixed-layer and decreases with depth in the upper water column (< 200 m).

The seasonal pattern of zooplankton biomass is similar from Station P (145°W) landward to station P16 (134°40’W), however, east of station P12 (130°40’W) it becomes much more distinct. This variability results not from differences in winter biomass, but from late spring variability, as observed in samples from May cruises. The explanation for more variable late spring biomass east of station P12 may lie in the physical and chemical characteristics of the water column. Although the dilute domain extended beyond Station P on all cruises where salinity data were available (as defined by the 32.6 isohaline, Favorite et al. (1976)), there appears to be another more intense dilute region east of about 130°W. The landward decrease in salinity and shoaling of the mixed-layer indicates that a dilute (> 0.7 lower salinity) surface region extends from the coast to about station P7 (128°10’W) and possibly as far as station P10 (129°40’W). Lower salinity may indicate less intense winter mixing in this region. Increasing NO₃⁻ concentration from station P4 to Station P supports this suggestion since more intense winter mixing near Station P would increase the upward vertical flux of nitrate. However, there may be other explanations for the landward decrease in salinity and increase in NO₃⁻ concentration—such as coastal runoff from the North American west coast.

Using the Sverdrup ‘critical depth’ model, Parsons & LeBrasseur (1968) conclude that the timing of the spring bloom in the eastern subarctic Pacific is predicted in large part from mixed-layer depth. These authors suggest that the spring bloom generally
advances from the coast (in March) to the centre of the Gulf of Alaska (in May), and that increases in zooplankton standing stock coincide with the advent of the spring bloom. Thus, interannual variability in the extent of the dilute region could produce variability in the timing of the spring bloom along Line P. Lower interannual variability in mixed-layer salinity and mixed-layer depth beyond the dilute region could result in a more constant environment and less variability in zooplankton biomass. The single surface salinity value obtained for station P4 in May 1993 is dissimilar to that found in May 1994 at station P4, indicating that salinity at this station was variable. In contrast, salinity measurements taken seaward of station P4 in May 1993 were similar to those taken in May 1994. These findings suggest the possibility that variability in mixed-layer salinity and mixed-layer depth during the spring are in some way responsible for the variability in May zooplankton biomass. However, the lack of physical data from this cruise does not allow for a more detailed analysis of the effects of interannual (May) variability in mixed-layer temperature, salinity and depth on zooplankton biomass.

1.4.2 Timing of *Neocalanus* Development

As noted above, the bulk of the zooplankton biomass reported here is strongly influenced by the abundance of *Neocalanus* species. Thus, it is reasonable to expect that the timing of the spring bloom coincides with the timing of *Neocalanus* development. Indeed, high numbers of *Neocalanus* spp. C1–4 at station P4 in March 1993 suggest that these copepods arrive at the surface near the time of the spring primary productivity increase while their abundance is lower at Station P, presumably because the spring primary productivity increase does not occur there until May. May 1993 numbers suggest that copepodites have already developed to C5 at station P4 and most of these have already migrated to depth. Greater abundance of C5s at Station P compared to station P4 on both May cruises suggests that *Neocalanus* development occurs faster landward of Station P. In
addition, *Neocalanus* weight measurements indicate that copepods are heavier at station P4 than at Station P, for May 1993 and 1994 cruises, suggesting faster or earlier development of these copepods at Station P4. Thus the developmental timing of *Neocalanus* spp. along Line P may be linked to the seasonal timing of the spring phytoplankton bloom.

From an extensive study of life history, Miller *et al.* (1984) concluded that *N. plumchrus* mature almost immediately after reaching their diapausing depth, where reproduction soon commences. The life history strategy of this copepod is different near the coast where over half a year is spent at depth before spawning in February or early March (Fulton, 1973). The mechanism that triggers maturation and spawning is not known, although it may be linked to the timing of the spring bloom (Fig. 1.25). Sedimenting live and dead phytoplankton cells are known to trigger egg release and spawning in some benthic invertebrates (Starr *et al.*, 1990; Starr *et al.*, 1994) suggesting the possibility of a similar mechanism in overwintering copepods. The timing of increased primary production and of copepod abundance in the Strait of Georgia are consistent with such a mechanism. Typically, there is a marked increase in primary production in February and a large increase in mixed-layer *Neocalanus* biomass in March (Parsons *et al.*, 1970). By the time *Neocalanus* has developed to stage C5, the production of phytoplankton is at its greatest (Fulton, 1973).

In the subarctic Pacific, this mechanism could also occur because Miller *et al.* (1984) note that *N. plumchrus* C5 begin to mature (molt to C6) in late June, and begin to spawn at depth in July. Spawning thus coincides with the small July 'bloom' in diatoms (6000 cells·L⁻¹: Clemons & Miller, 1984). From sediment trap (near Bermuda) analyses, Asper *et al.* (1992) show that after the onset of the spring phytoplankton bloom it takes only a few days for a particle flux signal to reach a depth of 500 m, the depth of diapausing *Neocalanus* spp. C5. This coupling between the small diatom 'bloom' and copepod spawning would allow C5s to be most abundant in late spring (Miller *et al.*, 1984) of the
Figure 1.25: Illustration of a possible mechanism for the timing of *N. plumchrus* development at Station P in the subarctic Pacific. Sinking cells from a small bloom (6000 cells-L\(^{-1}\)) of large diatoms in July trigger spawning in *Neocalanus*. Integrated (0–50 m) primary productivity values (1960–1966) are those of McAllister (1969) taken from Parsons & Lalli (1988). Monthly averages of copepod biomass (0–150 m) were calculated from LeBrasseur (1965a) using the carbon conversion given by Raymont (1983). Mean monthly mixed layer protozoan biomass was averaged from Frost’s (1993) simulated model data. Details of the timing of life history events of *N. plumchrus* were taken from Miller et al. (1984). Note that the above mechanism is for the earliest spawning schedule and that spawning is known to continue into winter. See text for details.
following year, when protozoan prey (Gifford & Dagg, 1991; Gifford, 1993a) production is also at its highest (Frost, 1993). Although a similar mechanism may exist in the Strait of Georgia and the subarctic Pacific, the result may be quite different. In the Strait of Georgia, *Neocalanus* in the mixed-layer would utilize phytoplankton as a food source, whereas in the subarctic Pacific, the source of nutrition might come from protozoan prey. Such a mechanism would allow a species to respond to different environmental conditions (temperature changes, intensity of winter mixing ...) by ensuring that its developmental timing is synchronized with the production of its food supply. These possibilities should be evaluated both in the laboratory and in the field, especially in a coastal environment where sampling can be done more frequently to ascertain the timing of both the phytoplankton spring bloom and the spawning of copepods. Attempts could be made to induce spawning or egg release in the laboratory using typical levels (as found in sediment traps) of degraded phytoplankton cells. There are other possible explanations for the difference in developmental schedule between coastal and oceanic *Neocalanus* populations. As Miller *et al.* (1984) noted, this difference could be due to subspecific differences between these populations. If this is the case, there may even be a cline along Line P in genetic traits linked to developmental timing.

1.4.3 Other copepods and Chaetognaths

Other large calanoid copepods did not show a seasonal pattern so clear as that of *Neocalanus* in the upper 100 m. The low May abundance and the general absence of *E. bungii* in the upper 100 m observed in winter along Line P is consistent with their pattern of development. Miller *et al.* (1984) observed adult and C5 *E. bungii* below 100 m from August until the end of March and in low numbers in the upper 100 m from April until the end of July. At Station P, the maximum numerical abundance of C5 and adult stages
was never more than 20% that of \textit{N. plumchrus} and \textit{N. flemingeri} C5, similar to the average proportion reported by Miller \textit{et al.} (1984). In May 1994, \textit{E. bungii} was virtually absent from the mixed-layer at Station P, suggesting some interannual variability in the timing of \textit{E. bungii} development. This variability, however, does not have an appreciable effect on the total zooplankton biomass in the mixed-layer.

Adult and C5 stage females of \textit{Metridia} spp. showed seasonality in numerical abundance at Station P, although this was less clear along Line P. Combined adult and C5 female numbers of \textit{Metridia} were greater than those of males in May at Station P. This is consistent with Batchelder's (1985) observations that, although male and female C5s are equally abundant in the upper 100 m in May, adults are not. Adult females are present at the surface during all months except November and December, whereas males are found almost exclusively between 250 and 1000 m throughout the year (Batchelder, 1985). The presence of high numbers of males during the February 1994 cruise at station P23 (141°40'W) was somewhat unusual, although Batchelder (1985) does document higher numbers of male C5 than female C5 during February. The general abundance pattern of \textit{Metridia} spp. along Line P is not consistent with that of Station P, suggesting that the timing of events in the life cycle of these species at Station P is out of phase with those near the slope region. A similar mechanism to that proposed for \textit{Neocalanus} may also be responsible for these differences. Alternatively, differences in developmental schedules could be caused by interspecific differences in open ocean species and more coastal ones. This has not yet been investigated, although a number of species probably make up what has been previously reported as \textit{M. pacifica} (Thorp, 1980).

Copepods of the species \textit{Oithona} were not significant in terms of total zooplankton biomass, but were occasionally important numerically. \textit{Oithona} numbers were high in May 1993 although this copepod was generally absent in May 1994. The abundance of the chaetognath \textit{S. elegans} at Station P is correlated with that of \textit{Oithona}. Indeed, from
gut content analyses and distribution patterns, Sullivan (1980) determined that *Oithona* comprises 86% of the diet of juvenile *S. elegans*. The correlation observed between *S. elegans* and *Neocalanus* spp. C1–4, additionally suggests that the early copepod life stages may also be a source of food for this chaetognath, although this was not verified by gut content analyses.

If the seasonal abundance of *Oithona* along Line P is similar to that observed at Station P during the four cruises, then *Oithona* numbers could potentially be explained by the presence of salps, since salps are known to produce large fecal pellets (Caron *et al.*, 1989) and *Oithona* is believed to be partially coprophagous (González & Smetacek, 1994). This possible relationship between cyclopoid and salp is partially supported by the high abundance of salps in 1993 and their absence in 1994 in the upper 100 m along Line P. However, the presence of *Oithona* at Station P in May 1993 is certainly not explained by salps because these were never present at that station. Clearly this association needs to be examined further because *Oithona* may be an important link in recycling nutrients at times when salps are abundant. In addition, the presence of salps along Line P could have an important impact on the ecology of the subarctic Pacific.

### 1.4.4 Distribution of Salps

Salps are indiscriminate filter feeders (Madin, 1974; Alldredge & Madin, 1982; Kremer & Madin, 1992) capable of responding quickly to short-lived phytoplankton blooms (Deibel, 1985) and of filtering particles as small as 1 μm (nominal diameter) in size (Harbison & McAllister, 1979). In 1984, the SUPER Group observed large numbers of aggregate and solitary zooids of the salp *Cyclosalpa bakeri* at Station P (Miller, 1993a). Using SCUBA, Purcell & Madin (1991) evaluated feeding behaviour of this salp in the late summer of 1987 and 1988, and concluded that the organism makes a nightly ascent to the surface—not to feed, but to facilitate the exchange of sperm at a thin surface layer. The presence
of *Cyclosalpa* at Station P in September 1984, and in late summer of 1987 and 1988 (Purcell & Madin, 1991; Madin & Purcell, 1992; Miller, 1993a) coincides with negative sea surface temperature (SST) anomalies (−1.5°C to −1°C) at the time of that study.² This is not surprising, because as Madin & Purcell (1992) note, *Cyclosalpa bakeri* occurs mainly in cold waters of the Pacific. In contrast, salps observed in 1993 (*Salpa* spp.) are associated with SST anomaly patterns characteristic of El Niño conditions in the North Pacific. The North American west coast had positive SST anomalies in March and May 1993 and in February and May 1994, whereas the central North Pacific registered negative SST anomalies during these months. The positive SST anomalies registered along the coast appear to lag SST anomalies in the equatorial Pacific³ by a few months. Although, *Salpa* are generally distributed in warm waters (Yount, 1958; Hubbard & Pearcy, 1971), the absence of salps in 1994 is difficult to explain since SST conditions were similar to those of 1993. Regardless of SST conditions in the North Pacific, it seems likely that the presence of salps along Line P in 1993 was caused by encroachment of transition waters since salps are abundant in these warmer southern waters (Berner, 1967). Increased salp abundance due to encroachment of warm waters has been noted in a number of studies on the distribution of salps (e.g., Thompson, 1948; Yount, 1958; Fraser, 1962). Hubbard & Pearcy (1971) observed that *Salpa* spp. were found at surface temperatures ranging from 8°C to 14°C off the Oregon coast, and that salps were more abundant during the summer than winter, similar to findings reported here. However, this does not explain the absence of salps in 1994, when winter and late spring sea surface temperatures were greater than in 1993.

²Determined from sea surface temperature anomaly database and viewing software provided by H. Freeland, IOS. All subsequent references to SST anomalies are based on this database.
³SST data near the equator were taken from Blumenthal (1995).
In the present study, salps were distributed east of 138°40'W in March 1993, when the mixed-layer depth was generally deep (60–110 m). In February 1994, the mixed-layer temperature was warmer and mixed-layer depth east of 138°40'W was generally shallower (Fig. 1.9). If this trend extended to May cruises of both years, as suggested by SST anomaly data (Fig. 1.26, 1.27) and May 1993 and 1994 temperature values from stations P4 to P12 (Fig. 1.10), then warmer temperatures could contribute to the absence of salps in May 1994 by more strongly stratifying the upper water column and consequently lowering the amount of primary production by decreasing the supply of macronutrients. A study of Mediterranean *Salpa* by Ménard *et al.* (1994) found that strong stratification of the water column lowers the probability of observing high salp abundance by decreasing the supply of macronutrients to phytoplankton. This argument may apply only to stations along Line P where macronutrients may limit the growth of phytoplankton. Low salinity east of station P8 (128°40'W), possibly due to coastal freshwater runoff, suggests that some factor associated with the run-off could also affect this ecosystem. In a north-south transect of the subarctic Pacific, Martin *et al.* (1989) showed that iron concentration is highest and NO$_3^-$ levels near zero off the Alaskan continental margin. In the present study, NO$_3^-$ levels also decrease landward of Station P. Thus the extent of winter mixing and the consequent resupply of macronutrients to the surface layer could have a greater influence on primary productivity within the dilute region compared to the more iron-limited and saline region. In the more productive, dilute region, salps would in turn be able to exploit a larger food source.

Even at Station P, conditions are occasionally suitable for salp populations. Le-Brasseur (1965a) reports some exotic, warm water species in net samples collected from Station P between 1958–1965, and the presence of *Salpa* in March and June of 1960 and in June and August of 1964. It is possible—even probable—that salps were present at Station P after the May cruise of 1993. If this is the case, the low abundance of salps
Figure 1.26: Map of sea surface temperature anomalies in the north Pacific for May 1993, showing positive SST anomalies along the North American coast and negative SST anomalies in the northeastern Pacific. A contour with a value of zero indicates no temperature anomaly. The location of Station P is marked with a star. Figure provided by H. Freeland, IOS, Sidney, B.C.
Figure 1.27: Map of sea surface temperature anomalies in the north Pacific for May 1994, showing positive SST anomalies along the North American coast and negative SST anomalies in the northeastern Pacific. A contour with a value of zero indicates no temperature anomaly. The location of Station P is marked with a star. Figure provided by H. Freeland, IOS, Sidney, B.C.
between stations P4–P20 in March 1993 and their high abundance at station P16 in May 1993, suggests that salps may advance towards the centre of the subarctic domain at the same time as the small, but incipient spring 'bloom.'

Nanoflagellate abundance in May 1993 was an order of magnitude greater than in May 1994 (Doherty, 1995) suggesting that food availability was sufficient in 1993 for the salp population to increase size. The ultimate impact of salps in the subarctic Pacific could be ecologically important. The lower size limit of particle retention of salps suggests that nanoflagellate abundance could be affected by higher predation pressures imposed on by salps. Assuming salps observed in May 1993 were similar in size and feeding characteristics to *C. bakeri* studied by Madin & Purcell (1992) in the subarctic Pacific in the 1980s, the salp population would ingest phytoplankton at a rate about equal to its production in the mixed-layer. With some additional grazing by other zooplankton species, the zooplankton community could track the phytoplankton population when salps are present. In contrast, Miller (1993a) finds that at Station P, zooplankton—mainly *Neocalanus* copepods—could not be responsible for the majority of the grazing required to control the phytoplankton population. Thus the food web dynamics of the subarctic Pacific could be entirely different in years when salps are present compared to years when they are absent.

The presence of salps no further west than 138°40'W in 1993 is associated with a concomitant decrease in the biomass of other zooplankton species at Station P (145°W). In fact, zooplankton biomass estimates (excluding salps) at Station P for February and May 1994, are about 10 mg C·m$^{-3}$ greater than the long term average biomass calculated from LeBrasseur (1965a), whereas the 1993 biomass estimates are much closer to this average (Fig. 1.28). Fraser (1949; 1962) also notes that lower copepod standing stocks are associated with the presence of salps. However, because May 1993 salp abundance was
Figure 1.28: Comparison of the total zooplankton biomass in the upper water column (0–150 m) at Station P during the four cruises from this study and the 8 year average biomass calculated from zooplankton wet weight data given by LeBrasseur (1965a). 8.3 mg wet weight were assumed to be equivalent to 1 mg C (Raymont, 1983).
greatest at station P16, but zooplankton biomass was as high there as it was at Station P, where salps were absent, it is not clear if salps are directly responsible for decreasing zooplankton abundance. The average late spring (May 1993 and 1994) zooplankton biomass at Station P is higher in comparison with the long term average biomass documented by LeBrasseur (1965a) for similar months. This is consistent with the decadal scale (1957–1980) increase in zooplankton biomass (113–194 g·1000 m$^{-3}$) noted by Brodeur & Ware (1992). These authors suggest that changes in wind pattern and intensity in the North Pacific could be responsible for increasing zooplankton biomass at Station P on a decadal scale, but that insufficient data are available to distinguish between possible mechanisms responsible for this increase.

1.4.5 Chapter Summary

This chapter documents the abundance and distribution of mesozooplankton along a transect from 48°39'N, 126°40'W to Ocean Station P at 50°N, 145°W. Zooplankton biomass is generally predominated by Neocalanus copepods although a number of other zooplankton species also appear to contribute to the total biomass. N. plumchrus appears to be developing earlier landward of Station P, and this may be the direct result of a coupling mechanism between small diatom ‘blooms’ and copepod spawning. Late spring zooplankton biomass (excluding salps) is more variable than winter biomass. In addition, interannual variability in late spring biomass along Line P appears to be greater east of 134°40'W, and coincides somewhat with the presence of salps. Salps were present only in 1993, and only east of 138°40'W. Salps may have a strong impact on phytoplankton populations in the eastern subarctic Pacific because of their ability to filter small cells. Zooplankton biomass at Station P during May cruises was greater than the long term (1957–1964) spring zooplankton biomass documented by LeBrasseur (1965a). This higher
present-day zooplankton biomass is consistent with the decadal scale increase in summer zooplankton biomass noted by Brodeur & Ware (1992), although the reasons for this increase remain elusive.
Chapter 2

*Neocalanus* Feeding Rates

2.1 Introduction

The grazing impact of copepods in the subarctic Pacific was traditionally thought to be responsible for cropping the phytoplankton stock during the spring primary production increase (Heinrich, 1962). However, recent evidence has modified our understanding of the copepod’s function in this region, where the bulk of the phytoplankton biomass is composed of cells $< 5 \mu m$ (Booth *et al.*, 1993; Doherty, 1995). Although large copepods can feed on this size fraction in monospecific laboratory algal cultures (Frost, 1972), and at low chlorophyll concentrations ($< 0.5 \text{ mg Chl} \cdot \text{m}^{-3}$: Frost *et al.*, 1983), their grazing rates and abundance are insufficient to regulate phytoplankton abundance in shipboard microcosm experiments in the subarctic Pacific (Landry *et al.*, 1993b). Furthermore, ingestion rates derived from gut pigment analyses and incubation experiments indicate that the large predominant copepods of the subarctic Pacific graze less than 15% of the daily primary production in this region (Dagg, 1993a). However, the fairly constant chlorophyll levels suggest that phytoplankton is being grazed at a rate roughly equal to that of the primary production rate (Frost, 1993).

This discrepancy may be explained by considering other grazers. Using an ecosystem model, Frost (1987; 1991; 1993) was able to duplicate seasonal chlorophyll standing stocks of the subarctic Pacific when microzooplankton were enlisted as the major grazers.
In shipboard mesocosm experiments, Landry et al. (1993b) showed that microzooplankton can in fact keep the abundance of small predominant nanoflagellates in check in the subarctic Pacific. These authors also observed that in the presence of copepods, the cyanobacterial population is maintained, presumably because of the suppression of zooflagellates by the copepods. These findings underscore the importance of the major copepods of the subarctic Pacific as key components of the food web in this region.

Although previous studies in the subarctic Pacific have focused on Neocalanus ingestion of chlorophyll (Dagg & Wyman, 1983; Frost et al., 1983; Dagg & Walser, 1987) and of ciliates (Gifford & Dagg, 1991; Gifford, 1993a), all have neglected to simultaneously evaluate the extent of feeding by these species on both autotrophic and heterotrophic flagellates (2–20 μm) as well as on ciliates. This distinction is important to properly describe the diet of Neocalanus, as well as the function of these large copepods as both herbivores and carnivores in the subarctic food web. In addition, comparatively few studies have examined feeding of N. flemingeri (Dagg, 1993a; Gifford, 1993a), a copepod that is at times more abundant than the closely related N. plumchrus (Miller, 1988; Miller, 1993b).

In this study, the ingestion rate of Neocalanus flemingeri, morphometrically similar to N. plumchrus (Miller, 1988), was measured in vitro in a shipboard bottle experiment using natural seawater samples. The goal of the experiment was to determine to what extent N. flemingeri C5 feeds on small (< 5 μm) and large (> 5 μm) autotrophic cells, ciliates, and other heterotrophic cells present in the subarctic Pacific.
Chapter 2. Neocalanus Feeding Rates

2.2 Materials and Methods

2.2.1 Shipboard Experimental Protocol

A single bottle experiment was conducted at Station P on 20 May, 1994, to estimate the feeding rate of the copepod *Neocalanus flemingeri* on prey items found in natural seawater samples. This experiment was similar in design to those described by Gifford & Dagg (1988; 1991) for *Neocalanus plumchrus*.

**Zooplankton Collection**

Mesozooplankton specimens were collected near the surface (\( z \approx 1 \text{ m} \)) at Station P (Fig. 1.3) using a fine mesh (45 \( \mu \text{m} \)) ring net with a closed cod-end to minimize damage to large copepods (Dagg, 1993a). Cod-end contents were immediately transferred to preconditioned 4 L polyethylene bottles containing natural seawater. These bottles were kept for about 2 h in a dark, on-deck incubator with a surface seawater flow-through system. Zooplankton were then sorted under dim light with a dissecting stereomicroscope. Fully plumose *N. flemingeri* C5 were placed in a separate 4 L polyethylene bottle filled with natural seawater that was then returned to the dark incubator until the time of the experiment (5 h).

**Natural Seawater Collection**

A natural seawater sample was collected near the surface with a pre-cleaned 30 L GoFlo water sampler on a Kevlar line, to ensure a clean sample. The sample was sieved underwater, through 202 \( \mu \text{m} \) mesh, into a 20 L carboy to exclude large mesozooplankton, and was acclimated in a dark incubator for 24 h (Gifford & Dagg, 1988). All 1 L polyethylene experimental (\( n = 3 \)), initial (\( n = 4 \)), and control (\( n = 4 \)) bottles were filled with the acclimated seawater. One stage C5 *N. flemingeri* was placed in each of
3 experimental bottles. The controls were incubated without copepods. Control and experimental bottles were topped off with the acclimated seawater, sealed with electrical tape and left free floating in the dark on-deck incubator at surface water temperature. Initial bottles were topped off with the acclimated seawater, but were not incubated.

**Incubation Protocol and Sampling Scheme**

Two water sample were taken from each of the four 1 L initial bottles filled with acclimated water. Samples were taken from the experimental and control bottles after 24 h. Following the respective incubation periods, copepods were removed from the experimental bottles using a clean 60 mL turkey-baster pipette and preserved in a 4% buffered formalin-seawater solution (Parsons *et al.*, 1984a) for laboratory examination. From each 1 L bottle, 250 mL was preserved with acid Lugol’s iodine for microplankton enumeration (Throndsen, 1978), and 250 mL with 1% filtered glutaraldehyde for nanoplankton enumeration by epifluorescence microscopy (Doherty, 1995).

Glutaraldehyde samples were processed within 24 h of preservation to minimize the loss of autofluorescence in the nanoplankton. An aliquot was stained with DAPI (4', 6-diamidino-2-phenylindole dihydrochloride hydrate: Porter & Feig, 1980) and proflavin hemisulfate (Hass, 1982), and was filtered onto a 25 mm, 0.8 μm porosity, black-stained Poretics polycarbonate filter. Although no stains are necessary to visualize autofluorescence under blue light (e.g., Booth *et al.*, 1988), the use of these stains helps distinguish between cells and background non-organic particulate matter (Doherty, 1995).

Because the nanoplankton abundance was expected to decrease over time, due to copepod feeding activity, the aliquot volume was varied accordingly; 50 mL was filtered for initial and control samples, and 100 mL for the 24 h samples. Once the aliquots were suctioned onto the black-stained filters, they were mounted on slides and sealed with clear

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1 Gifford & Dagg (1988) used 2 copepods in 2 L bottles.
nail polish. The slides were stored at $-20^\circ$C until microscopical counts were be made by S. Doherty (UBC) in the laboratory. Details of the staining and slide preparation procedures are given by Doherty (1995).

2.2.2 Laboratory Enumeration Protocol

Nanoplankton and bacterial enumeration by epifluorescence microscopy

Heterotrophic and autotrophic cells were separated into four size classes (2–5 $\mu$m, 5–10 $\mu$m, 10–20 $\mu$m and > 20 $\mu$m) to determine the size and type of prey consumed by *N. flemingeri* C5. For cells < 20 $\mu$m, a minimum of 100 cells of the most abundant nanoflagellate size group and 80 microscope fields were counted to ensure an adequate abundance estimate (cf. Venrick, 1978). For cells > 20 $\mu$m, all individuals were enumerated at x400 magnification and their dimensions were measured to determine carbon content based on cell volume (Strathmann, 1967). *Synechococcus* spp. cells were enumerated at 10 separate locations on the filter so that 200–300 cells were counted. All microscope fields were analyzed along two transects that crossed the centre of the circular field. Refer to Doherty (1995) for details of the enumeration procedures.

Microzooplankton Enumeration by Inverted Microscopy

The Utermöhl method was used to enumerate microzooplankton (20–200 $\mu$m) in the Lugol’s preserved samples (Hasle, 1978). Each 250 mL jar containing the microplankton was thoroughly shaken to resuspend and randomize its contents (Venrick, 1978). Samples were then quickly poured into 47–50 mL settling chambers, covered and left to settle at room temperature for at least 72 h. Entire chambers were analyzed for loricate and aloricate ciliates and dinoflagellates. Counts were divided by chamber volume to obtain cells·L$^{-1}$.
Carbon Conversions and Ingestion calculations

The biovolume of ciliates and flagellates was estimated from formulae given by Wetzel & Likens (1991) for general microplankton shapes. The carbon-to-volume ratio for ciliates was assumed to be 0.19 pg C·μm⁻³ (Putt & Stoecker, 1989). For flagellates and dinoflagellates > 4 μm, cell carbon was estimated by the equation in Strathmann (1967) for non-diatom phytoplankton. Carbon content of cells < 4 μm was estimated from the conversion 0.22 pg C·μm⁻³ (Mullin et al., 1966). Cell carbon of Synechococcus spp. was assumed to be 210 fg C-cell⁻¹ (Waterbury et al., 1986). Chlorophyll was calculated from carbon content using a C:Chl value of 70 for the mixed-layer. This value was used by Dagg (1993a) for his May feeding experiments, and is in the range (50–100) of C:Chl values given by Welschmeyer et al. (1993) for the subarctic Pacific.

Clearance and ingestion rates were calculated from formulae given by Frost (1972) and Omori & Ikeda (1984). The equation:

\[ I = F \times \frac{C_e' - C_i'}{(k - f)t} \]  

was used to calculate the ingestion rate \((I \text{ in } \mu g \text{ C.ind}^{-1} \cdot h^{-1})\) of \textit{N. flemingeri} on a given prey type. The clearance rate \((F)\) is in mL-ind⁻¹-h⁻¹, and \(C_e'\) and \(C_i'\) are the biomass \((\mu g \text{ C.L}^{-1})\) of the prey type in the experimental and initial bottles, respectively. The feeding coefficient \((f)\) is the change in cell concentration \((h^{-1})\) due to copepod feeding and the growth coefficient \((k)\) is the change in cell concentration \((h^{-1})\) in the absence of copepods (controls) over the course of the experiment \((t)\). The daily ingestion rate \((\mu g \text{ C.ind}^{-1} \cdot d^{-1})\) was calculated from \(I \times 24 \text{ h}\), assuming no diel feeding pattern in \textit{Neocalanus} feeding (Dagg & Walser, 1987). Community ingestion rates were calculated by multiplying daily ingestion rates with population abundance at Station P during the May 1994 cruise (Table 1.3).
Chapter 2. Neocalanus Feeding Rates

2.3 Results

2.3.1 Initial Conditions

Initial cell abundance was predominated by small (< 5 \( \mu \text{m} \)) autotrophic cells (Table 2.6). These contributed as much as 97% of autotrophic cells and 88% of all cells enumerated. In terms of chlorophyll, this small cell fraction made up 66% of the total initial chlorophyll \( a \) concentration (0.38 \( \mu \text{g} \cdot \text{L}^{-1} \)). Heterotrophic nanoflagellates < 5 \( \mu \text{m} \) were the second most abundant cells, contributing as much as 67% of heterotrophic cells and 6% of all cells enumerated. Although diatom abundance increased in both the experimental and control bottles (ANOVA: \( P < 0.01 \)), they never exceeded 0.2 \( \mu \text{g} \cdot \text{C} \cdot \text{L}^{-1} \). Initial numerical abundance and biomass of \textit{Synechococcus} cells averaged \( 7.4 \times 10^6 \) and 1.55 \( \mu \text{g} \cdot \text{C} \cdot \text{L}^{-1} \), respectively. Average initial ciliate abundance was 3211 cells·L\(^{-1} \) (Table 2.6), contributing 7.2 \( \mu \text{g} \cdot \text{C} \cdot \text{L}^{-1} \), or 37% of the total heterotrophic biomass (Table 2.7). Microscope measurements and observations of ciliates indicate that 60% of ciliates were > 25 \( \mu \text{m} \), and were predominantly of the genus \textit{Strombidium}, although strobilidids and haptorids were also important. Heterotrophic dinoflagellates > 5 \( \mu \text{m} \) were mostly \textit{Gyrodinium} species. The coefficients of variation for all counts made from control bottles ranged from 20% to 50% and were generally greater than those for initial bottle counts.

2.3.2 Individual Ingestion

The highest clearance rates for \textit{N. flemingeri} C5 were on cells > 5 \( \mu \text{m} \), although rates ranged from 10.6 to 62.9 mL·ind\(^{-1}·\text{h}^{-1} \) (Table 2.8). Autotrophic and heterotrophic cells < 5 \( \mu \text{m} \) were cleared at rates of 47.2 and 36.2 mL·ind\(^{-1}·\text{h}^{-1} \), respectively (Table 2.8). \textit{N. flemingeri} fed on autotrophic nanoflagellates with the highest daily ingestion rate (12.8 \( \mu \text{g} \cdot \text{C} \cdot \text{ind}^{-1}·\text{day}^{-1} \)), and on ciliates with the second highest daily ingestion rate
Table 2.6: Cell densities in incubation bottles during the 24 h feeding experiment with *N. flemingeri* C5. Sample size for the initial, experimental, and control bottles are *n* = 4, *n* = 3, and *n* = 4, respectively. All values are means and all units are cells·L⁻¹.

<table>
<thead>
<tr>
<th>Fraction (μm)</th>
<th>Initial (time zero)</th>
<th>Experimental (after 24 h)</th>
<th>Control (after 24 h)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autotrophic Nanoflagellates</td>
<td>&lt;5</td>
<td>2 340 000</td>
<td>908 000</td>
</tr>
<tr>
<td></td>
<td>5–10</td>
<td>56 825</td>
<td>10 300</td>
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<tr>
<td></td>
<td>&gt;10</td>
<td>4850</td>
<td>8133</td>
</tr>
<tr>
<td>Autotrophic Dinoflagellates</td>
<td>&gt;10</td>
<td>18 950</td>
<td>3233</td>
</tr>
<tr>
<td>Heterotrophic Nanoflagellates</td>
<td>&lt;5</td>
<td>165 825</td>
<td>199 667</td>
</tr>
<tr>
<td></td>
<td>5–10</td>
<td>56 825</td>
<td>10 300</td>
</tr>
<tr>
<td></td>
<td>&gt;10</td>
<td>19 075</td>
<td>38 767</td>
</tr>
<tr>
<td>Heterotrophic Dinoflagellates</td>
<td>&gt;10</td>
<td>1627</td>
<td>1139</td>
</tr>
<tr>
<td>Ciliates</td>
<td>&gt;5</td>
<td>3211</td>
<td>2470</td>
</tr>
<tr>
<td>Total Autotrophic</td>
<td></td>
<td>2 420 625</td>
<td>929 666</td>
</tr>
<tr>
<td>Total Heterotrophic</td>
<td></td>
<td>246 563</td>
<td>252 343</td>
</tr>
</tbody>
</table>
Table 2.7: Initial carbon concentrations in incubation bottles for the 24 h feeding experiment with *Neocalanus flemingeri* C5. All units are μg C·L$^{-1}$.

<table>
<thead>
<tr>
<th>Fraction (μm)</th>
<th>Initial</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autotrophic</td>
<td></td>
</tr>
<tr>
<td>Nanoflagellates</td>
<td>&lt;5</td>
</tr>
<tr>
<td></td>
<td>5–10</td>
</tr>
<tr>
<td></td>
<td>&gt;10</td>
</tr>
<tr>
<td>Autotrophic</td>
<td>&gt;10</td>
</tr>
<tr>
<td>Dinoflagellates</td>
<td></td>
</tr>
<tr>
<td>Heterotrophic</td>
<td>&lt;5</td>
</tr>
<tr>
<td>Nanoflagellates</td>
<td>5–10</td>
</tr>
<tr>
<td></td>
<td>&gt;10</td>
</tr>
<tr>
<td>Heterotrophic</td>
<td>&gt;10</td>
</tr>
<tr>
<td>Dinoflagellates</td>
<td></td>
</tr>
<tr>
<td>Ciliates</td>
<td>&gt;5</td>
</tr>
<tr>
<td>Total Autotrophic</td>
<td></td>
</tr>
<tr>
<td>Total Heterotrophic</td>
<td></td>
</tr>
</tbody>
</table>
Table 2.8: *Neocalanus flemingeri* C5 consumption of autotrophic and heterotrophic cells in natural seawater samples.

<table>
<thead>
<tr>
<th>Fraction (μm)</th>
<th>Clearance Rate (mL·ind⁻¹·h⁻¹)</th>
<th>Ingestion Rate (μg C·ind⁻¹·day⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autotrophic</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt;5</td>
<td>47.2</td>
<td>12.8</td>
</tr>
<tr>
<td>5-10</td>
<td>60.0</td>
<td>2.5</td>
</tr>
<tr>
<td>&gt;10</td>
<td>24.6</td>
<td>≈ 0</td>
</tr>
<tr>
<td>Autotrophic</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&gt;10</td>
<td>62.9</td>
<td>0.7</td>
</tr>
<tr>
<td>Dinoflagellates</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Heterotrophic</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt;5</td>
<td>36.2</td>
<td>0.4</td>
</tr>
<tr>
<td>5-10</td>
<td>60.0</td>
<td>2.5</td>
</tr>
<tr>
<td>&gt;10</td>
<td>14.4</td>
<td>0.8</td>
</tr>
<tr>
<td>Heterotrophic</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&gt;10</td>
<td>10.6</td>
<td>0.2</td>
</tr>
<tr>
<td>Dinoflagellates</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ciliates</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&gt;5</td>
<td>15.8</td>
<td>3.4</td>
</tr>
<tr>
<td>Total Autotrophic,</td>
<td></td>
<td>16.0</td>
</tr>
<tr>
<td>Total Heterotrophic</td>
<td></td>
<td>7.3</td>
</tr>
</tbody>
</table>
(3.4 \mu g \text{C-ind}^{-1}\text{-day}^{-1}). These two groups contributed 70\% of \textit{N. flemingeri}'s daily ingestion. There was no detectable difference in the abundance of \textit{Synechococcus} among the initial (1.6 \mu g \text{C-L}^{-1}), control (2.3 \mu g \text{C-L}^{-1}), and experimental (2.8 \mu g \text{C-L}^{-1}) bottles. Including all size fractions, \textit{N. flemingeri} consumed, 16.0 \mu g \text{C-ind}^{-1}\text{-day}^{-1} and 7.3 \mu g \text{C-ind}^{-1}\text{-day}^{-1} of autotrophs and heterotrophs, respectively.

2.3.3 Population Ingestion

Assuming that \textit{N. flemingeri} and \textit{N. plumchrus} C5 have equal ingestion rates, the combined population ingestion rate for these copepods was 2.8 mg \text{C-m}^{-3}\text{-day}^{-1} (Table 2.9). The most heavily preyed upon group was the autotrophic nanoflagellates < 5 \mu m, which made up 55\% of all predated cell biomass (Table 2.9). The next most heavily-predated group was the ciliates, which made up 15\% of consumed cell biomass (Table 2.9). In total, the \textit{N. flemingeri} and \textit{N. plumchrus} C5 population consumed 69\% of autotrophic and 31\% of heterotrophic biomass.

2.4 Discussion

The grazing\textsuperscript{2} and total ingestion rates of \textit{N. flemingeri} reported here are roughly double those reported earlier for this species in the subarctic Pacific (Dagg & Walser, 1987; Dagg, 1993a), whereas ciliates and heterotrophic nanoflagellates are ingested at rates similar to those measured by Gifford (1993a). Total carbon ingestion measured in the present study was sufficient for daily metabolic requirements and for growth, although the estimated growth rate was near the maximum value that Dagg \textit{et al.} (1982) calculated using maximum ingestion rates. In summary, individual and community ingestion rates of phytoplankton were not consistent with previous average estimates for the subarctic

\textsuperscript{2}Here, 'grazing' refers to the ingestion of phytoplankton cells.
Table 2.9: Population ingestion rates for *Neocalanus flemingeri* and *Neocalanus plumchrus* C5 feeding on autotrophic and heterotrophic cells. Copepod abundance estimates from Chapter 1 were used to calculate ingestion rates. *N. plumchrus* ingestion rates were assumed to be the same as those of *N. flemingeri*.

<table>
<thead>
<tr>
<th>Fraction (μm)</th>
<th>Ingestion Rate (μg C·m⁻³·day⁻¹)</th>
<th><em>N. flemingeri</em></th>
<th><em>N. plumchrus</em></th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Autotrophic</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt;5</td>
<td>535</td>
<td>1014</td>
<td>1549</td>
<td></td>
</tr>
<tr>
<td>5-10</td>
<td>103</td>
<td>196</td>
<td>299</td>
<td></td>
</tr>
<tr>
<td>&gt;10</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td><strong>Nanoflagellates</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&gt;10</td>
<td>29</td>
<td>55</td>
<td>85</td>
<td></td>
</tr>
<tr>
<td><strong>Dinoflagellates</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Heterotrophic</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt;5</td>
<td>18</td>
<td>33</td>
<td>51</td>
<td></td>
</tr>
<tr>
<td>5-10</td>
<td>103</td>
<td>196</td>
<td>299</td>
<td></td>
</tr>
<tr>
<td>&gt;10</td>
<td>34</td>
<td>64</td>
<td>98</td>
<td></td>
</tr>
<tr>
<td><strong>Dinoflagellates</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&gt;10</td>
<td>9</td>
<td>17</td>
<td>27</td>
<td></td>
</tr>
<tr>
<td><strong>Ciliates</strong></td>
<td>&gt;5</td>
<td>352</td>
<td>267</td>
<td>407</td>
</tr>
<tr>
<td><strong>Total Autotrophic</strong></td>
<td></td>
<td>667</td>
<td>1265</td>
<td>1933</td>
</tr>
<tr>
<td><strong>Total Heterotrophic</strong></td>
<td></td>
<td>516</td>
<td>577</td>
<td>882</td>
</tr>
</tbody>
</table>
Pacific. However, despite the high ingestion rates, the data imply that copepod ingestion can balance neither phytoplankton nor ciliate growth rates in the subarctic Pacific.

The chlorophyll standing stock measured from initial experimental samples was typical of late spring Station P values (Parsons & Lalli, 1988). In addition, fluorometric analysis of water samples taken within one day of the experiment gave a chlorophyll concentration (0.35 µg Chl·L$^{-1}$; P. Boyd, UBC, pers. comm.) similar to the initial experimental sample (0.38 µg Chl·L$^{-1}$). In terms of carbon, initial conditions were comparable to mixed-layer biomass estimates reported by Booth et al. (1993) for the same month in 1984 and 1988. Thus chlorophyll and carbon estimates indicate that phytoplankton standing stock during the May 1994 cruise was typical of Station P during this time of year, and that the prey population in the incubation vessels approximated that found naturally.

The initial heterotrophic biomass (2–200 µm) was predominated by nanoflagellates and ciliates, and their biomass was similar to the average reported by Booth et al. (1993) for their May cruises. Initial ciliate biomass (7.24 µg C·L$^{-1}$) also agrees with Strom et al. (1993) who reported ciliate biomass of 5.93 µg C·L$^{-1}$ for the same day in May 1988, although this was also the maximum biomass they observed at Station P over four month-long cruises in 1987 and 1988. Their estimates of ciliate numerical abundance indicate that the high biomass they observed for that day resulted from higher than average ciliate numbers, whereas ciliate numbers from the present study were near average. Assuming a constant carbon-to-volume ratio for ciliates (Putt & Stoecker, 1989), the similar biomass but lower ciliate numbers observed here suggests that ciliates from the present study were about twice the size compared to May 1988, when Strom et al. (1993) sampled. In fact, ciliates from the present study were generally > 25 µm, contrary to previous work that described the majority of ciliates as < 24 µm (Booth et al., 1993). Therefore, the
slightly greater ciliate biomass observed here is due not to a greater number of cells, but to larger than average ciliate body size.

### 2.4.1 *N. flemingeri* Individual Ingestion

Copepods from this study had the highest clearance rates on cells < 5 μm, although cells > 5 μm were also cleared at relatively high rates. High clearance rates and the predominance of < 5μm autotrophic cells in the mixed-layer resulted in a calculated grazing rate an order of magnitude greater than the bottle-derived grazing rates reported by Dagg (1993a) for *N. flemingeri* and *N. plumchrus* feeding at Station P. However, feeding on small cells is consistent with findings by Frost *et al.* (1983) who showed that these copepods can indeed capture cells 2–3 μm in size. Dagg (1993a) noted that *N. flemingeri* and *N. plumchrus* generally do not feed at maximum rates in the subarctic Pacific, suggesting that the vertical distribution of both food and consumer allows for potential sporadic feeding events. Indeed, the biomass of small autotrophic cells is generally greatest in the mixed-layer (Booth *et al.*, 1993; Doherty, 1995), coinciding with the known vertical distribution of *N. flemingeri* within the upper mixed-layer (Mackas *et al.*, 1993). Furthermore, from a 20 year copepod sample series, Miller *et al.* (1992) suggested that variation in food availability may be the cause of interannual variability in the size of *N. flemingeri* at Station P. It appears that conditions in May 1994 were ideal for near maximal clearance rates and resulted in copepod weight being greater in May 1994 (129 μg C, Section 1.3.3) compared to the average weight (87 μg C) calculated from Miller (1993b) for copepods collected in late May of 1988.

Heterotrophic prey are also ingested by *N. flemingeri* (Gifford & Dagg, 1991; Gifford, 1993a; Table 2.8), and their importance to the copepod’s diet can be quantified by
estimating the organism’s respiratory needs. Respiratory requirement can be calculated from Dagg et al.’s (1982) equation:

\[ R = 0.101 W_c^{0.884}, \]  

where \( R \) is respiration as \( \mu g \text{C-ind}^{-1} \cdot \text{d}^{-1} \) and \( W_c \) is the animal weight as \( \mu g \text{C} \). Assuming the assimilation efficiency is 70% (in the range given by Conover, 1968), \( N. \ flemingeri \) weighing 129 \( \mu g \text{C-ind}^{-1} \) in May 1994 (Section 1.3.3) requires ingestion of 10.6 \( \mu g \text{C-d}^{-1} \) to satisfy its basic respiratory requirements \( (R = 7.4 \ \mu g \text{C-d}^{-1}) \). Since \( N. \ flemingeri \) obtains 7.3 \( \mu g \text{C-ind}^{-1} \cdot \text{d}^{-1} \) from heterotrophic prey, 69% of its respiratory requirements are satisfied from heterotrophic prey alone. This estimate is not dissimilar from Gifford’s (1993a) estimate of 77% for \( N. \ plumchrus \), derived from a similar bottle experiment conducted at Station P, albeit without measuring the contribution of autotrophic cells. In the present study, it was phytoplankton that accounted for the majority of ingested food, supplying ample carbon for growth.

Assuming that any assimilated carbon that exceeds daily requirements for respiration contributes to copepod growth (Dagg et al., 1982), growth could be calculated by subtracting respiration requirements \( (7.4 \ \mu g \text{C-ind}^{-1} \cdot \text{d}^{-1}) \) from assimilated carbon. Copepods from this experiment ingested 23.3 \( \mu g \text{C-d}^{-1} \) (assimilated 16.3 \( \mu g \text{C-d}^{-1} \)), leaving 8.9 \( \mu g \text{C-d}^{-1} \) for growth, equivalent to 6.9% daily body carbon growth. This rate is in agreement with growth rates calculated by Dagg et al. (1982) for Station P copepods using maximum ingestion rates. Thus it seems that the estimated growth rate is also high, possibly representing near-maximum growth. Alternatively, copepods could be accumulating lipids at a high rate (non-somatic growth), in preparation for their ontogenetic migration to depth (Miller & Clemons, 1988). Support for this comes from Miller’s (1993b) data that shows a doubling of \( N. \ flemingeri \)’s dry weight between late May and early June is principally due to lipid enrichment.
A salient feature of calculated clearance rates is their inequality, specifically the lower clearance rates observed on some large cells (> 10 μm). The general understanding of calanoid feeding is that clearance rates should be greater on larger cells, presumably because copepods handle and eat large cells more efficiently than small cells (Frost, 1972). The calculation of Chesson’s α (Chesson, 1978) is useful in determining if there is selectivity for different prey types. Selectivity for a prey occurs when the relative frequency of an ingested prey type differs from its relative frequency in the environment. Chesson’s α is calculated as:

$$\alpha_j = \frac{d_j/p_j}{\sum (d_j/p_j)}$$  \hspace{1cm} (2.5)

where $d_j$ and $p_j$ are the proportion of the $j^{th}$ prey item ingested and in the environment, respectively. The $\alpha_j$ selectivity index for the $j^{th}$ prey item is compared to a value of $1/N$, where $N$ is the number of prey classes. If $\alpha_j < 1/N$ then the $j^{th}$ prey type was rejected, and if $\alpha_j > 1/N$, the prey type was preferred.\(^3\) The calculated $\alpha$ for all prey types considered in the present experiment indicates that ciliates and all prey types > 10 μm were rejected, except for autotrophic nanoflagellates > 10 μm. When the prey types are divided into two groups, autotrophic and heterotrophic, Chesson’s $\alpha$ indicates a preference for autotrophic cells and rejection of the heterotrophic cells. It is difficult to reconcile the general preference for autotrophs over heterotrophs because animal food is assimilated more efficiently than plant food in other calanoid copepods (Corner \textit{et al.}, 1972; 1976). The preference for smaller cells (< 10 μm) is also difficult to reconcile with the known feeding behaviour of calanoid copepods. Nonetheless, \textit{N. flemingeri} exhibited some feeding preference for autotrophs over heterotrophs, and for cells < 10 μm over larger cells.

\(^3\)Here, ‘rejected’ and ‘preferred’ are quantitative terms, not qualitative. They do not refer to actual rejection and preference of prey, but to whether a prey type was ingested in lesser or greater proportion to what its proportion is in the environment.
2.4.2 Population Impact

The species *N. flemingeri* and *N. plumchrus* are here assumed to have identical specific rates of ingestion and excretion. Although this is certainly erroneous, it allows for some speculation of the effect these copepods have on the subarctic Pacific food web. Comparing the calculated combined *N. plumchrus* and *N. flemingeri* C5 ingestion rate on autotrophs (1.9 mg C·m\(^{-3}\)·d\(^{-1}\)) to a phytoplankton production measurement (529 mg C·m\(^{-2}\)·d\(^{-1}\)) taken in the upper mixed-layer (0–45 m) a day prior to the feeding experiment (P. Boyd, UBC, *pers. comm.*), these copepods consumed 16.4% of the daily primary production. Assuming that these copepods contributed about half of the total community ingestion (see Fig. 12 in Dagg, 1993a), during the present study community grazing would be approximately 33% of the daily phytoplankton production. Although this rate is twice that of previous estimates (*e.g.*, Dagg & Wyman, 1983; Dagg, 1991; Dagg, 1993a), it remains insufficient to control phytoplankton stock alone. The inability of the copepod community to balance phytoplankton growth agrees with most of the recent literature regarding Station P (Landry & Lehner-Fournier, 1988; Miller & SUPER Group, 1988; Parsons & Lalli, 1988; Dagg, 1991; Dagg, 1993a; Frost, 1993).

Another source of phytoplankton grazing may come from microzooplankton (Parsons & Lalli, 1988; Frost, 1993). Strom *et al.* (1993) showed that ciliates graze about 20% of the phytoplankton production at Station P. These authors noted that other protozoans likely contribute to herbivory in the subarctic Pacific, including heterotrophic nanoflagellates and dinoflagellates, which contributed more than 60% to the total heterotrophic biomass in the present study.

In the present study, *N. flemingeri* and *N. plumchrus* obtained one third of their carbon from heterotrophic cells. In light of the importance of protozoans as grazers in the subarctic ecosystem (Frost, 1993), it is important to determine if these copepods can
control the protozoan population. For example, copepods from this experiment cleared ciliates at a rate of 0.38 L·ind\(^{-1}\)·d\(^{-1}\). Combined with copepod abundance in the mixed-layer, this specific clearance rate yields a population clearance rate of 0.05 L·d\(^{-1}\), or 5% of the mixed-layer daily. From shipboard mesocosm experiments at Station P, Landry et al. (1993b) estimated ciliate specific growth rate as 0.1 d\(^{-1}\). However, Montagnes (in press) compared maximal growth rates achieved in the laboratory to those calculated from empirical relationships in the literature, and found that the maximal in situ growth rate of ciliates from the genera *Strobilidium* and *Strombidium* are best predicted from the cell volume and temperature-dependent formula given by Müller & Geller (1993). Assuming a cell volume of ca. 4000 \(\mu\text{m}^3\) and an ambient water temperature of 7.8°C (Section 1.3.1), the calculated maximal specific growth rate of these ciliates is 0.57 d\(^{-1}\). Ciliate growth rate thus exceeds their rate of removal by copepods by an order of magnitude, indicating that the major copepod species are not capable of controlling the ciliate population at Station P in May. This finding is supported by Frost’s (1993) modeling results, that the control of heterotrophic microzooplankton lies in predation pressures from groups other than copepods.

Dagg (1993b) has suggested that it is not unreasonable for *N. cristatus* living at the bottom of the mixed-layer to monitor an area as large as 3 cm\(^2\) for sinking fecal particles. This coprophagous behaviour requires sufficient sinking fecal matter from above, most likely large fecal pellets produced by large copepods. Assuming an assimilation efficiency of 70% (Conover, 1968), the remaining unassimilated 30% is egested as fecal pellets. Since the total ingestion rate of *N. flemingeri* C5 is 23.3 \(\mu\text{g C·ind}^{-1}·\text{m}^{-3}·\text{d}^{-1}\)), the amount of carbon egested as fecal matter is 7.0 \(\mu\text{g C·ind}^{-1}·\text{m}^{-3}·\text{d}^{-1}\). Assuming that *N. plumchrus* egestion is about the same, the total daily carbon egested by these copepods in the mixed-layer is a product of their abundance and their specific egestion rate. Given an abundance of 121 ind·m\(^{-3}\) (Table 1.3), the biomass of fecal matter produced in the
mixed-layer is 846 \( \mu g \text{ C} \cdot \text{m}^{-3} \cdot \text{d}^{-1} \). If the mixed-layer is 65 m deep, the production of fecal matter is 55 mg C \cdot m^{-2} \cdot d^{-1}, or 61\% of the 90 mg C \cdot m^{-2} \cdot d^{-1} downward vertical flux of carbon at 100 m typically found at Station P in May.\(^4\) This flux is equivalent to 5.5 \( \mu g \text{ C} \cdot \text{cm}^{-2} \cdot \text{d}^{-1} \). \textit{N. cristatus} could thus obtain approximately 16.5 \( \mu g \text{ C} \cdot \text{ind}^{-1} \cdot \text{d}^{-1} \) of its nutrition from sinking fecal matter produced by \textit{N. flemingeri} and \textit{N. plumchrus} C5 in the upper mixed-layer.

The estimated respiration rate of \textit{N. cristatus} C5 weighing an average of 889 \( \mu g \text{ C} \) (for May 1993 and 1994: Section 1.3.3) is 40.8 \( \mu g \text{ C} \cdot \text{ind}^{-1} \cdot \text{d}^{-1} \) (Eq. 2.4). Thus \textit{N. cristatus} can obtain about 28\% of its daily metabolic requirements from this source alone. If \textit{N. cristatus} consume protozoa at a rate of up to 12.2 \( \mu g \text{ C} \cdot \text{ind}^{-1} \cdot \text{d}^{-1} \) (Gifford, 1993a), then it could receive half of its metabolic needs from both sources. Thus, although \textit{N. flemingeri} and \textit{N. plumchrus} contribute substantially to the vertical carbon flux at 100 m, these species are probably not the only source of sinking food particles for \textit{N. cristatus}. The remainder of \textit{N. cristatus}'s metabolic needs could come from sinking fecal pellets produced by the large fraction of 'other' zooplankton species (Figs. 1.23, 1.24) and sinking phytoplankton present in the mixed-layer along Line P.

An important aspect of the subarctic ecosystem is the year-round high NO\(_3^-\) concentration, partially due to NH\(_4^+\) inhibition of NO\(_3^-\) uptake (Wheeler & Kokkinakis, 1990). A relevant question then, is whether copepods excrete sufficient NH\(_4^+\) to supply phytoplankton with NH\(_4^+\). Nitrogen excretion can be predicted from the body size dependent relationship

\[
E = 0.072 W_N^{0.902},
\]

where \( E \) is ammonium excretion as mgNH\(_4^+\) \cdot \text{ind}^{-1} \cdot \text{d}^{-1} \) and \( W_N \) is copepod weight in \( \mu g \text{ N} \) (Dagg \textit{et al}., 1982). Using conversion factors from Miller (1993b), a 129 \( \mu g \text{ C} \)

\(^4\)The May organic carbon flux value is an average of shallow sediment trap data from May 1990 and 1993, provided by C.S. Wong, IOS, Sidney, B.C.
A copepod is equivalent to a maximum of 20.5 µg N. At this weight, a copepod excretes 1.1 µg NH₄⁺·d⁻¹, recycling about 5% of its weight in nitrogen daily, assuming that urea excretion is minimal compared to that of ammonium (Corner et al., 1976). Combining this excretion rate with mixed-layer abundance of *N. flemingeri* and *N. plumchrus* yields a combined population excretion rate of 7.35 µg-atoms NH₄⁺·m⁻³·d⁻¹, or 3.3% of the ambient ammonium concentration in the mixed-layer (220 µg-atoms NH₄⁺·m⁻³; Section 1.3.2) per day. If phytoplankton uptake of NH₄⁺ in the mixed-layer is assumed to be 97.1 µg-atoms NH₄⁺·m⁻³·d⁻¹, NH₄⁺ excretion by these copepods represents only 8% of the NH₄⁺ uptake by phytoplankton at Station P. Such a low value supports the idea that NH₄⁺ is being recycled by a mechanism other than by copepod excretion, namely microzooplankton nitrogen excretion (Frost, 1993).

A number of important caveats are associated with the use of bottle experiments in measuring ingestion rates of copepods. Although no other method allows for detailed measurements of the size and type of food particles consumed, the incubation method does not provide *in situ* grazing rates, as in the case of the gut pigment method (Mackas & Bohrer, 1976). This is an important distinction, especially for species that do not derive most of their nutrition from particles in the mixed-layer. For example, *N. cristatus* lives just below the thermocline (Mackas et al., 1993) and feeds on sinking fecal matter from above (Dagg, 1993b). Such a feeding strategy would not be detected in an incubation experiment.

An equally serious problem with incubation experiments is that bottle conditions may alter prey and water characteristics, thus modifying the feeding strategy of copepods. Phytoplankton and protozoan cells may break (Harbison & McAlister, 1980; Gifford, 1993a,b), or some cells may sink to the bottom portion of the container, altering the copepod's ability to filter these potential food items. An additional difficulty related to

---

5 This value is a weighted average calculated from raw data provided by D. Varela, UBC.
containing a parcel of water, is the sometimes contrived abundance of copepods needed to
detect a feeding signal. In this experiment, the combined number of *N. flemingeri* and
*N. plumchrus* was 0.12 ind-L⁻¹, whereas the experimental 1 L bottles each contained
1 copepod. However, practical limitations do not easily permit a replicated shipboard
experiment using 12 copepods in 100 L containers.

Additional experiments should be conducted since interexperimental variability in
clearance rates is reasonably high (see Table 2 in Gifford, 1993a). However, time did
not permit for this, or for experimental verification using other methods. Without such
verification, it is difficult to validate estimates made from the present study. Nonetheless,
the results presented here are consistent with the understanding that copepods from the
subarctic Pacific do not graze sufficiently to control the phytoplankton stock.

In terms of copepod diet, this experiment is the first to attempt a detailed evaluation
of *Neocalanus* ingestion of various size fractions of both autotrophic and heterotrophic
cells in the subarctic Pacific Ocean. Future studies should consider the transition in
feeding ecology of copepods along Line P, from an iron-replete to an iron-limited regime.
Changes in iron regimes could alter the growth rates of copepods and other zooplankton
species by changing the phytoplankton species composition, the size of cells, and their
abundance. The contribution of other, occasionally abundant animals, such as salps
(Section 1.3.3), to total zooplankton grazing has not been evaluated along Line P. Since
they require a more gentle approach in evaluating ingestion, contingent experimental
schemes should be considered under circumstances when salps are abundant. The gut
fluorescence method has been used previously to examine grazing in salps (Madin &
Cetta, 1984) and this method has been used on the salp *C. bakeri* at Station P (Madin
& Purcell, 1992). In combination with detailed abundance estimates, this method could
be used to determine the impact of salps on the phytoplankton population.
2.4.3 Chapter Summary

Copepods from this study do not clear all size fractions at equal rates, ostensibly implying some feeding preferences or capabilities. The calculated Chesson's selectivity index (Chesson, 1978) indicates that N. flemingeri feeds preferentially on autotrophic cells, and on cells < 10 μm. Large ciliates (> 60 μm) are cleared at low rates compared to smaller autotrophic and heterotrophic cells. Phytoplankton is ingested at rates twice those previously determined by Dagg (1993a). However, the copepod community does not consume more than 33% of the daily primary production. Ciliates are ingested at rates comparable to those previously reported by Gifford (1993a), but their stock does not appear to be controlled by copepods. 28% of N. cristatus's metabolic needs could be accounted for by sinking fecal matter produced by N. flemingeri and N. plumchrus. Although these copepods are estimated to contribute about 61% to the downward vertical carbon flux at 100 m via their fecal pellets, they do not contribute extensively to NH₄⁺ recycling, suggesting that another mechanism must exist for this process.
Chapter 3

Conclusions and Future Research

3.1 Distribution and Abundance of Mesozooplankton

- In the upper water column (< 200 m) at Station P in May, zooplankton biomass was concentrated in the mixed-layer.

- Zooplankton biomass was much more variable along Line P among late spring cruises than among winter cruises. The variability in late spring was greatest east of about 134°W.

- Species of *Neocalanus* contributed more to the total zooplankton biomass during late spring compared to the winter.

- Zooplankton species other than those considered in the present study made important contributions to the total zooplankton biomass. These species need to be examined more carefully, especially in late summer when *Neocalanus* is not as abundant in the mixed-layer.

- *Oithona* were often abundant when salps were present. This association could be important to nutrient cycling in the mixed layer when salps are present. In addition, *Oithona* was associated with its chaetognath predator, *Sagitta elegans*.

- Salps (*Salpa* spp.) were present during late spring and winter of 1993, but were never observed at Station P during that year. Salps were absent from all late spring and winter 1994 samples. Although *Salpa* spp. are typically found in warm water,
they were not present in 1994 when water temperatures were generally higher than in 1993. Nonetheless, the presence of salps in 1993 is likely due to a north-south shift in oceanic boundaries because *Salpa* are typically more southern species.

- The presence of salps was generally associated with much lower biomass of other zooplankton species, suggesting that salps may be important in changing the dynamics of the food web. The importance of salps in the subarctic Pacific requires further attention. The gut fluorescence method seems ideal for quantifying grazing in this group since their fragility makes them difficult to study in routine shipboard bottle experiments.

- The development of *N. plumchrus* is different at Station P than in the Strait of Georgia. Along Line P, *N. plumchrus* and *N. flemingeri* appear to develop progressively later seaward to Station P. The reason for this could involve a mechanism whereby small 'blooms' in large diatoms could trigger spawning or egg release in copepods at depth. This general mechanism could be most easily evaluated in a coastal environment where sampling can be done more frequently. An alternative explanation for the difference in developmental timing could be that of subspecific differences between coastal and oceanic populations. This possibility could be evaluated by conducting a population survey of genetic traits in *Neocalanus* along Line P and in other regions of the subarctic Pacific.

### 3.2 Copepod Feeding and Community Impact

- Despite high ingestion rates measured in *N. flemingeri* C5, this species and the closely related *N. plumchrus* accounted for 33% of the daily primary production in May 1994. Ciliates were ingested by *N. flemingeri* at a rate of 3.4 μg C·ind$^{-1}$·d$^{-1}$. 
Assuming a similar ingestion rate by *N. plumchrus*, a comparison of clearance rate and maximal growth rate of ciliates indicates that these copepods do not control ciliate stocks.

- Clearance rates calculated for *N. flemingeri* were not equal for all prey sizes and types. Smaller cells (< 10 \(\mu m\)) were generally ingested preferentially over larger cells. This is contrary to the general understanding of calanoid feeding behaviour. In addition, *N. flemingeri* ingested autotrophic cells preferentially over heterotrophic cells despite the fact that other copepods species are known to assimilate animal food more efficiently than plant food.

- There are few detailed bottle experiments combining epifluorescence and light microscopical counts in the literature. Although this method is labour intensive, it is the only method that allows for a detailed breakdown of copepod diet. The present experiment needs to be replicated at Station P. Experimentation of this type along Line P would allow for analysis of diet shifts from the coast to the open ocean.

- Calculations of copepod excretion based on a weight specific relationship indicate that the *N. plumchrus* and *N. flemingeri* community contributed about 8% to the total NH\(_4^+\) uptake by phytoplankton at Station P in May 1994. This result suggests that another mechanism exists for recycling ammonium in the mixed-layer.

- Egestion by *N. plumchrus* and *N. flemingeri* C5 contributed to about 61% of the downward vertical flux at 100 m measured by sediment traps. Comparing respiration requirements to potential ingestion of fecal pellets suggests that *N. cristatus* receives about 28% of its daily metabolic requirement from this source by capturing sinking particles in the lower mixed-layer. Including the consumption of microzooplankton prey, this species could meet half of its metabolic requirements. Other
sources of food for this copepod may come from fecal pellets produced by other zooplankton species living in the upper mixed-layer.


Dagg, M. 1993a. Grazing by the copepod community does not control phytoplankton production in the subarctic Pacific Ocean. Prog. Oceanogr. 32: 163-183.


Appendix A

Depth Distribution Graphs

The bar graphs presented in this Appendix are intended to illustrate depth distributions, day and night differences in abundance (for March 1993 cruise only), and nightly variability (for May 1993 cruise only). The height of bars are means ($\bar{X}$) and error bars are standard errors ($\pm$SE). Graphs for the 1993 data include three depth strata, whereas graphs for February 1994 have only one strata and those of May 1994 have two strata. Note that graphs that are without bars are included for consistency, but represent the absence of zooplankton (e.g. Fig. 1.11 *N. plumchrus* and *N. flemingeri* C5 in March 1993, and February 1994).
Figure A.29: Abundance estimates ($\bar{X} \pm SE, n = 3$) of *Eucalanus bungii* C1–4 at Station P during the two winter and summer cruises. Filled bars as in Fig. 1.11.
Figure A.30: Abundance estimates ($\bar{X} \pm SE, n = 3$) of *Eucalanus bungii* male C5 stages and adult males, and female C5 stages and adult females at Station P during the two winter and summer cruises. Filled bars as in Fig. 1.11.
Figure A.31: Abundance estimates ($\bar{X}$±SE, $n = 3$) of *Metridia* spp. C1–4 at Station P during the two winter and summer cruises. Filled bars as in Fig. 1.11.
Appendix A. Depth Distribution Graphs

**Figure A.32:** Abundance estimates ($\bar{X} \pm SE$, $n = 3$) of *Metridia* spp. male C5 stages and adult males stages, and female C5 stages and adult females at Station P during the two winter and summer cruises. Filled bars as in Fig. 1.11.
Figure A.33: Abundance estimates ($\bar{X} \pm SE, n = 3$) of *Eukronia hamata* and *Sagitta elegans* (all stages) at Station P during the two winter and summer cruises. Filled bars as in Fig. 1.11. Note different scales.
Figure A.34: Abundance estimates (X±SE, n = 3) of Parathemisto pacifica (all stages) at Station P during the two winter and summer cruises. Filled bars as in Fig. 1.11.
Appendix B

Details of all Line P Stations

This appendix contains a single table of all Line P stations with their corresponding latitude, longitude, depth and other station details.
### Table B.10: Cruise track and details of stations along Line P.

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<th>Depth</th>
<th>Notes</th>
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Appendix C

Temperature Profiles Along Line P

This appendix contains temperature profile graphs from all cruises, except May 1993 when there was a CTD failure. Only every other station along Line P is included. See Fig. 1.3 in Chapter 1 for the location of each station.
Figure C.35: Temperature profiles of some stations along Line P during the March 1993 cruise.
Figure C.36: Temperature profiles of some stations along Line P during the February 1994 cruise.
Figure C.37: Temperature profiles of some stations along Line P during the May 1994 cruise.