Title: Population Dynamics and Feeding Ecology of the Copepod, Metridia pacifica, in the Subarctic Pacific Ocean.

Abstract approved: Charles B. Miller

Abundances of the life stages of Metridia pacifica were followed at Ocean Station P in the eastern subarctic Pacific from February 1980 to March 1981. All stages were present throughout most of the year, but spawning was most concentrated during late winter, summer and autumn. Three cohorts appeared to be completed during the study period. Each cohort proceeded through development from early nauplii to adults at the same rate. This was probably achieved, in spite of substantially warmer sea surface temperatures during summer, because the third copepodite and older life stages (except adult males) migrate vertically during the day from the surface layer occupied at night to depths below 250 m, where water temperature does not vary seasonally.

The recommencement of reproduction in February and March, following a hiatus in female reproduction from November to January, initiates a cohort and provides an impetus for a cycling of the population age structure. Cyclic variation of the female reproductive condition, whereby few females are reproducing during
late May to June and in August, may reinforce the synchrony by restricting egg laying to short intervals.

Ingestion and respiration by *Metridia pacifica*, the dominant large copepod during autumn and winter in the subarctic Pacific, were investigated by shipboard and laboratory experiments. Diel variation in the rate of grazing on phytoplankton by *M. pacifica* was determined from measurements of gut pigment content and gastric evacuation rate. Both adult females and C₅ copepodites exhibited marked diel variation in gut contents, and thus feeding intensity. Nighttime gut pigment values were ten times greater than daytime values. Ingestion rates during May 1984 were 51.7 and 9.8 ng chl-a copepod⁻¹ day⁻¹ for adult females and fifth copepodites, respectively. Estimated filtering rates were 76 ml female⁻¹ day⁻¹ and 15 ml C₅⁻¹ day⁻¹. Feeding rates at low food concentrations in incubation bottles were similar to estimates obtained from in situ studies. Adult females consumed approximately 7.5% of body carbon day⁻¹, and C₅ copepodites only 2.5% day⁻¹.

Respiration was 4 to 10% of body carbon day⁻¹ for both C₅ and adults, indicating approximate energy balance for females but higher daily energy expenditure than gain for C₅. Based on the respiration measurements, a model was developed to evaluate the seasonal grazing impact of *M. pacifica* on the phytoplankton standing crop in the subarctic Pacific. During peak phytoplankton production in summer, the low densities of *M. pacifica* require less than 10% of daily primary production to satisfy metabolic, growth and reproduction
requirements. In contrast, the *M. pacifica* population requires 36 to 57% and exceptionally 175% of daily primary production to satisfy their energy requirements during autumn and winter. *M. pacifica* contributes significantly to the total grazing potential responsible for maintaining low stocks of phytoplankton during the unproductive, fall-winter, season in the eastern subarctic Pacific.

A numerical population dynamics model has been developed and used to investigate the functional response parameters of the copepod, *Metridia pacifica*. Equations describing growth, mortality, and reproduction are formulated and used to describe the development of individuals and generate a population dynamics history for year long model runs. Growth was described using an energetics based input-output model. Mortality was implemented as a constant daily per capita predation rate. Reproductive parameters of clutch size, clutch frequency, and total number of clutches were chosen to provide lifetime egg production rates similar to rates previously reported for other calanoid copepods. The model assumes that growth of *Metridia pacifica* in the subarctic Pacific is food-limited, and that temperature is unimportant.

Seasonal abundance and life history data for *Metridia pacifica* from Station P in the subarctic Pacific were used to evaluate the output of the model. The timing of life processes, such as the time for development from egg to egg, was considered the most important criterion for judging the suitability of the model and the choices made for the functional response parameters. "Reasonable" parameter
sets provided growth rates which allowed completion of development in a generation time of approximately 100 days; the generation time observed in the field. Development rate of *M. pacifica* in the model was very sensitive to food availability. This sensitivity may be responsible for the large year-to-year differences in abundance of *M. pacifica* at Station P.
Population Dynamics and Feeding Ecology of the Copepod, Metridia pacifica, in the Subarctic Pacific Ocean.

by

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A THESIS submitted to Oregon State University in partial fulfillment of the requirements for the degree of Doctor of Philosophy

Completed November 21, 1985
Commencement June 1986
ACKNOWLEDGEMENTS

Much of my development as a scholar has been influenced by my association and interaction with my major professor, Charlie Miller. Thank you Charlie for not holding back your thoughts and opinions about science and scientists. I would also like to thank Larry Small, Bill Pearcy, and Pete Dawson for their comments on this thesis.

Much of this thesis could not have been accomplished without the kindness and cooperation of many individuals and organizations. In particular I wish to thank the Offshore Oceanography Group (particularly Cor deJong) of the Institute of Ocean Sciences, Patricia Bay, and the officers and crew of the CCGS Quadra and CCGS Vancouver for permitting collection of the 1980-1981 zooplankton samples. Special thanks to Martha Clemons and Richard Conway, who helped in the collection of those samples. I also thank the participants of the SUPER program for their help and camaraderie during the May and August 1984 cruises.

Thank you also to the OSU biological oceanography group, but particularly, Mark Brzezinski, Dreas Nielsen, and Steve Ellis, for listening to my ideas and reading and commenting on early drafts of this thesis. Finally, thank you Diane for your friendship, love and understanding during a stressful period of our lives.

This research was funded by National Science Foundation Contracts OCE-7981687, OCE-8201899, and OCE-8309078 awarded to C. Miller.
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CHAPTER I

Introduction

Copepods are the dominant animals of the plankton in the world's oceans. Raymont (1983) goes so far as to state "They [copepods] must rank as the world's most abundant metazoans." (p. 166). It is because of their high abundances in planktonic systems that it is important to know their distribution, life cycles and feeding ecology if we wish to fully understand the pelagic ecosystem.

Numerous species of copepods are found in the plankton, yet feeding ecology has been studied for very few, and fewer still are studies of their life cycles or population dynamics. The studies which have been done have concentrated on a few species only, most notably *Calanus* spp. and *Acartia* spp. The former has been studied principally because of its large size and its presumed importance as food for many commercially valuable fishes. *Acartia* spp. commonly dominate the zooplankton of estuarine ecosystems and are, therefore, relatively accessible to researchers at marine laboratories.

The planktonic fauna of the subarctic Pacific ocean is strongly
dominated by relatively few species. The large copepods, *Neocalanus cristatus*, *Neocalanus plumchrus*, *Eucalanus bungii*, and *Metridia pacifica* constitute a large fraction of the herbivorous biomass in this oceanic region. Together with the chaetognaths, *Eukrohnia hamata* and *Sagitta elegans*, and the euphausiids, *Euphausia pacifica* and *Thysanoessa longipes*, these copepods probably comprise 80 to 90% of the zooplankton biomass of the subarctic Pacific (Vinogradov, 1970).

Physical Oceanography of the Subarctic Pacific

The review of the physical oceanography and water column characteristics of the subarctic Pacific which follows is from Favorite et al. (1976). The southern boundary of the subarctic domain of the North Pacific Ocean was defined by Dodimead et al. (1963) by the latitude where the 34 % isohaline descends vertically from the surface to intermediate depths (Fig. I.1). The location of the southern boundary is commonly near 38 to 45°N latitude varying somewhat both seasonally and interannually. Occasionally it meanders north of 50°N at 145°W. Favorite et al. (1976) used T-S curves and surface circulation features to define five distinct domains in the eastern subarctic Pacific: Coastal, Transition, Upwelling, Ridge, and Dilute (Fig. I.2). The Coastal Domain occurs adjacent to shore in regions influenced strongly by river discharge, usually not extending beyond the shelf. The Transition Domain lies just north of the subarctic boundary. Surface salinity in this
Figure I.1

Vertical sections of long-term mean temperature (A) and salinity (B) along 159°W. (From Favorite et al., 1976).
Figure I.1
Surface domains and current systems in the subarctic Pacific region. ACS - Alaska Current System; AG - Alaskan Gyre; BCS - Bering Current System; BSG - Bering Sea Gyre; CCS - California Current System; CPG - Central Pacific Gyre; DD - Dilute Domain; OKCS - Okhotsk Kurile Current System; OSG - Okhotsk Sea Gyre; P - Station Papa; RD - Ridge Domain; SCS - Subarctic Current System; TD - Transition Domain; UD - Upwelling Domain; WSG - Western Subarctic Gyre. (Redrawn from Favorite et al., 1976).
domain remains higher than 33.0 %. year-round. Most of the region is characterized by slow transpacific zonal flow from west to east. The region of upwelling off the coast of Northern California, Oregon, Washington and Southern British Columbia in summer defines the Upwelling Domain. During summer upwelling, surface temperatures there are 5°C lower than in offshore waters which have not been influenced by upwelling. The Ridge Domain is not well defined by surface features, but is clearly evident in subsurface features. The northward flow of deep water in the Pacific is deflected toward the surface when it interacts with the Aleutian-Commander Island Arc, injecting a vertical tongue of cold, saline, nutrient-rich, and oxygen-poor water into the more dilute surface water.

The Upwelling, Transition, and Ridge Domains, having greater than 33.0 % surface salinity, border the central Dilute Domain which is characterized by surface salinities less than 33.0 %. Low salinity water of the Dilute Domain appears to form from the interaction of the diverging Subarctic Current with the westward extension of relatively fresher plumes from the Columbia River, Strait of Juan de Fuca, and Queen Charlotte Sound. The lens of fresh water extends from the surface to approximately 100 m. Below 300 m the features of this domain are indistinguishable from the adjacent Ridge and Transition domains. Ocean Station Papa (P) at 50°N, 145°W, the site for much of the work in this thesis, is within the Dilute Domain. Temperature-salinity curves from several months during 1980 and 1984, the field periods of this study, are shown in
Temperature–salinity plots from Station P. (A) March 1980; (B) May 1980; (C) August 1980; (D) May 1984; (E) August 1984. Deepest depth for each date is 600 m; tick depths as in (A).
Figure 1.3
The lens of low salinity surface water in the Dilute Domain provides a permanent pycnocline near 100 m depth, which acts as a barrier to deep convective overturn during the winter. The seasonal cycle of water column temperature is shown in Figure 1.4. A shallow thermocline and secondary pycnocline begin to develop above the permanent pycnocline during April. The seasonal mixed layer warms and shallows during spring and summer, until in September the temperature is close to 14°C at the surface and the thermocline is near 25 m. From October to March the surface layer cools and deepens by winter mixing. The surface lens of dilute water is sufficiently light that winter mixing is unable to mix it through the permanent pycnocline at 100 m. The subarctic Pacific never experiences the deep convective winter overturn typical of the subarctic Atlantic.

Biological Oceanography of the Subarctic Pacific

Miller et al. (1984) recently summarized the regional ecology, especially that pertaining to primary production by phytoplankton, and grazing by zooplankton, of the oceanic realm of the eastern subarctic Pacific Ocean. In order to provide a conceptual framework, within which the current study fits, I shall provide an abbreviated overview of the ecology of this ocean region.

Long term time series of chlorophyll observations from the
Figure I.4

Thermal structure of the water column at Station P for the period from January 1980 to March 1981. (From Miller et al., 1984; data originally from Institute of Ocean Sciences, 1981).
Figure I.4
Canadian Weather Station Papa (P), located at 50°N, 145°W in the eastern subarctic Pacific, have established the absence of spring blooms. There are few reports of chlorophyll concentrations which exceeded 1.0 mg m⁻³. Chlorophyll concentrations remain in the relatively narrow range of 0.1 to 0.6 mg m⁻³ throughout the year, with most values close to 0.3 mg m⁻³ (Fig. 1.5). The seasonal constancy of phytoplankton stocks of the oceanic subarctic Pacific differs substantially from the large amplitude cycles of plant stocks in the Coastal Domain of the subarctic Pacific and in the oceanic North Atlantic. Plant stocks in those two regions during the spring bloom are 15 to 20 times greater than concentrations preceding the bloom.

The species composition of the phytoplankton in the subarctic Pacific was relatively unknown until recently. Preservation and microscopic techniques advanced sufficiently during the last decade to allow better quantification and more rigorous description of the smaller species of phytoplankton. Most of the plants in the subarctic Pacific are smaller than 5 μm (Booth et al., 1982). Occasional blooms of much larger cells, Corethron hystrix, Thalassiothrix longissima, or Rhizoselenia alata, sometimes occur (Clemons and Miller, 1984), but cell numbers in those instances are never sufficient to be evident in measures of chlorophyll-a concentration.

Although plant stocks do not accumulate seasonally, phytoplankton primary production varies seasonally, increasing from
Figure I.5

Annual cycle of chlorophyll-a (ug Chl liter$^{-1}$) at Station P (50°N, 145°W). Data from many years summarized in Anderson, et al. (1977).
Figure I.5

Station 'P'
1959-1970
low values during winter to higher values in spring and summer (Stephens, 1968). Nitrate concentration in the upper mixed layer exhibits the seasonal cycle that would be expected from the productivity cycle, with nitrate concentration decreasing from April to October (Anderson et al., 1977), the period of high phytoplankton production (Fig. I.6).

The now "classical" explanation for the absence in the subarctic Pacific of a spring phytoplankton bloom, in spite of increased phytoplankton growth rates during spring and summer, is that zooplankton grazers crop the spring and summer plant production as it occurs. Thus the high spring and summer phytoplankton production becomes evident as an increase in zooplankton biomass rather than in phytoplankton biomass (Fig. I.7). Heinrich (1957, 1962) suggested that *Neocalanus plumchrus* and *N. cristatus*, the two dominant zooplankton grazers, produced young in early spring before the increase in plant production, using lipid reserves stored during the previous year's growing season. The abundant early copepodite stages present from mid-winter through spring represented an enormous grazing potential which affected immediate cropping of the spring production.

The life cycles of three of the dominant herbivorous copepods at Station P, *Neocalanus plumchrus*, *N. cristatus* and *Eucalanus bungii*, have been described recently (Miller et al., 1984). Subsequent work has revealed that the *N. plumchrus* of that study is in fact comprised of two very similar species, *N. plumchrus* and
Seasonal cycle of nitrate concentration (ug-at liter$^{-1}$) at Station P. (From Anderson et al., 1977).
Figure I.6
Long-term seasonal cycle of zooplankton biomass at Station P. (Data summary by J. Fulton; vertical hauls (0-150 m) made during the day with 350 um mesh and 0.5 m diameter net).
ZOPLANKTON BIOMASS

(mg/m³)

Figure I.7
Neocalanus n. sp., having slightly different timing of life cycle events. The season of maximum growth and development for all four species was April to mid-July, corresponding to the period of maximum phytoplankton production. The population cycles of all the species, but especially of *N. plumchrus*, appear to be suitably timed to effect control of plant stocks in the spring and early summer.

Density of *N. plumchrus* (both species) in the upper mixed layer in 1980 declined during June to September. At that time *N. plumchrus* grazing pressure upon the plant stocks must be low compared to earlier in the year, yet stocks of phytoplankton increased only slightly (Clemons and Miller, 1984). Since plant production is still substantial, other herbivores must increase in density or grazing activity during late summer and autumn to replace the grazing activity of *N. plumchrus*. Potentially important herbivores in late summer and autumn are the intermediate sized copepods *Pseudocalanus* spp., *Calanus pacificus*, and *Metridia pacifica*, the euphausiids *Euphausia pacifica* and *Thysanoessa longipes*, and several species of salps. Zooplankton data collected from the weatherships suggests that the principal consumers during the fall may differ from year to year (Fulton, unpubl.). During some autumns *Calanus pacificus* increase in abundance, while in other years *Metridia pacifica* or some other species becomes abundant. Zooplankton collections from the Canadian weatherships at Ocean Station P during autumn and winter 1980-1981 were dominated by *Metridia pacifica*. From population abundance and biomass estimates it appeared that *M.*
pacific could be responsible for maintaining low phytoplankton stocks during the autumn.

Species of the genus Metridia are abundant, vertically migrating herbivores and omnivores in many high latitude ocean ecosystems. Metridia lucens and M. longa are abundant in Gulf of Maine (Haq, 1967) and Scotian Slope waters (Sameoto, 1982). Metridia longa, the larger of the two species, has a wide geographic distribution in the North Atlantic, ranging from Baffin Bay and the Northern Labrador Sea (Huntley, Strong and Dengler, 1983; Harrison et al., 1985) to deep Norwegian fjords (Tande and Gronvik, 1983; Gronvik and Hopkins, 1984). The seasonal abundance, life cycle, and reproductive maturity of M. longa have been documented for the population in Balsfjorden, Norway (Tande and Gronvik, 1983; Gronvik and Hopkins, 1984). In the North Pacific, Metridia pacifica is abundant in oceanic regions of the Bering Sea (Dagg et al., 1982; Cooney and Coyle, 1982), central Gulf of Alaska (Marlowe and Miller, 1974), and has also been found in the California Current off the shelf of Oregon (Peterson and Miller, 1976) and California (Enright and Honegger, 1977). In the southern hemisphere, Metridia gerlachei is one of the dominant copepods in waters near the Antarctic peninsula (Schnack, 1983). Many Metridia spp. migrate vertically several hundred meters daily (Vinogradov, 1970; Marlowe and Miller, 1974; Enright, 1977). Thus, the center of distribution and abundance of Metridia spp. is usually over deep water; rarely are they abundant over the continental shelf.
Metridia spp. may be key components in the transfer of energy from primary producers to secondary consumers (carnivores) in oceanic systems. Metridia pacifica is an important prey of chaetognaths (Sullivan, 1980) and myctophid fishes (McCrone, 1981) in the subarctic Pacific. The chaetognaths Sagitta elegans and Eukrohnia hamata were the most abundant zooplanktonic carnivores found at Station P by Marlowe and Miller (1974). In nearly all size classes of Stenobrachius leucopsarus and many of the Diaphus theta examined by McCrone (1981) M. pacifica juveniles (copepodites) and adult females were the most abundant food item. In addition to its potential key role in the transfer of organic matter to higher trophic levels, M. pacifica, through its daily vertical migration, may be an important pathway in the transfer of matter to the deep-sea.

The feeding and metabolism of Metridia spp. are not well known. Haq (1967) investigated feeding and metabolism of M. lucens and M. longa from the Gulf of Maine, and Schnack (1983) measured ingestion and particle selection by M. gerlachei. Also, the nitrogen metabolism of Metridia spp. (probably M. longa) in the eastern Canadian Arctic has been measured (Harrison et al., 1985).

In view of the widespread distribution, abundance, and potential trophic importance of Metridia spp., surprisingly little is known about their biology and ecology. Thus, the goal of this thesis is to investigate and document the biology of Metridia pacifica. Specifically, this thesis addresses three major
objectives. First, to document the population abundance, vertical
distribution, and life cycle of *M. pacifica* in the subarctic
Pacific, using samples collected during 1980 and 1981. Second, to
investigate the feeding ecology and energetics of this species.
Third, to evaluate from population abundance estimates and
energetics, the role of *M. pacifica* in maintaining the constant low
standing stocks of phytoplankton observed in the oceanic subarctic
Pacific.
Chapter II

Seasonal Abundance, Vertical Distribution, and Life History of *Metridia pacifica* (Copepoda: Calanoida) in the Oceanic Subarctic Pacific.

Abstract

Abundances of the life stages of *Metridia pacifica* were followed at Ocean Station P in the eastern subarctic Pacific from February 1980 to March 1981. All stages were present throughout most of the year, but spawning was most concentrated during late winter, summer and autumn. Three cohorts appeared to be completed during the study period. Each cohort proceeded through development from early nauplii to adults at the same rate. This was probably achieved, in spite of substantially warmer sea surface temperatures during summer, because the third copepodite and older life stages (except adult males) migrate vertically during the day from the surface layer occupied at night to depths below 250 m, where water temperature does not vary seasonally.

The recommencement of reproduction in February and March, following a hiatus in female reproduction from November to January, initiates a cohort and provides an impetus for a cycling of the population age structure. Cyclic variation of the female reproductive condition, whereby few females are reproducing during late May to June and in August, may reinforce the synchrony by restricting egg laying to short intervals.
Introduction

Life histories of marine copepods are known best for coastal and estuarine species. *Acartia clausi* (Landry, 1978; Uye, 1982) and *A. californiensis* (Johnson, 1981) have been particularly well studied. The life cycles of *Eurytemora herdmani* (McLaren and Corkett, 1981), *Calanus finmarchicus* (Tande, 1982), *Euchaeta norvegica* (Bakke, 1977), *Neocalanus plumchrus* (Fulton, 1973), and the small copepods of Loch Striven (Marshall, 1949; McLaren, 1978) are also fairly well known. Several features are common to these studies. First, advective inputs and losses from the population were minimized by studying isolated populations in relatively closed bodies of water. Second, tracking of cohorts in the field, and thus the study of population dynamics, was facilitated by proximity to coastal laboratories, which permitted frequent sampling of the population relative to the generation time of the copepods.

Study of the population dynamics of oceanic species is more difficult, and there are no investigations comparable to those of the coastal forms listed above. The sibling species, *Metridia pacifica* Brodskii and *M. lucens* Boeck, are common, vertically migrating copepods in oceanic waters of the subarctic North Pacific and North Atlantic, respectively (LeBrasseur, 1965; Marlowe and Miller, 1974; Sameoto, 1982). Despite their high numerical abundance, no data are available that permit quantitative description of the seasonal dynamics or life history of either species. Heinrich (1962b) has shown that, in the Bering Sea, where
there is a substantial spring phytoplankton bloom, *M. pacifica* had up to four broods during summer and autumn. Koeller et al., (1979) found only older copepodite stages of *M. pacifica* in British Columbia coastal waters during autumn and early winter; early copepodites first appeared in January. However, neither of these studies included the fine-mesh sampling required to provide data for naupliar stage abundance, which are necessary for a thorough evaluation of the life history of copepods.

The remoteness of oceanic habitats generally prohibits the sampling frequency requisite for quantitative evaluation of zooplankton life histories. However, at a few sites weatherships have provided extended time-series data. The site most thoroughly exploited for this purpose is Ocean Sta. P (50°N, 145°W) in the subarctic Pacific. It was occupied continuously by weatherships from World War II to June 1981, primarily to gather meteorological and oceanographic observations. As part of this program, vertical plankton hauls have been taken regularly (usually twice weekly) from 150m to the surface since 1956 (Fulton, 1983). However, these collections are not suitable for a comprehensive life history study of *M. pacifica* because the 350µm mesh net used does not quantitatively capture *M. pacifica* life stages younger than fourth copepodites and because no night-time hauls were taken. The lack of night-time sampling is the greater problem as *M. pacifica* females and older copepodites are strong diel vertical migrators (Vinogradov, 1970; Marlowe and Miller, 1974; Enright, 1977).
However, during the last year of operation of the weatherships at Ocean Sta. P, a sampling program was designed for the examination of the population dynamics of the large herbivorous copepods residing in the subarctic Pacific. The population dynamics of *Neocalanus plumchrus*, *N. cristatus*, and *Eucalanus bungii* have been described from the new data set (Miller et al., 1984). The life history and population dynamics of another large herbivorous copepod, *M. pacifica*, is described herein.
Methods

Field sampling

Zooplankton were sampled using opening-closing 73 um and 333 um mesh "Puget Sound" nets of 0.7 m mouth diameter (Miller, et al., 1984). Nets were hauled vertically at 1 m s\(^{-1}\) and closed by messenger without stopping on ascent. Weekly sampling with nets of both mesh sizes, except when net losses or inclement weather prevented sampling with one or both mesh sizes, began in February 1980 and continued for 14 months. The 73 um net was given priority over the 333um net when only one sample series was possible. A 211 um mesh net was used instead of the 73 um net during March 1980. During June 1980 both 73um mesh nets were lost so only 333um samples are available. Sampling of the water column was divided into the following depth intervals: surface to thermocline depth (TH), TH to 100 m, 100 to 250 m, 250 to 500 m, 500 to 1000 m, and 1000 to 2000 m. To minimize diel vertical migration effects, only samples collected at night (2100 to 0100 h) were used for the description of seasonal population dynamics. Several daytime sample series (0900 to 1300 h) were used to evaluate the diel vertical migratory behavior of *M. pacifica*. Samples were preserved in 10% formalin-seawater, buffered with sodium borate.

Flow of water through the net was not measured for most samples. Attempts to meter the flow of water through the net met
with little success. Flowmeters mounted in the mouth of the net were often damaged when the net closed. Since evidence of clogging was not observed and wire angles rarely exceeded 15° from vertical and were usually <5°, the volume of water filtered by the net was estimated as the vertical distance of the haul times the mouth area of the net.

Hydrographic data were collected on all cruises (Institute of Ocean Sciences, 1981). CTD casts to 1200 m were made daily and bottle casts for temperature, salinity, oxygen, and chlorophyll a weekly.

**Determination of life stages of *M. pacifica***

The abundances of third copepodite and older stages of *M. pacifica* were estimated from subsamples obtained by a Folsom splitter (McEwen et al., 1954). Examination of 1/32 to 1/2 of a sample provided adequate numbers (100's) of the older (larger) life stages. Counts of nauplii and first and second copepodites were obtained from 73um mesh samples after subsampling with a 1 ml piston pipette; subsampling fractions ranged from 1/400 to 1/50 of the entire sample. When the intended sampling depths were not met, densities were corrected to the standard depths. Abundances are expressed as the water column sum of individuals m⁻² (0 to 500 m for N₁-C₂; 0 to 2000 m for C₃-C₆), to facilitate comparison among sampling dates.
The six copepodite stages \((C_1, C_2, \ldots, C_6)\) of \(M.\) pacifica were readily distinguished. Sexes of fifth copepodites and adults are differentiated. The naupliar stages \((N_1, N_2, \ldots, N_6)\) of \(M.\) pacifica have not been described; however \(N_1\) to \(N_6\) of the closely related \(M.\) lucens from the North Atlantic have been described (Ogilvie, 1953). The nauplii of \(M.\) lucens are morphologically similar to those of Neocalanus plumchrus (=Calanus tonsus (Campbell, 1934), one of the dominant copepods at Ocean Sta. P. However, an attempt to rear \(M.\) pacifica was successful, so the nauplii more readily can be distinguished from \(N.\) plumchrus in field samples. The morphology of the naupliar stages of \(M.\) pacifica will be reported in detail in a subsequent paper. In the present paper the two youngest naupliar stages \((N_1\) and \(N_2)\) of \(M.\) pacifica are considered together.
Results

Hydrography and Chlorophyll

The seasonal cycle of temperature (Fig. II.1) is typical of the subarctic Pacific region, with surface temperature warming from 5.6°C in late March to April to a maximum of 13.9°C in mid-September 1980. Thermal stratification was established abruptly at 60 m between 1 June and 6 June, as surface temperature rose from 7.2°C to 9.2°C. The thermocline gradually intensified and the mixed layer shoaled to 25m by early July. Maximum temperature difference between the upper mixed layer and deeper water occurred in mid-September. The mixed layer began cooling in late September with erosion and deepening of the thermocline through March. Salinity profiles (Miller et al., 1984) showed the strong permanent halocline between 100 and 125m that is characteristic of the subarctic Pacific region (Favorite et al., 1976).

The distribution of chlorophyll concentration with season and depth over the 14 month study period is reported by Clemons and Miller (1984). Chlorophyll values were consistently low, varying little throughout the year, as reported previously for Ocean Sta. P (McAllister et al., 1960; Anderson et al., 1977). Maximum chlorophyll concentrations, up to 0.8 mg Chl-a m⁻³, were observed in October and November. Values exceeding 0.3 mg m⁻³ in the mixed layer were common during autumn and winter (September to January) but were
Figure II.1

Thermal structure of the water column at Station P during the study period, January 1980 to March 1981. (From Miller et al., 1984)
Figure II.1
rare during spring and summer.

Seasonal dynamics

All life history stages of *M. pacifica* were present throughout the year, except during January 1981, when naupliar stages were absent. Most stages exhibited distinct patterns of abundance with time. The data indicate three peaks in reproduction: early spring, summer, and autumn.

**Nauplii.** Naupliar stages N₁ to N₄ increased in abundance from February to April 1980 and remained abundant during May (Fig. II.2). Naupliar stages N₅ and N₆ increased logarithmically into May (Fig. II.3), although N₄ remained the most abundant stage during May. No naupliar data are available for June 1980 due to the loss of the 73um net, however, the data on copepodite stages C₃ and C₄ suggest that a second cohort was initiated during late May and June.

Densities of N₁+2, N₃ and N₄ in early July, like those in April and May, were high (Fig. II.2). Density decreased by one and a half to two orders of magnitude later in July as they progressed to older stages. Abundances of N₅ (7700 m⁻²) and N₆ (3700 m⁻²) in early July were substantially lower than in mid-May (34,000 N₅ m⁻²; 17,000 N₆ m⁻², respectively), but increased for a short period, with N₅ peaking at 86,000 m⁻² and N₆ at 14,000 m⁻² on 19 July (Fig. II.3). By 20 August the densities of N₅ and N₆ had declined to approximately 1000 m⁻². The decline and density minima of the four
Figure II.2

Number m$^{-2}$ of first four naupliar stages of *Metridia pacifica* from 0 to 500 m. □ indicate N$_1$ and N$_2$ combined, ▲ N$_3$, ○ N$_4$, ◇ no nauplii found.
Figure II.2
Figure II.3

(A) Percentage of all naupliar stages ($N_1$ to $N_6$) of *Metridia pacifica* between given depths. "TH" indicates thermocline depth.

(B) Number $m^{-2}$ of $N_5$ and $N_6$ from 0 to 500 m. ▲ indicates $N_5$, ○ $N_6$, ∅ no nauplii found.
Figure II.3
youngest naupliar stages preceded the decline and minima of $N_5$ and $N_6$ by about a week. From August to November, numbers of $N_{1+2}$, $N_3$ and $N_4$ remained constant, or increased only slightly, as mortality and maturation were balanced by recruitment. Numbers of both $N_5$ and $N_6$ peaked (40,000 m$^{-2}$; 25,000 m$^{-2}$, respectively) in late November. Stocks of all naupliar stages began to decline rapidly in late November (Figs. II.2 and II.3), resulting in their absence from the water column in January 1981. The data indicate a progression, in which the $N_{1+2}$ and $N_3$ disappeared first, followed in succession by $N_4$, $N_5$ and $N_6$. On 3 February 1981 all naupliar stages were again abundant, $N_4$ and $N_5$ being most numerous.

Copepodite stages $C_1$ and $C_2$. The patterns of abundance of $C_1$ and $C_2$ stocks through the year (Fig. II.4) were similar to those observed for the later naupliar stages ($N_5$ and $N_6$). No $C_1$ were found in the water column when sampling was initiated on 6 February 1980. The stock of $C_1$ increased rapidly during March and April, attaining a density of approximately 10,000 m$^{-2}$ in May. Abundance of $C_2$ declined between 6 and 19 February, the minimum occurring two weeks later than that of $C_1$. The stock of $C_2$ then increased until May (7000 m$^{-2}$). Unfortunately, $C_1$ and $C_2$ (like naupliar stages) are not captured, and $C_3$ are not sampled quantitatively with a 333 μm mesh net; thus no data are available for late May and June. Density of $C_1$ remained high during summer, ranging from 5000 to 17,000 m$^{-2}$, whereas that of $C_2$ was somewhat lower during this period. Both stocks decreased in October; densities were roughly 2000 m$^{-2}$ (Fig.
Figure II.4

(A, B) Percentages of *Metridia pacifica* C₂ and C₁, respectively, between given depths. (C), Number m⁻² of C₁ and C₂ from 0 to 500 m. ▲ indicates C₁, ○ C₂, Ø no copepodites found.
Figure II.4
From October to early December, stocks of C₁ and C₂ increased, attaining maximum values of 41,000 m⁻² and 24,000 m⁻², respectively, on 4 December. These high densities occurred one and a half to two weeks later than the maxima of N₅ and N₆, which by 4 December were already well into decline (Fig. II.3). The dramatic decline in C₁ and C₂ density during winter is similar to that of the naupliar stages. The stocks of C₁ decreased rapidly to a minimum in mid-January at the time when N₅ and N₆ were absent. The C₂ stock declined more slowly and did not reach a minimum until mid-February 1981, a full month after the C₁ minimum. The time when the density of C₂ was least in 1981 closely corresponded to that of the minimum in 1980 (Fig. II.4). Unlike nauplii, neither C₁ nor C₂ was absent totally from the water column during January and February 1981. By March 1981, C₁ and C₂ were both numerous, each having densities of roughly 20,000 m⁻². Although the timing of the midwinter minimum was similar in the two years, the recovery from low abundance was much more rapid in 1981 than in 1980. Nauplii and early copepodites reached densities in March 1981 that were not attained in 1980 until April and May. Throughout the study, fewer C₂ were found than C₁, except during periods when both stages declined in abundance. At these times, the rate of decline of C₁ exceeded that of C₂, resulting in temporary predominance of C₂.

Copepodite stages C₃ and C₄. The data for C₃ (Fig. II.5) and C₄ (Fig. II.6) show three distinct peaks of abundance during April to
(A) Percentages of *Metridia pacifica* C3 between given depths (0 to 500m only). (B) Number m⁻² of C3 from 0 to 2000 m. ○ indicates estimates from 333um, ● from 73um mesh.
Figure II.5
(A) Percentages of *Metridia pacifica* C₄ between given depths. (B) Number m⁻² of C₄ from 0 to 2000 m.
Figure II.6
May, August, and December, suggesting that three cohorts occurred during the year. Times of peak abundance were separated by periods when densities were lower by a factor of 5 to 10. The April to May population peak was the smallest and the midwinter peak the largest for both stages. The data for C₃ and especially for C₄, provide strong evidence for there being three main periods (peaks) of reproduction in *M. pacifica*. It is primarily from these data that I infer a peak in reproduction (initiation of the second cohort) in late May and June. The low abundance of C₄ in late March 1980 followed periods of low abundance of all younger stages in February. Assuming a similar pattern in summer, the low C₄ densities of June and early July almost certainly were preceded by low densities of nauplii, C₁ and C₂, in late May and early June. Abundances of C₃ and C₄ were an order of magnitude greater in February to March 1981 than in February to March 1980, indicating that substantial interannual variability may occur in the abundance of *M. pacifica*.

Copepodite stage C₅ and adults. Cohorts, such as those observed for C₃ and C₄ life stages, are not clearly defined in the seasonal abundance data for C₅ (Fig. II.7) or adults (Fig. II.8). An increase of both sexes of C₅ began in early July 1980 and continued through mid-December. After December the stocks of both sexes declined through the remainder of the sampling program. The C₅ sex ratio significantly (p<.001; Paired t-test) favored males throughout the study; on average, males comprised 60% of the C₅ population.

Adult males and females were more abundant during autumn than
Figure II.7

(A, B) Percentages of *Metridia pacifica* C5 males and C5 females, respectively, between given depths. (C) Number m$^{-2}$ of C5 males (solid circles) and C5 females (open circles) from 0 to 2000 m.
Figure II.7
Figure II.8

(A, B) Percentages of *Metridia pacifica* adult males and females, respectively, between given depths. (C) Number m$^{-2}$ of adult males (solid circles) and adult females (open circles) from 0 to 2000 m. Dashed vertical lines delimit times of changed sex ratios.
Figure II.8
at other times of the year (Fig. II.8). Peak female density occurred in late November and preceded the peak abundance of males by a month. As only a 10-fold amplitude in the abundance of males and females was observed during the study period, it was difficult to evaluate the significance of individual highs and lows of abundance. Thus, cohort analysis could not be based solely on adult abundances.

The yearly average sex ratio of adults was not significantly different from 1:1. However, the pattern of the sex ratio (Fig. II.8) was nonrandom with time (p<.001; Runs test). Not only were there significant changes in the sex ratio during the year, but the sex ratio during February to March 1981 differed from that during February to March 1980.

Seasonal variation of nighttime vertical distribution

Naupliar abundance was evaluated on several sampling dates for all depths to 2000 m. However, because nauplii were seldom found in samples deeper than 500 m, usually only samples shallower than 500 m were evaluated for naupliar abundance. During April and May more than 80% of all nauplii in the water column were shallower than 100 m (Fig. II.3). The upper 100 m, during summer when a shallow seasonal thermocline (TH) was present, was divided into two sampling intervals, 0 m to TH and TH to 100 m. On 4 July, the first date for which naupliar abundance is available following the June sampling
hiatus, roughly equal numbers of nauplii were found above and below the seasonal thermocline. A week later, most of the nauplii (>85%) were below the thermocline, where they remained until 22 September. After this date nauplii were again more numerous in the surface layer than in deeper, colder water. Although the temperature of the upper mixed layer is probably the major factor determining summer depth distribution, additional factors may be involved since the mixed layer remains warm, generally exceeding 10°C, into early November.

The seasonal depth distributions of C₁ and C₂ stocks were similar to those observed for the nauplii. Density of C₁ and C₂ decreased with increased depth (Fig. II.4). Throughout the year roughly 70% of the stocks of both stages were collected from depths shallower than 100 m, and few individuals were deeper than 250 m. The distribution of C₃ copepodites with depth is shown for the upper 500 m only (Fig. II.5), since <1% were ever deeper than 500 m. More than 90% of the C₄ individuals were found in the upper 500 m at all times; they were equally abundant in the 0 to 100 m and 250 to 500 m depth strata throughout the year, while comparatively few were collected between 100 and 250 m (Fig. II.6). The underlying cause of this feature is obscure but may be related to the pattern of diel vertical migration. If only some individuals of a migrating species migrate to the surface each night, the resultant nighttime vertical distribution will appear bimodal. The temporal pattern of C₃ depth distribution was not as regular as that of the C₄. Roughly 50 to 60%
of the C₃ individuals were shallower than 100 m from March to December 1980; in contrast, C₃ were most abundant at 250 to 500 m during midwinter (December 1980 to February 1981).

From March to August, 80% of C₅ males occurred shallower than 500 m (Fig. II.7). During September the depth distribution shifted, with 50% of the population below 500 m. Roughly equal numbers of C₅ males were collected shallower and deeper than 500 m from September 1980 to March 1981. Most of the increase in C₅ male density during late 1980 (Fig. II.7) reflects increased numbers in the 250 to 500 m and 500 to 1000 m samples. Density at depths shallower than 250 m increased only 3- to 4-fold during the latter half of 1980, whereas density at 250 to 500 m and 500 to 1000 m increased 10- and 20-fold, respectively, at that time. The depth distribution of C₅ females varied in a manner similar to that of C₅ males, except the density increase deeper than 500 m was not as great and occurred slightly later during the autumn (Fig. II.7). Since both sexes of C₅ copepodites engage in diel vertical migration (see below), the increased percentage of C₅ males and C₅ females below 500 m in winter may reflect a decreased proportion of individuals actively migrating to the surface at night, either because some individuals are no longer migrating at all, or because the frequency of migration by an individual to the surface has decreased.

Adult male and female distributions with depth are shown in Figure II.8. Males were found almost exclusively between 250 m and 1000 m at all seasons. Seventy percent (on average) of the adult
females were collected in the upper 100 m, except during November and December, when <25% were near the surface, and females were most abundant at 250 to 500 m. Hence, males and females are seldom found at the same depth at night.

Day-night depth distributions

Diel vertical migratory behavior by nauplii and copepodites C₁ and C₂ was not investigated in this study. Day-night comparisons of depth distributions of older copepodite and adult stages for July and August 1980 and January 1981 are shown in Table II.1. The data imply that all copepodite life stages (C₃-C₆), except adult males, undergo diel vertical migratory behavior during July and August. A greater fraction of the stock of each stage was found near the surface at night than during the day. The seasonal thermocline apparently did not inhibit vertical migration to the surface of any life stage. Smaller fractions of the total population of each life stage were near the surface at night in January than during midsummer. This was particularly evident for stocks of C₄ and C₅ females. There was no difference in the day-night depth distribution of C₃ in January. During winter this stage apparently ceases migrating to the surface at night. Substantial numbers of adult females remained below 100 m at night during the winter, in contrast to the very few remaining deeper than 100 m during summer. Adult males were seldom found near the surface during either day or night, thus mating presumably occurs at depth.
Table II.1. Day-night vertical distribution of life stages (C₃ to adult) of *Metridia pacifica* for three periods at Station P.

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<td></td>
<td>1000-2000</td>
<td>0</td>
<td>0</td>
<td>NS</td>
</tr>
</tbody>
</table>

* Th indicates the depth of the thermocline.

† NS indicates no sample available.
Discussion

Three cohorts of *M. pacifica* developed at Sta. P during 1980. Peaks of reproduction, which established the cohorts, occurred in early spring (March), summer (late June and July), and early autumn (September to early October). The seasonality of the reproductive condition of female *M. pacifica* in the subarctic Pacific during February 1980 to March 1981 (Fig. II.9) will be reported elsewhere (Batchelder, paper submitted). The percentage of the adult female population in "fully spawning" condition in the upper 100 m exhibited seasonal trends similar to those observed for the youngest naupliar stages. The low percentage of "fully spawning" females during May and early June suggests that the abundance of young nauplii may be lower in late May and June than was observed in early May and early July (Fig. II.2). Such a decline in naupliar abundance during May and June would be consistent with the observed seasonal pattern of copepodite C₃ and C₄ abundance (Figs. II.5 and II.6), which showed distinct minima during June and early July, respectively.

The three cohorts developed at the same rate, each requiring 3 to 4 months. The seasonally constant cohort development rate was probably achieved, even though the surface layer warmed during summer, because *M. pacifica* migrate vertically. During the day, most of the later life stages are below 250 m (Table II.1) where temperatures do not vary seasonally (Fig. II.1). Thus, for much of the time individuals in all three cohorts develop at the same,
Percentages of reproductively mature adult females in the 0 to 100 meter depth interval.
19% OF FEMALES IN "FULLY SPAWNING" CONDITION

Figure II.9
constant low temperatures below 250 m. This provides a mechanism by which the three cohorts could have equal-length generation times, despite substantially warmer surface temperature during summer.

The strongest evidence for a generation time of 3 to 4 months is provided by analysis of the third and largest cohort. Table II.2 provides the estimated water column abundances for all life stages of *M. pacifica* for the period from 22 September 1980 to 3 February 1981. The data indicate that this cohort began at the end of September or early October, when stages N_{1+2} and N_3 were abundant. By November, the 15 October pulse of N_3 had progressed to N_4, N_5, and N_6, which developed to early copepodite stages by December, while naupliar abundance declined. In early January, the population was mostly late stage copepodites, and nauplii were very scarce. No nauplii were found on 11 January, yet all naupliar stages were present in substantial numbers on 3 February. Assuming that the time of peak N_{1+2} abundance was 1 October, the generation time can be estimated to be at least 104 days and less than 126 days. Because the midwinter hiatus in reproduction occurred at the end of this cohort it is likely that 126 days is an overestimation of the generation time. The consistently high counts of C_5 (Table II.2) probably reflect a substantially longer and more variable intermolt period in that stage than in the other stages. Similar trends have been observed for intermolt periods of other copepods, such as *Calanus* spp. (Peterson, 1980; Landry, 1983). Cohorts in the C_5 and adult female stages are not well defined because of the long and
Table II.2. Water column abundance (No. m\(^{-2}\)) of all life stages of *Metridia pacifica* from 0 to 1000 m from 22 September to 3 February 1981.

<table>
<thead>
<tr>
<th>Date</th>
<th>(N_{1+2})</th>
<th>(N_3)</th>
<th>(N_4)</th>
<th>(N_5)</th>
<th>(N_6)</th>
<th>(C_1)</th>
<th>(C_2)</th>
<th>(C_3)</th>
<th>(C_4)</th>
<th>(C_5)</th>
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<td>7509</td>
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<tr>
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<td>3118</td>
<td>6236</td>
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<td>4158</td>
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<td>333</td>
<td>4989</td>
<td>9313</td>
<td>12639</td>
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variable stage duration of C₅ copepodes.

A similar analysis was not possible for the early spring and summer cohorts as they were not as clearly demarcated as the autumn cohort. Also, there were periods in March, late May, and June, when abundances of nauplii and early copepodes could not be estimated.

For the cycling stage structure of the population to persist as distinct cohorts over several generations, some process must operate to reinforce the synchrony of the population. Without reinforcement, individual variation in development rate would result in continuous recruitment and ultimately a stable age distribution, which is not observed.

The progression of clearly demarcated cohorts through the year appears to be structured initially by an annual hiatus of reproduction by adult females during winter (Fig. II.9). This is particularly evident for December 1980 and January 1981, but also can be assumed for the previous winter, when only the tail end of the event could be observed. The decline in percentages of adult females in "fully spawning" condition began in early October, preceding the decline in naupliar abundance by approximately 2 months, and was surely responsible for the absence of nauplii during January 1981. Note that the declining naupliar abundances in December and January proceeded from the youngest stages to the older stages (Table II.2), as the youngest nauplii continued to develop while N₁ recruitment ceased.
The return of conditions permitting egg production and laying by females in late January or February, after several months of no reproduction, assures formation of a cohort. The individuals of this cohort proceed with development through the spring period; however a subsequent well-defined cohort can be generated only if reproduction by maturing adult females is restricted to a short interval. There must be few instances of repeated reproduction by individual females. Studies of *Acartia clausii* in Jakle's Lagoon, Washington (Landry, 1978) and *A. californiensis* in Yaquina Bay, Oregon (Johnson, 1981) indicated that repeated egg laying by individuals was infrequent because of severe predation. *Acartia* adult females were preyed upon by fishes to a significantly greater extent than the younger life stages, thereby preventing repeated reproduction which resulted in a succession of distinct cohorts throughout the growth season.

Females of *M. pacifica*, like estuarine *Acartia* spp., also may be more heavily preyed upon than their younger life stages. McCrone's (1981) data on the feeding habits of the myctophid fishes, *Stenobrachius leucopsar*us, and *Diaphus theta*, in the subarctic Pacific, indicate *M. pacifica* (*his lucens*) females to be one of the most abundant prey. *C*₄ and *C*₅ copepodites were also eaten, but the selectivity of the myctophids for these stages was not as great as for the adult females.

A more intriguing explanation for the clear demarcation of the second (summer) and third (autumn) cohorts of *M. pacifica* is
indicated by the cycling in adult female reproductive condition (Fig. II.9). During May to June, late July to August, and November to January, reproductively immature females comprised a large part of the adult female population. It is not known what caused the reproductive condition of adult females to cycle in such a regular fashion. It probably is not water temperature, since the three cycles occurred at widely different temperatures. Nor can the cycling be explained by cycling of food stocks or productivity. The pattern could arise, however, if there is an extended period when the female is not capable of producing eggs, followed by a relatively short period of active reproduction. Undoubtedly, laboratory experiments on maturation and egg laying would help to understand the mechanism responsible for the cycling in adult female reproductive condition.

It is important to understand why the abundance of older copepodites and adults of *M. pacifica* is greater in autumn and winter than in spring and summer. This is unusual; most large oceanic copepods in temperate regions increase to maximum population size during the spring and summer, generally in direct response to increasing productivity and therefore favorable feeding conditions. Several mechanisms may account for the unusual timing of the maximum population size. Specifically, food may be more available or predatory interactions may be less severe during autumn than at other seasons.

The annual maximum of chlorophyll a concentration in the
subarctic Pacific occurs during September, October, and November (Clemons and Miller, 1984), instead of during spring and early summer, as is typical of other high latitude oceans. Heinrich (1962a) postulated that the large herbivores, *Neocalanus cristatus* and *N. plumchrus*, by extensive grazing, prevented the accumulation of phytoplankton stocks during spring and summer. Miller et al. (1984) confirmed that the life histories of these copepods, in which reproduction occurs prior to the onset of the spring bloom, are suitable for preventing an increase in standing crop of phytoplankton during the spring, provided reasonable grazing capabilities are assumed for the copepods (Frost et al., 1983). According to Miller et al. (1984), entrance to the diapause phase for both *Neocalanus* spp. occurred during July in 1980. The reduction of grazing pressure upon the phytoplankton when *Neocalanus* spp. leave the surface waters and enter diapause may permit a build-up of phytoplankton stocks (at least as measured by chlorophyll a) during the autumn. Estimates of plant biomass (carbon) are affected by temporal and spatial variations in chlorophyll a content per cell (i.e., carbon:chlorophyll ratios), and thus are imprecisely estimated from chlorophyll a values alone. For example, McAllister (1969) estimated the carbon:chlorophyll ratio at Sta. P to range from 15 in winter to 50 in summer. A lower carbon:chlorophyll ratio in September and October than during summer implies that phytoplankton biomass may not be greater during autumn than at other times of the year. It should be noted, however, that oceanographic conditions in the subarctic Pacific appear to remain
favorable for the growth of phytoplankton during autumn. An estimate of the vertical extent of mixing indicates that it remains shallower than the critical depth (Sverdrup, 1953) into September and October (Parsons et al., 1966). Moreover, incident photosynthetically active radiation (PAR) for September remains moderately high, being 65% of the PAR of May and June. During October, however, PAR is reduced to only 44% of the midsummer maximum (Parsons et al., 1966). The shallow mixed layer (50 to 60 m), the fairly high light field, and the presence of abundant nutrients (>7.0 ug-at NO₃⁻¹) (Anderson et al., 1977) in September provide conditions favorable for the growth of phytoplankton populations. If, in fact, the increased chlorophyll concentration during this period reflects increased carbon as well, then the large winter population of M. pacifica may have resulted from feeding conditions in autumn that enhanced the production of eggs and decreased starvation mortality of the then developing nauplii and young copepodites.

Alternatively, the large winter population of M. pacifica may be a consequence of fewer predators during autumn and early winter than at other times of the year. If predation upon naupliar stages is lessened, an increase in population size can occur. Frost et al. (1983) observed that both Neocalanus plumchrus and N. cristatus supplemented their predominantly herbivorous diet by eating small copepodites. Consequently, if older copepodites of Neocalanus spp., which are abundant at Ocean Sta. P during spring and early summer
(Miller et al., 1984), feed carnivously upon small microplankton including *M. pacifica* nauplii; predation pressure would be reduced when they enter diapause, thereby permitting the development of the large cohort observed in autumn and early winter.

The results from the present study differ substantially from previous reports on the population dynamics of *M. pacifica*. Heinrich (1962b) found *M. pacifica* to be a common constituent of the plankton of the northern and western regions of the Bering Sea. In the warmer western region four generations (broods) from May through November were noted; progression of the last cohort during winter was slow, reaching adulthood in the following April to May. In the northern region, a single brood was spawned in midsummer. Heinrich presumed that *C.5* overwintered until the following spring. Naumenkô (1979) observed a lengthy summer reproductive period and a single generation per year for *M. pacifica* in the southeast Bering Sea. *M. pacifica* at Sta. P in the eastern subarctic Pacific appears to have progressed through three generations during 1980 to 1981, and no overwintering or diapause phase was observed. There was, however, a marked reduction in the frequency of vertical migration to the surface during winter that may be somewhat analogous to the diapause phase observed for *M. pacifica* in the Bering Sea and the *Neocalanus* and *Eucalanus* spp. at Sta. P (Miller et al., 1984).

In Saanich Inlet, British Columbia, stocks of young copepodite stages of *M. pacifica* begin to increase during January (Koeller et al., 1979). Sampling was not conducted during summer (May to August)
in the inlet, so it is difficult to compare the population dynamics of *M. pacifica* at that site to that observed at Sta. P. However, in Saanich Inlet, young copepodites were never found from September to December, whereas in the oceanic population all naupliar and copepodite stages were present continuously, except during January. In the coastal habitat, development of the shallow seasonal thermocline and surface water warming occur earlier, beginning in late March (Institute of Ocean Sciences, 1980), and the phytoplankton community, with several spring and autumn blooms, is much more dynamic than that of the oceanic habitat. Local differences in the timing and magnitude of such environmental features are probably responsible for the differences in the population dynamics of *M. pacifica* in the Bering Sea, Saanich Inlet, and the eastern subarctic Pacific.
References


Batchelder, H. P. (in review) A staining technique for determining copepod gonad maturation. (Submitted to Journal of Crustacean Biology)


Heinrich, A. K. (1962b) On the production of copepods in the Bering


A Staining Technique for Determining Copepod Gonad Maturation:
Application to *Metridia pacifica* from the Northeast Pacific Ocean.
Abstract

Fast Green is used to selectively stain the reproductive system and ova of adult female *Metridia pacifica*. Reproductive maturity of *M. pacifica* adult females in the subarctic Pacific exhibited a marked seasonal cycle during 1980 to 1981. Seasonal variation of female reproductive condition agreed well with that expected from the abundance of naupliar stages in plankton collections.
Introduction

The seasonal timing and intensity of reproduction in pelagic marine copepods is difficult to evaluate in the field. Two approaches are used commonly to discern cohorts and infer the timing of reproduction in marine copepods. They are 1) evaluation of the abundance of early (naupliar) life stages in a time series of plankton samples (Nicholls, 1933; Marshall, 1949), and 2) evaluation of gonad maturity, egg number or egg development within the body of the adult females (Marshall and Orr, 1955; Tande and Hopkins, 1981). While the eggs, ovaries and oviducts of some adult female copepods, eg. *Calanus marshallae* (Peterson, 1980) and *Neocalanus plumchrus*, *N. cristatus* and *Eucalanus bungii* (Miller et al. 1984), are more opaque than muscle and other tissues and readily can be seen using transmitted illumination, the eggs of other copepod species, eg. *Metridia* spp., are not easily distinguished from other body tissues, either prior to or after preservation. For such species, a stain is required which either selectively stains ova or is retained by gonadal material upon clearing.

Several different stains have been used in previous studies investigating the development of the reproductive system in copepods. Marshall and Orr (1960) tested the suitability of several stains for the ova and reproductive system of *Calanus finmarchicus*. A celestine blue staining method was judged to be superior to either borax carmine or methylene blue, although the borax carmine method "proved fairly satisfactory". Tande and Hopkins (1981) used borax
carmine in their investigation of gonad development and overwintering in *Calanus finmarchicus*, and their method was subsequently used to describe gonad development in *Metridia longa* (Tande and Gronvik, 1983). This paper describes a staining technique which was developed to study the seasonal timing and intensity of reproduction of the copepod, *Metridia pacifica*, in the oceanic subarctic Pacific. The results obtained are compared to those obtained by evaluation of naupliar abundance from fine mesh plankton sampling. The new staining procedure was also compared to the borax carmine and celestine blue methods.
Materials and Methods

A solution of Fast Green (Michrome No. 135; Gurr, 1960) (one percent by weight in distilled water) is used to stain whole female copepods. Formaldehyde preserved adult females are sorted into 1.5 cm polycarbonate tubes with 333 μm Nitex mesh bottoms. When enough females (generally fifty) have been sorted from a sample, the tube is transferred to a shallow dish containing the Fast Green staining solution. After 30 minutes, the tube and animals are removed and briefly rinsed with distilled water. At this point, all body tissues are uniformly dark blue and require destaining and dehydration by serial transfer from distilled water through 15, 40, 75, and 95% ethanol. The females are left in each solution for 5 to 15 minutes. During destaining the specimens are examined frequently to evaluate the progress of stain removal. Loss of stain from the body tissues is most rapid in distilled water but occurs also at slow rates in the alcohol solutions. If destaining proceeds too far, it is possible to rehydrate the specimens and restain. It is important that the females remain in the 95% ethanol for at least 15 minutes to prevent collapse of the specimen upon transfer to a clearing reagent. Several clearing reagents were tried, including turpentine, clove oil, glycerine and lactic acid. Turpentine was superior to the others. The stained and dehydrated females are individually transferred from the staining tube into a glass depression plate containing turpentine. After clearing in turpentine for 4-12 hours, the females are examined under a stereo microscope.
at 25X or 50X. The stained and cleared specimens have been stored in turpentine in tightly capped vials for up to 18 months with no loss or change of the stain. Females stained with Fast Green were compared to other females which were stained with borax carmine (Tande and Hopkins, 1981) and celestine blue (Marshall and Orr, 1960) to evaluate selectivity and restriction of the stains to the reproductive system and ova.

Females of Metridia pacifica were sorted from samples collected during a 15 month study of the zooplankton assemblage at Ocean Station Papa (50°N 145°W) (see Miller, et al., 1984, and Batchelder, 1985, for details on sampling and preservation methods). Thirty-five to fifty Metridia pacifica females were sorted from 0-100 m plankton collections from 23 dates between 6 February 1980 and 18 March 1981. For comparison with the seasonal cycle of female maturity, naupliar stages of M. pacifica were enumerated from samples spanning 0-500 m (Batchelder, 1985).
Results and Discussion

After staining in fast green and clearing in turpentine, the ovary, posterior oviducts and anterior diverticula of the genital system of *Metridia pacifica* are greenish-blue, while other body tissues have little color. The genital system of adult female *M. pacifica* is similar to that described for *M. longa* by Tande and Gronvik (1983). The ovaries are located dorsally in the region of the first and second thoracic segments (Fig. III.1). Two anterior diverticulae extend forward into the head region from the ovary. In reproductively mature females the diverticula are large and contain numerous, closely packed eggs. In other females the diverticula do not extend very far forward from the ovary, are narrow, and do not contain masses of large eggs, although a single row of small eggs may be present. Oviducts extend laterally and ventrally before continuing posteriorly to the genital opening.

The stained *M. pacifica* females were classified into three groups based on the size and development of the reproductive products and genital system. "Immature" females (Fig. III.1.A) have anterior diverticula which do not extend forward beyond the attachment of the second antennae. Additionally, there are no large eggs or egg masses present in the diverticula, although in some individuals each diverticulum contains a single row of small (∼40 um diameter) eggs. Posterior oviducts of "immature" females are narrow with no evidence of lateral pouches. The anterior diverticula of individuals classified as "partly mature" (not shown) also do not
Figure III.1

*Metridia pacifica.* (Drawings of formalin preserved and Fast Green stained individuals.) (A) Lateral and dorsal view of genital system in "immature" adult female. (B) Lateral and dorsal view of genital system in "mature" adult female. Eggs within the oviducts are 50-60 um in diameter. Scale bar is 2.0 millimeters.
Figure III.1
extend forward of the second antennae, but contain masses of eggs, often in multiple rows. "Partly mature" females have oviducal pouches which extend ventrally from the posterior oviducts between the extensor muscles of the swimming feet. These often have larger (50-60 μm diameter) eggs within them. Females classified as "mature" (Fig. III.1.B) have oviduct pouches containing large eggs, similar to those of "partly mature" females, but in addition contain robust egg masses which extend forward into the head, beyond the second antennae.

The percent of the females considered "mature", which are those presumably most actively reproducing, for each sampling date is shown in Figure III.2. There were three major peaks in the percentage "mature" during 1980. Times of peak spawning when greater than 75% of the _M. pacifica_ females were "mature" were April, late June to early July and late September to early October. Times of peak egg production were separated by periods in which the percentage of "mature" females rarely exceeded 60% and was at times below 20%. Following the September and October peak there was a rapid decline until 11 December when none of the females were "mature". The fraction of females "mature" remained less than 5% until 3 February.

The seasonal variation of the percent of _M. pacifica_ females in "mature" condition agrees well with the seasonal variation in abundance of early naupliar stages (Fig. III.3., from Batchelder, 1985). Through most of the year, the correspondence between the
Figure III.2

Percentage of *Metridia pacifica* adult female population within the 0 to 100m depth interval which is reproductively mature at Station P during 1980 to early 1981.
Figure III.2

% OF FEMALES IN "FULLY SPAWNING" CONDITION

0-100 m

0 20 40 60 80 100

J F M A M J J A S O N D J F M

1980 1981
Figure III.3

Number m$^{-2}$ of first four naupliar stages of *Metridia pacifica* from 0 to 500 m. □ indicates $N_1$ and $N_2$ combined, ▲ $N_3$, ○ $N_4$, ⌀ no nauplii of missing symbol found.
Figure III.3
peaks in the proportion of "mature" female *M. pacifica* and naupliar abundance was offset by one to two months. This relationship is not unexpected, since the percent of females which are "mature" is an estimate of future nauplii, which will appear at a later date.

Certainly the two major features of the two time series, the increases in "mature" females and nauplii number during February to April 1980 and the dramatic decline to zero percent "mature" and the absence of nauplii at the end of 1980, are cause and effect relations. The decline in naupliar abundance during December 1980 reflects the earlier cessation of egg production by the adult females. In addition to the correspondence of the major features of the time series of reproductive condition and naupliar abundance, several of the less pronounced features of the two time series could be traced. The peak of "mature" females during the first week of July, the rapid decline from this peak, and the subsequent gradual increase which continued until late September are evident also in the naupliar data from early July to November. There is not perfect agreement. The low percent of females which are "mature" on 20 August has no counterpart in the naupliar abundance data.

In comparison tests, the fast green and celestine blue staining procedures were judged to be equally reliable as a reproductive stain for pelagic marine copepods, while the borax carmine method was considered inferior to either of the others. One drawback to the borax carmine method as described by Tande and Hopkins (1981) is the lengthy staining time. They found that a minimum of one week
was necessary for the gonads to become clearly visible. In the present study, borax carmine was not found to selectively stain the gonads, but rather stained the entire animal including the carapace. Furthermore, once stained with borax carmine it was impossible to destain specimens with either water or ethanol washes.

The fast green staining method is rapid and suitable for selectively staining gonadal products of copepods in which the ovaries and oviducts cannot be distinguished from other body tissues in unstained specimens. Staining and destaining with fast green required only 2.5 to 3 hours and clearing in turpentine an additional 4 to 12 hours. An additional benefit is that the specimens can be stored in turpentine for up to 18 months without loss or change in the distribution of the stain. The method has been applied successfully to an oceanic copepod population to determine the seasonal timing of reproduction and the results agreed well with independently derived estimates from other life cycle data.
References


CHAPTER IV

Phytoplankton Balance in the Oceanic Subarctic Pacific:
the Grazing Impact of *Metridia pacifica*.
Abstract

Ingestion and respiration by *Metridia pacifica*, the dominant large copepod during autumn and winter in the subarctic Pacific, were investigated by shipboard and laboratory experiments. Diel variation in the rate of grazing on phytoplankton by *M. pacifica* was determined from measurements of gut pigment content and gastric evacuation rate. Both adult females and C₅ copepodites exhibited marked diel variation in gut contents, and thus feeding intensity. Nighttime gut pigment values were ten times greater than daytime values. Ingestion rates during May 1984 were 51.7 and 9.8 ng chl-a copepod⁻¹ day⁻¹ for adult females and fifth copepodites, respectively. Estimated filtering rates were 76 ml female⁻¹ day⁻¹ and 15 ml C₅⁻¹ day⁻¹. Feeding rates at low food concentrations in incubation bottles were similar to estimates obtained from in situ studies. Adult females consumed approximately 7.5% of body carbon day⁻¹, and C₅ copepodites only 2.5% day⁻¹.

Respiration was 4 to 10% of body carbon day⁻¹ for both C₅ and adults, indicating approximate energy balance for females, but higher daily energy expenditure than gain for C₅. Based on the respiration measurements, a model was developed to evaluate the seasonal grazing impact of *M. pacifica* on the phytoplankton standing crop in the subarctic Pacific. During peak phytoplankton production in summer, the low densities of *M. pacifica* require less than 10% of daily primary production to satisfy metabolic, growth and reproduction requirements. In contrast, the *M. pacifica* population
requires 20 to 40%, and exceptionally 175%, of daily primary production to satisfy their energy requirements during autumn and winter. *M. pacifica* contributed significantly to the total grazing potential responsible for maintaining low stocks of phytoplankton in the eastern subarctic Pacific during autumn and winter 1980-1981.
Introduction

The oceanic region of the subarctic Pacific has a close temporal and spatial coupling between primary production and herbivore consumption (Cushing, 1959). As a result, the summer increase in primary production does not increase phytoplankton stocks, it increases zooplankton stocks, and the strong seasonal peak of plant biomass, typical of most temperate and boreal ocean regions does not occur in the subarctic Pacific.

A previous numerical model of the phytoplankton and zooplankton dynamics of the subarctic Pacific (Parslow, 1981) represented Neocalanus plumchrus and N. cristatus as the herbivores primarily responsible for cropping plant production. This principal role of Neocalanus was suggested by Heinrich (1957, 1962) because the overwintering strategy and reproduction of these two copepods prior to the spring bloom appeared appropriate for immediate grazing control of the spring phytoplankton bloom. Miller et al. (1984) documented the life cycles of the two Neocalanus spp. at Station P (50°N, 145°W) and concluded that the timing of their life cycles was suitable for grazing control of the spring bloom in the subarctic Pacific. However, models which relied solely upon Neocalanus grazing for control of phytoplankton stocks became unbalanced during the autumn after the Neocalanus spp. descended to depth and entered diapause. Parslow (1981) concluded that grazing control after the departure of the large grazers from the euphotic zone must be provided by smaller herbivores, but it was difficult to simulate a
smooth transition of grazing pressure from the larger *Neocalanus* to smaller unspecified grazers. The copepod *Metridia pacifica* may be an important grazer during autumn in the subarctic Pacific, since its population size increases soon after the *Neocalanus* spp. depart from the euphotic zone in July (Batchelder, 1985). Except for the very small copepods, such as *Oithona* spp., *Metridia* copepodites and adults were the most abundant herbivores in the surface mixed layer during autumn and winter 1980-1981 (Batchelder, 1985; Miller, et al., 1984).

In this study a carbon budget for stage C₅ and female *M. pacifica* is presented based upon experimental determination of ingestion and respiration rates. These results are used to model the potential of these smaller herbivores to maintain constant, low phytoplankton stocks in the subarctic Pacific.
Methods

Collection of Animals

*Metridia pacifica* for experimental studies were collected during summer 1982 and 1983 from coastal Oregon waters (44°40'N), in summer 1984 from Station P (50°N, 145°W), and in fall 1984 from Dabob Bay, Washington (47°45'N, 122°49'W). Zooplankton were sampled using an 0.7 m diameter net of 243 um mesh equipped with a large volume, slow-filtering cod-end. Vertical or oblique hauls from 50, 70 or 100 meters to the surface provided animals for grazing and respiration incubations. Animals were either gently poured into a five gallon plastic pail, from which they were sorted, or sorted directly from the cod-end into 0.5 – 1.0 liter containers of surface seawater screened at 64 or 200 um, or Whatman GF/C filtered. Sorting began immediately after collection and was completed within 2-3 hours.

Diel variation of phytoplankton pigments in gut contents

*In situ* ingestion rate was estimated by measurement of the amount and turnover rate of phytoplankton pigment in the guts of freshly collected copepods. Zooplankton samples collected from the upper 50 to 100 m at Station P every three hours over a 27 hour period on 16-17 May 1984 were used to evaluate phytoplankton pigments in the guts of *Metridia pacifica*. After each collection, up
to five replicates of 8 to 16 individuals of both adult females and C₅ copepodites were sorted into small tubes and kept in the dark. Sorting was completed within ten to fifteen minutes from the time of collection. The method of Mackas and Bohrer (1976), as modified by Dagg and Grill (1980), was used to measure copepod gut fluorescence. For each analysis, the copepods were homogenized in 4-6 ml of 90% acetone, filtered through a Whatman GF/C glass fiber filter, and the fluorescence of the filtrate measured with a Turner Designs Model 10 fluorometer, before and after acidification. The pigment content per copepod was calculated according to the equations:

\[
\text{ng chlorophyll cop}^{-1} = \frac{V (F_0 - F_a) C}{N} \tag{1}
\]

\[
\text{ng phaeopigment cop}^{-1} = \frac{V (T F_a - F_0) C}{N} \tag{2}
\]

where \(F_0\) and \(F_a\) are the fluorescence readings before and after acidification, respectively; \(N\) is the number of copepods; \(T\) is the maximum acidification ratio; \(V\) is the volume of acetone used to extract the pigments; and \(C\) is a machine-dependent calibration factor. The phaeopigment content of the gut was multiplied by 1.51 to correct for the molar conversion of chlorophyll-a to phaeophorbide (Shuman and Lorenzen, 1975), and added to the measured chl-a content of the gut to estimate the amount of chlorophyll-a originally ingested by the copepod (chlorophyll-a equivalent).
Experiments to determine the gut evacuation rate of *M. pacifica*, and thus estimate ingestion from observed *in situ* gut contents, were done both at sea and ashore. Copepods, previously fed on unialgal cultures of either *Thalassiosira weissflogii* (10-15 um diameter) or *Corethron hystrix* (approx. 25 um by 70 um), were transferred to filtered seawater. Groups of four to ten animals were removed intermittently over the following one to three hours and analyzed for gut pigment content.

Incubation Grazing Experiments

*Metridia pacifica* females collected from off the Oregon coast (Summer 1983), from Dabob Bay, Washington (September 1984), and from Station P (May, August 1984) were used to investigate grazing capabilities. The functional response curve of *M. pacifica* females feeding on *Thalassiosira weissflogii* was determined from 24 hour incubations. Initial and final cell concentrations for experiments during summer 1983 were determined using a model ZBi Coulter Counter equipped with a 70 um aperture tube. A Particle Data electronic counter, fitted with either a 95 um or 190 um aperture tube, was used to determine cell densities during 1984. In addition, *Corethron hystrix* was used as food in one experiment to investigate the effect of particle size on ingestion. Cell counts and cell volumes for this experiment were determined microscopically.

For each functional response experiment, two replicate
containers with 10 to 15 copepods, and one control lacking animals, were prepared for each of four to five food levels. Animals were incubated in 700 ml glass beakers or 500 ml polycarbonate bottles containing 500 ml of the food medium. The differential effect of ammonia excretion by the animals on phytoplankton growth was minimized by adding 5-10 umol NH₄Cl l⁻¹ to each container at the beginning of each experiment. Incubations lasted 20 to 30 hours, and were conducted in a constant temperature cold room. All containers were gently stirred several times hourly by a plunger-stirrer, which maintained the phytoplankton in suspension. Incubations during 1983 were conducted at 10 to 12.5 °C under constant cool-light illumination (60 to 80 uE m⁻² sec⁻¹). The September 1984 experiments were performed in constant darkness at 8, 12, and 15 °C. Shipboard experiments were conducted in on-deck incubators at sea surface temperature with the natural daylight cycle. Ingestion and filtration rates were calculated by the equations of Frost (1972). Ingested particle volume was converted to carbon using the equation of Mullin et al. (1966). All food levels and ingestion rates are presented on a carbon basis to facilitate comparison among experiments.

Respiration experiments

Respiratory rate of M. pacifica was measured in bottle incubations during May and August 1984 at Station P. Animals were collected by net hauls as described above. Fifteen to thirty C₅
copepodites or adult females were sorted into 300 ml BOD bottles filled with 64 μm or 200 μm screened surface seawater. Control bottles, filled with identical water but lacking animals, were run concurrently. The bottles were placed in deck incubators for 12 to 24 hours. Oxygen consumption by adult females was measured at 8, 9 and 14.6 °C, but only at 8 to 9 °C for C₅ copepodites. The oxygen concentration in initial, final experimental and final control bottles was measured by Winkler titration. The measured respiration rates in μl O₂ cop⁻¹ hr⁻¹ were converted to ug carbon cop⁻¹ hr⁻¹ using a respiratory quotient of 0.9 (Parsons et al., 1984).

Seasonal length variation and length-weight relations

Seasonal variation of body size of Metridia pacifica was described from samples collected at Station P from February 1980 to March 1981. Total length, excluding caudal setae, of N₄, N₅, C₃, C₄, C₅ males and females, and adult females were measured using a calibrated ocular micrometer. Usually 25 to 50 individuals of each life stage were measured from each 0-100 meter sample. On dates when the depth of the mixed layer was shallower than 100 meters, 25 to 50 individuals of each stage were measured from both the 100m to thermocline sample and the thermocline to 0m sample. An abundance weighted size distribution was then calculated for the 100 meter layer.

A length-weight relation for M. pacifica was determined from
freshly collected individuals of the older life stages ($C_4$ to adult) and from formalin preserved $C_1$ to $C_3$ copepodites. Animals were measured for total length, rinsed briefly in distilled water, transferred to precombusted Whatman QM/A quartz fiber filters, and dried at 60°C. Carbon contents for both live sorted and formalin preserved samples were analyzed ashore using a Perkin Elmer Model 240C Elemental Analyzer.
Results

Diel variation of gut content fluorescence

The variation of chlorophyll-a equivalent per C5 and female Metridia pacifica during a 27 hour period in May 1984 is shown in Figure IV.1. During daytime, adult females contained little pigment, ranging from 0.4-0.6 ng chl-a female\(^{-1}\); whereas females collected at 2200 h and 0100 h averaged 5.7 and 5.9 ng chl-a female\(^{-1}\), respectively. The diel cycle of gut pigment of C5 copepodites was similar, but of lower amplitude (Fig. IV.1). Daytime values were always less than 0.24 ng chl-a C5\(^{-1}\), compared to 0.8 to 1.2 ng chl-a C5\(^{-1}\) at night.

Since only individuals from the upper mixed layer were analyzed for gut pigment content, and the percent change in ambient water chlorophyll (Fig. IV.1) was much less than was observed for gut chlorophyll, the temporal change of chlorophyll equivalent per copepod implies a real difference in feeding intensity between day and night, not an artifact of vertical migration.

The time course of pigment loss from the guts of adult females after transfer to filtered seawater is shown in Figure IV.2 for five experiments. Pigment content declined rapidly over the first hour. The gut evacuation rate was described by the exponential relation:

\[ S_t = S_0 e^{-Et} \]  

(3)
Figure IV.1

Diel variation of water chlorophyll-a and pigment content of *Metridia pacifica* at Station P during 16-17 May 1984. (A) water chlorophyll; (B) adult female; (C) C₅ copepodite.
Figure IV.1

Graph A: 
- Y-axis: pg Chl a L\(^{-1}\)
- X-axis: Time (0000-1200)

Graph B: 
- Y-axis: pg Chl a ind\(^{-1}\)
- X-axis: Time (0000-1200)

Graph C: 
- Y-axis: pg Chl a ind\(^{-1}\)
- X-axis: Time (0000-1200)
Time course of gut pigment evacuation for *Metridia pacifica* adult females. Symbols as in Table IV.1.
Figure IV.2
where $S_0$ is the amount of pigment in the gut at time zero; $S_t$ is the pigment content at time $t$; and $E$ is the instantaneous (min$^{-1}$) gut evacuation rate (Dagg and Wyman, 1982). Gut evacuation rate ranged from 1.4 to 2.4% min$^{-1}$ (Table IV.1), with no consistent relation to temperature, food type or initial gut fullness.

Gut evacuation rate of adult females was independently estimated from the decline in mean gut pigment value from 0158 to 0436 hr on 17 May 1984, assuming the decline during that interval resulted from cessation of feeding activity. If the copepods stopped feeding at 0153 h, the gut evacuation rate necessary to decrease the gut contents to 0.54 ng pigment cop$^{-1}$ at 0436 h, is calculated from equation (3) to be 1.53% min$^{-1}$ in good agreement with the laboratory results.

In situ ingestion rate was determined from the diel cycle of gut pigment (Fig. IV.1) using an instantaneous gut evacuation rate of 1.8% per minute (Table IV.1). Total consumption ($C_t$) for each time interval ($t$) was calculated from:

$$C_t = \frac{(S_t - S_0e^{-Et}) Et}{1 - e^{-Et}}$$

(Elliot and Persson, 1978) where $S_0$ and $S_t$ are the amount of pigment in the gut at the beginning and end of the time interval, respectively; and $E$ is the instantaneous gut evacuation rate. This
Table IV.1. Results of adult female *Metridia pacifica* gut evacuation experiments. Tw -- *Thalassiosira weissflogii*; Ch -- *Corethron hystrix*.

<table>
<thead>
<tr>
<th>Date</th>
<th>Temp. °C</th>
<th>Food</th>
<th>Evacuation min</th>
<th>$R^2$</th>
<th>Symbol in Fig. IV.2.</th>
</tr>
</thead>
<tbody>
<tr>
<td>6-16-83</td>
<td>10.2</td>
<td>Tw</td>
<td>.016</td>
<td>0.538</td>
<td>+</td>
</tr>
<tr>
<td>6-22-83</td>
<td>10.2</td>
<td>Tw</td>
<td>.024</td>
<td>0.616</td>
<td>X</td>
</tr>
<tr>
<td>7-23-83</td>
<td>13.5</td>
<td>Ch</td>
<td>.014</td>
<td>0.861</td>
<td>□</td>
</tr>
<tr>
<td>5-19-84</td>
<td>8.4</td>
<td>Tw</td>
<td>.022</td>
<td>0.766</td>
<td>•</td>
</tr>
<tr>
<td>11-16-84</td>
<td>12.0</td>
<td>Tw</td>
<td>.017</td>
<td>0.762</td>
<td>△</td>
</tr>
</tbody>
</table>
relation assumes that the evacuation rate is exponential and that consumption rate during the interval remains constant. Ingestion rate of both females and C5 appears to have been greatest near midnight (Table IV.2). Total daily consumption was 9.8 and 51.7 ng chl-a for C5 and adult females, respectively. Since the specific depth at which the animals were feeding was not known from vertical collections, the highest chlorophyll-a concentration of the mixed layer was used to provide conservative estimates of filtration rate for each sampling time (Table IV.2). Daily volume swept clear was 76 ml animal⁻¹ for adult females and 15 ml animal⁻¹ for C5.

Grazing incubations

Table IV.3 summarizes the experimental conditions and phytoplankton used in the feeding experiments. Functional response curves in most experiments appeared curvilinear and were described by the Ivlev (1955) equation as modified by Parsons et al. (1967):

\[ I = I_{\text{max}} (1 - e^{a(P_0 - P)}) \]  

(5)

where \( I_{\text{max}} \) is the maximum ingestion rate; \( a \) is a constant related to the initial slope of the curve; and \( P_0 \) is the threshold food level below which ingestion ceases. \( P_0 \) was not significantly different from zero in any experiment. Ingestion rates of M. pacifica females feeding on Thalassiosira weissflogii were higher in the dark than in the light (Fig. IV.3A,B).
Table IV.2. Diel cycle of ingestion and filtration rate of *Metridia pacifica* C$_5$ and females at Station P during May 1984. Values in parentheses are the number of replicates. * -- interpolated water chlorophyll values

<table>
<thead>
<tr>
<th>Date</th>
<th>Time</th>
<th>chl-a ng ml$^{-1}$</th>
<th>Ingestion ng an$^{-1}$ hr$^{-1}$</th>
<th>Filtration ml an$^{-1}$ hr$^{-1}$</th>
<th>Ingestion ng an$^{-1}$ hr$^{-1}$</th>
<th>Filtration ml an$^{-1}$ hr$^{-1}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>16 May</td>
<td>1345</td>
<td>0.80</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>0.10-0.27 (3)</td>
</tr>
<tr>
<td></td>
<td>1622</td>
<td>0.80*</td>
<td>0.19-1.12 (5)</td>
<td>0.24-1.40</td>
<td>0.16-0.21 (2)</td>
<td>0.20-0.27</td>
</tr>
<tr>
<td>1930</td>
<td>0.79</td>
<td>1.12-1.80 (4)</td>
<td>1.42-2.28</td>
<td>0.18-0.26 (3)</td>
<td>0.23-0.33</td>
<td></td>
</tr>
<tr>
<td>2228</td>
<td>0.96</td>
<td>5.54-10.16 (5)</td>
<td>5.77-10.58</td>
<td>0.99-1.70 (3)</td>
<td>1.03-1.32</td>
<td></td>
</tr>
<tr>
<td>17 May</td>
<td>0158</td>
<td>0.74*</td>
<td>4.66-10.23 (6)</td>
<td>6.30-13.82</td>
<td>1.54-1.75 (3)</td>
<td>2.08-2.37</td>
</tr>
<tr>
<td>0436</td>
<td>0.74*</td>
<td>0.53-1.06 (3)</td>
<td>0.72-1.43</td>
<td>0.07-0.14 (3)</td>
<td>0.09-0.19</td>
<td></td>
</tr>
<tr>
<td>0737</td>
<td>0.52</td>
<td>0.52-1.08 (4)</td>
<td>1.00-2.08</td>
<td>0.13 (1)</td>
<td>0.25</td>
<td></td>
</tr>
<tr>
<td>1045</td>
<td>0.57*</td>
<td>0.49-0.66 (3)</td>
<td>0.86-1.16</td>
<td>0.19-0.22 (3)</td>
<td>0.33-0.39</td>
<td></td>
</tr>
<tr>
<td>1352</td>
<td>0.62</td>
<td>0.45-0.59 (3)</td>
<td>0.73-0.95</td>
<td>0.25-0.38 (3)</td>
<td>0.41-0.62</td>
<td></td>
</tr>
<tr>
<td>1620</td>
<td>0.62*</td>
<td>0.34-0.61 (3)</td>
<td>0.55-0.98</td>
<td>0.19-0.24 (3)</td>
<td>0.30-0.39</td>
<td></td>
</tr>
</tbody>
</table>
Table IV.3. Experimental conditions, collection site, and dates of *Metridia pacifica* ingestion rate incubations. Tw -- Thalassiosira weissflogii; Ch -- Corethron hystrix; FSW -- Filtered seawater

<table>
<thead>
<tr>
<th>Date</th>
<th>Collection Site</th>
<th>Temp. $^\circ$C</th>
<th>Light $\mu$E m$^{-2}$ sec$^{-1}$</th>
<th>Precondition</th>
<th>Food Type</th>
<th>Symbol in Fig. IV.3a</th>
</tr>
</thead>
<tbody>
<tr>
<td>9-19-81</td>
<td>Oregon</td>
<td>8.0</td>
<td>5-20</td>
<td>None</td>
<td>Tw</td>
<td>•</td>
</tr>
<tr>
<td>5-18-83</td>
<td>Oregon</td>
<td>12.5</td>
<td>60-80</td>
<td>36 hr @ 450 $\mu$gC L$^{-1}$</td>
<td>Tw</td>
<td>+</td>
</tr>
<tr>
<td>6-14-83</td>
<td>Oregon</td>
<td>10.0</td>
<td>60-80</td>
<td>12 hr in FSW</td>
<td>Tw</td>
<td>X</td>
</tr>
<tr>
<td>6-21-83</td>
<td>Oregon</td>
<td>10.2</td>
<td>60-80</td>
<td>6 hr in FSW</td>
<td>Tw</td>
<td>◯</td>
</tr>
<tr>
<td>7-22-83</td>
<td>Oregon</td>
<td>13.5</td>
<td>low light</td>
<td>18 hr in FSW</td>
<td>Ch</td>
<td></td>
</tr>
<tr>
<td>9-11-84</td>
<td>Dabob Bay</td>
<td>8,12,15</td>
<td>dark</td>
<td>None</td>
<td>Tw</td>
<td></td>
</tr>
</tbody>
</table>
Ingestion rates of *Metridia pacifica* adult females. Curves in (A) and (C) are best Ivlev fit to the data. (A) feeding on *Thalassiosira weissfloggi* in the light (lower curve - high food preconditioned; upper curve - low food preconditioned); Symbols as in Table IV.3); (B) feeding on *T. weissfloggi* in the dark (x - 8°C; □ - 12°C; o - 15°C)); (C) feeding on *Corethron hystrix* (Temperature=13.5 °C; Low light) (Note scale change from (A) and (B))
Figure IV.3
*Metridia pacifica* adult females exhibited an hunger response (Runge, 1980). Females preconditioned for 36 hr at 450 ug carbon l⁻¹ of *T. weissfloggi* had lower ingestion rates than females which were not preconditioned or were preconditioned in filtered seawater for 6 to 18 hours (Fig. IV.3A). *I*ₘₐₓ for the animals preconditioned on high food was 1.92 ug C cop⁻¹ day⁻¹, compared to 4.75 ug C cop⁻¹ day⁻¹ for animals starved prior to the experiment.

Ingestion rates of *M. pacifica* feeding on *T. weissfloggi* in the dark showed significant temperature dependence (Fig. IV.3B). At the two lowest food concentrations, 25 and 75 ug C l⁻¹, ingestion rates were similar at 8.0 °C and 12.0 °C. However at 250 and 570 ug C l⁻¹, ingestion was higher at 12 °C than at 8 °C. *I*ₘₐₓ was 4.9 ug C cop⁻¹ day⁻¹ at 8 °C and 8.2 ug C cop⁻¹ day⁻¹ at 12 °C. Ingestion at 15 °C was linearly, rather than curvilinearly, related to food abundance. Apparently food levels exceeding 570 ug C l⁻¹ are needed to saturate feeding at 15 °C. Although ingestion at the highest food level was greatest at 15 °C, ingestion at intermediate food levels was lower at 15 °C than at 8 °C or 12 °C.

*M. pacifica* ingested three to four times more carbon per day when fed *Corethron hystrix* than when fed *T. weissfloggi* (Fig. IV.3C). Daily ingestion was 15 to 20 ug C cop⁻¹ at 500 ug C l⁻¹ of *Corethron*, compared to 2.5–6 ug C cop⁻¹ when fed *Thalassiosira*. Maximum ingestion (*I*ₘₐₓ) was 31.3 ug C cop⁻¹ day⁻¹ on the large cell, which is four to six times and 6 to 15 times greater than when feeding on *Thalassiosira* in the dark and light, respectively.
Respiration experiments

Oxygen consumption rates of *M. pacifica* females and *C₅* copepodites are shown in Table IV.4. Adult female respiration was not clearly related to temperature. Water temperature in the deck incubators during the May and August 1984 cruises was slightly (1 to 3 °C) warmer than that of the surface water. Thus, the animals experienced higher temperatures in the respiration experiments than they would encounter normally in surface waters at that time; the poor relationship of metabolic rate to temperature might be explained by the animals not being acclimatized to higher than ambient temperatures. Respiration by *C₅* copepodites at 8–9 °C was approximately half that of adult females at the same temperature. Respiration as fraction of body weight was 4–10% day⁻¹ for both *C₅* copepodites and adult females.

Seasonal variation in length and length-weight relations

Seasonal variation in total length was most pronounced for adult females (Fig. IV.4; mean, SE shown). Mean length of adult females was greatest, 3.23 mm, on 21 June and 10 July 1980, and least, 2.31 mm, on 1 January 1981. Mean length of *C₃* to *C₅* copepodites also varied seasonally, although the amplitude of the seasonal pattern was far less than that of adult females (Fig. IV.4). Length of *N₄* and *N₅* did not vary seasonally.
Table IV.4. Respiration of *Metridia pacifica*.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Temp. °C</th>
<th>N</th>
<th>uL O₂ cop⁻¹ hr⁻¹</th>
<th>ug C cop⁻¹ hr⁻¹*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>9.0</td>
<td>6</td>
<td>0.397 (0.070)</td>
<td>0.191 (0.034)</td>
</tr>
<tr>
<td>Female</td>
<td>8.0</td>
<td>6</td>
<td>0.267 (0.140)</td>
<td>0.129 (0.067)</td>
</tr>
<tr>
<td>Female</td>
<td>14.6</td>
<td>2</td>
<td>0.326</td>
<td>0.157</td>
</tr>
<tr>
<td>C5</td>
<td>8-9</td>
<td>6</td>
<td>0.155 (0.028)</td>
<td>0.075 (0.014)</td>
</tr>
</tbody>
</table>

* - respiratory quotient of 0.9 assumed.
Seasonal length of *Metridia pacifica* during February 1980 to February 1981. (Sample mean and standard deviation; N=50).
Figure IV.4
The length-weight relation for *M. pacifica* is shown in Figure IV.5. Values represented by triangles were determined from formalin preserved samples, which according to Landry (1978) and Omori (1978) underestimate the true carbon values by approximately 30 percent. The measured carbon contents of N4 to C3 have been multiplied by 1.43 to correct for this weight loss. The corrected values are indicated by squares. For C1 to adults, the length-weight relation, fit by least-squares regression to the log transformed data, was best described by:

\[ W = 3.828 L^{2.462} \]

\[ R^2 = 0.940 \quad N = 27 \]  

(6)

where \( L \) is total length in mm; and \( W \) is body weight as ug carbon.
Figure IV.5

Length-weight relation for *Metridia pacifica*. ● - live sorted; ▲ - formalin preserved; □ - corrected formalin preserved.
Figure IV.5
Discussion

Feeding rates

*Metridia pacifica* C5 and females exhibited a marked diel feeding periodicity during May 1984 at Station P; ingestion and filtration rates were an order of magnitude greater at night than during the day. Diel variation in gut pigment content of copepods has been reported previously for *Centropages hamatus* (Nicolajsen, et al., 1983; Head, et al., 1984), *Centropages typicus* (Mackas and Bohrer, 1976; Dagg and Grill, 1980), *Metridia lucens* (Mackas and Bohrer, 1976), *Pseudocalanus* sp. (Nicolajsen, et al., 1983) and *Temora longicornis* (Head, et al., 1984). In several of these earlier gut content studies, however, it was not possible to separate the effects of (1) daytime, downward migration away from high food concentration from (2) diel variation in individual feeding behavior. Since chlorophyll-a values of the upper 70 to 100 m were nearly homogeneous (Lorenzen, 1984) in the present study, the diel cycle of gut pigment content reflects a real day-night difference in feeding intensity, similar to that found by Baars and Oosterhuis (1984) for *Temora, Pseudocalanus, Centropages* and *Calanus*.

The pigment content of each *M. pacifica* female during the daytime represented the filtration of 1 to 2 ml of the surrounding water, whereas the pigment content at night represented filtration of 6 to 8 ml of water. Ingestion of chlorophyll by adult females in
May 1984 was 51.7 ng Chl-a copepod\(^{-1}\) when summed over twenty-four hours. Assuming a carbon to chlorophyll-a ratio of 60 (Welschmeyer, pers. comm.), daily ingestion was 3.10 ugC female\(^{-1}\). For adult females of 43 ugC, this ration is equal to 7.2 percent of body carbon per day. A similar calculation for C\(_5\) reveals that daily ingestion was 0.59 ugC, which amounts to only 2.4 percent of body carbon.

Clearance rates determined for *M. pacifica* females in bottle incubation experiments were lower than in situ rates estimated from gut pigment content. When food concentrations in bottle incubations were significantly higher than ambient food levels at Station P, daily ration of adult females ranged from 3.9 percent of body weight when preconditioned on a high concentration of *Thalassiosira weissflogii*, to 62 percent when fed the large diatom, *Corethron hystrix*. However, in containers with food concentrations comparable to those observed at Station P, daily consumption was generally less than 1 percent of body carbon.

The results of gut fluorescence analyses and laboratory incubation experiments were consistent in that both indicated that *M. pacifica* have relatively low ingestion rates. Ingestion as a fraction of body weight was usually less than 7% day\(^{-1}\), except when the animals were offered unnaturally high food concentrations.

There are relatively few studies of other pelagic crustacea with which the present feeding results of *M. pacifica* may be
compared. Haq (1967) measured the feeding rate of *Metridia lucens* upon several foods, including both phytoplankton cells and *Artemia* nauplii. Ingestion rates depended upon the quantity and type of food offered. Maximum ingestion of phytoplankton food was less for small cells than large ones. The present results agree with those earlier experiments, since maximum ingestion rates were much higher when *M. pacifica* were offered *C. hystrix* than when offered *T. weissflogii*. Moreover, daily consumption of phytoplankton by *M. lucens* was similarly low; ingestion ranged from 0.44 ugC cop⁻¹ day⁻¹ when fed *Dunaliella* to 2.10 ugC cop⁻¹ day⁻¹ when fed *Thalassiosira nordenskioldii* (Haq, 1967).

Other pelagic crustaceans similar in size to *M. pacifica* and *M. lucens* have much greater daily rations. Paffenhofer (1971) reported daily ration of *Calanus helgolandicus* (=*pacificus*) of 60 ug carbon body weight to be 55% of body carbon day⁻¹. Mullin and Brooks (1970), also working on *Calanus pacificus* (= 45 ug C), reported the ration as roughly 40% day⁻¹. *Euphausia pacifica* furcilia of 25-50 ug C ingested 17-30% day⁻¹ (Ross, 1982). It is not clear why the measured ingestion rates of Metridia species are so much lower than those of other crustacea of similar size, but it may be related to the size of the food particles. Most of the studies of *Calanus pacificus* and *Euphausia pacifica* ingestion were conducted using relatively large (19-64 um diameter) phytoplankton cells as food. In the present study, *Metridia pacifica* offered large cells (*Corethron hystix*) had ingestion rates as high as 62% of body carbon
Metabolic rate

Figure IV.6 indicates that the respiration rates of *M. pacifica* measured in the present study are comparable to previously published data for this species and *M. lucens*. Dagg, et al. (1982) present a relation between metabolism and body size determined for zooplankton, including *M. pacifica*, from the Bering Sea. The slope of their relation (b = 0.884) is similar to the slope of boreal (b = 0.834) and subtropical (b = 0.867) species reported by Vidal and Whitledge (1982). Vidal and Whitledge (1982) concluded that the slopes of the allometric equation describing metabolism as a function of body weight did not differ for pelagic crustacea of boreal and subtropical habitats. In contrast, the intercept of the relation between weight and metabolism increased with increased habitat temperature.

In the present study, respiration of *Metridia pacifica* was measured at a few temperatures only, and only for adult females and *C₅* copepodites (Table IV.4). Respiration rates of younger copepodite stages were assessed indirectly by a relation developed to express respiration as a function of habitat temperature and body size. Adult female respiration increased linearly with temperature over the temperature range from 2 to 18 °C (Fig. IV.6). *Metridia pacifica* females in the Bering Sea were larger (~ 100 µg C) (Dagg, et al.)
Summary of respiration rates of adult female *Metridia pacifica* and *M. lucens*. *M. lucens* data from ■ - Marshall and Orr (1962); ○ - Haq (1967); △ - Ikeda (1976); *M. pacifica* data from X - Dagg, et al. (1982); + - present study.
Figure IV:6

[Graph showing a linear relationship between temperature (°C) and respiratory rate (ug C ind⁻¹ day⁻¹)]
1982) than those from coastal Oregon or Station P; thus, respiration for females from the Bering Sea was calculated for 45 ug individuals using the equations provided by Dagg, et al. (1982). Assuming the allometric equation appropriately describes the relation between metabolism and body size, and assuming also that the respiration data shown in Figure IV.6 were obtained from adult females of constant body size, an empirical relation was derived to describe the temperature (T) dependence of the respiration constant (a) of the allometric equation. The equation best describing this relation is:

\[ a = 0.037 + 0.006 \, T \]

\[ R^2 = 0.60 \quad p < 0.005 \] (7)

Using 0.884 (Dagg, et al. 1982) as the slope of the allometric equation then:

\[ R = (0.037 + 0.006 \, T)w_c^{0.884} \] (8)

where \( R \) is respiration rate in \( \text{ug C day}^{-1} \); \( T \) is temperature in \( ^\circ C \); and \( w_c \) is body weight in \( \text{ug carbon} \).

An empirical relation such as (8) must be applied with caution, particularly when it is derived from a small set of data. It is desirable to compare predictions of the equation with experimentally measured values. Since the dependence of the respiration constant (a) on temperature was derived from data on adult females only, a
test is to compare the predicted respiration of C₅ copepodites (approximately 25 ug C) at 8.5 °C to that reported in Table IV.4. The respiration rate of 1.544 ug carbon cop⁻¹ day⁻¹ predicted by the equation falls within the 95 percent confidence interval of the experimentally determined rate for C₅ copepodites (X = 1.797; S = 0.325; N = 6).

Carbon budget of C₅ copepodites and adult females

From the data on respiration and in situ feeding rates in May 1984, a carbon budget was constructed to evaluate the ability of M. pacifica to survive at rations available in the field. Daily carbon ingestion of adult females and C₅ copepodites at Station P during May was estimated from the in situ gut content results, and compared to calculated metabolic demands. Assuming that feeding occurs at night at the surface and that days are spent at 250 meters, metabolic demands are calculated to be 1.90 and 1.13 ug C copepod⁻¹ day⁻¹ for females and C₅, respectively. If assimilation efficiency is 70%, ingestion of 2.71 and 1.61 ug C copepod⁻¹ day⁻¹ is required for metabolism. Given the carbon to chlorophyll ratio of 60, the daily ingestion per female and C₅, estimated from in situ gut pigment determinations and a gut evacuation rate of 1.8% min⁻¹, are 3.10 and 0.59 ug C copepod⁻¹, respectively. Thus, adult females ingested sufficient food to support their metabolism and have a little left for growth or reproduction, while C₅ obtained food for only 37% of their daily metabolic needs with no provision for
growth.

Several assumptions were made to enable these comparisons, and errors in them, alone or in concert, may cause the poor agreement between metabolic requirements and daily ingestion of the fifth copepodites. The possibilities include the following: the carbon to chlorophyll ratio is in error; respiration rate is overestimated; gut evacuation rate is underestimated; the animals supplement their diet by feeding at depth on animals or seston; assimilation efficiency is greater than 70%; or during this particular day M. pacifica C5 did not get enough to eat. The last possibility is difficult to test, can only work on the short term, and is not discussed further. The other hypotheses are testable and can be evaluated for C5. The carbon to chlorophyll value may be in error, but other plausible values for this parameter (20 to 100) also fail to balance the energy budget. Assimilation efficiency, even if assumed to be 100%, an unlikely value, could not by itself balance the energy budget.

Respiration estimates from several sources (Fig. IV.6) were used to derive the respiration equation. The container size, acclimation and incubation times, and methods used to measure respiration varied widely, yet the results agree reasonably well. This reduces, but does not eliminate, the possibility of error; the respiration rates from all sources may be elevated above those found in situ. Considering the possibility that Metridia supplement their diet with animal prey, the guts of a few C5 and several dozen
females were examined microscopically for evidence of animal remains, and none, except a very few nasselarian radiolaria, were found (Batchelder, pers. obs.), although both Mullin (1966) and Haq (1967) found that *Metridia* readily ingest and grow on *Artemia* nauplii.

The carbon budget balance turns out to be sensitive to the choice of gut evacuation rate. The gut evacuation rate of 1.8% min\(^{-1}\) that was used in this analysis was determined using adult females only. It may not be appropriate to apply that rate to younger life stages. Furthermore, in the evacuation rate experiments described above the animals were transferred to filtered seawater to follow the time course of pigment loss from the gut, and perhaps animals so treated retain the food already in the gut longer than when other food is available (Murtaugh, 1984). If so, evacuation rates would be underestimated. All other parameters being unchanged, the carbon budget of C\(_5\) can be balanced so that assimilated carbon equals respired carbon if evacuation rate is increased from 1.8% min\(^{-1}\) to 5.0% min\(^{-1}\). Although this gut evacuation rate is twice the highest rate (2.4% min\(^{-1}\)) measured for adult females, gut evacuation rates as high as 4% min\(^{-1}\) have been reported for *Neocalanus plumchrus* (Dagg and Wyman, 1983) and *Temora, Pseudocalanus, Centropages, and Calanus* spp. (Baars and Oosterhuis, 1984).
Potential contribution of *M. pacifica* in control of plant stocks

The agreement between the measured and predicted respiration of C5 copepodites encouraged me to use the equation to estimate the metabolism of the C3 to C5 copepodite and adult female populations of *M. pacifica* at Station P from seasonal abundance estimates (Batchelder, 1985), and size distribution. All of these life stages migrate vertically, spending the night near the surface and the day at depth. During this migration, individuals pass through a marked temperature gradient, the intensity of which varies with season. A simple model was developed using temperature of the surface mixed layer and temperature at 250 meters, for night and day periods, respectively. Migration from the surface to 250 meters and back were considered to occur instantaneously at sunrise and sunset (U. S. Naval Observatory, 1979), respectively.

Respiration by the C3 to adult populations of *M. pacifica* was calculated for eight dates from 6 February 1980 to 15 February 1981 (Table IV.5). Predicted respiration varied from 0.08 mg C m−2 day−1 for C3 in June 1980 and February 1981, to 5.2 mg C m−2 day−1 for the adult female population in June 1980. Adult female respiration generally accounted for 30 to 50% of the sum of the respiration of all stages. Exceptions were June 1980, when copepodite density was low and 73% of the total respiration was by females, and January 1981, when copepodite stages were numerous and adult female respiration was only 19% of total respiration. Total daily consumption by C3 to adult *M. pacifica* was estimated assuming no
<table>
<thead>
<tr>
<th>Date</th>
<th>C3</th>
<th>C4</th>
<th>C5M</th>
<th>C5F</th>
<th>Fem.</th>
<th>Sum</th>
<th>(A) Cons.*</th>
<th>(B) Cons.**</th>
<th>(C) Primary Prod.</th>
<th>Fraction of Production Consumed (A/C)X100</th>
<th>(B/C)X100</th>
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<td>1.40</td>
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<td>3.62</td>
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<td>12.6</td>
<td>35.4</td>
<td>24.9</td>
<td>35.6</td>
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</tbody>
</table>

* - Daily consumption calculated using 70% assimilation efficiency, and assuming no growth or reproduction.

** - Daily consumption calculated assuming 70% assimilation efficiency and 70% of assimilated carbon respired, leaving 30% for growth and reproduction.
growth or reproduction and an assimilation efficiency of 70% and compared to seasonal average daily primary production (Stephens, 1968) (Table IV.5). The percentage of total daily primary production ingested by the older copepodite stages of *M. pacifica* ranged from 5% during the spring peak of primary production to 175% during midwinter.

It is important to remember that the consumption estimates discussed to this point provide for neither growth nor reproduction. Yet, development progressed, and growth occurred throughout the year except possibly during late December 1980 to early February 1981 (Batchelder, 1985). By making the additional assumption that 70% of the food assimilated is respired (Sushchenya, 1970), with the remaining 30% channeled to growth and reproduction, an estimate of consumption which provides for growth and reproduction as well as metabolism was obtained (Table IV.5). Only 8 to 9% of daily primary production is required by *C_3* to adults to meet their growth, reproduction and metabolic needs during summer, while in autumn and winter 36 to 57% of daily production is required. On 1 January 1981, however, consumption to meet metabolic demands alone was 1.7 times production. Batchelder (in press) found that adult female *M. pacifica* failed to produce eggs during late December to early February. The results of the model presented here suggest that there was insufficient food at that time to satisfy the metabolic requirements of the copepods, much less provide for growth or reproduction.
The respiration rate of the adult female population was calculated for all dates for which the length distribution was known, and compared to daily primary production (Fig. IV.7). The results confirm the conclusions derived from the fewer data on the younger stages; less than 5% of spring and summer daily primary production and roughly 20 to 40% of autumn and winter production was consumed by adult females. The increased fraction of production which was consumed by females in autumn and winter was due in part to lower primary production, and in part to the increased number of females. The large fluctuations, as low as 3% and as high as 80%, in the percent of primary production consumed by *M. pacifica* females during autumn and early winter are caused by the highly variable estimates of population size. These calculations suggest that the *M. pacifica* population had the grazing potential in 1980-1981 to maintain phytoplankton stocks at a low level during autumn and early winter but had relatively little impact on plant populations during the spring and summer peak of primary production.
(A) Seasonal cycle of primary production at Station P. (Approximate mean compiled from Stephens, 1968); (B) Seasonal cycle of water column respiration by the population of adult female *Metridia pacifica*. 
Figure IV.7

**A**
Prod. (mg C m\(^{-2}\) d\(^{-1}\))

**B**
Resp. (mg C m\(^{-2}\) d\(^{-1}\))

1980

J A J O J A
References


Heinrich, A. K. (1962). The life history of plankton animals and...


inferring feeding rate from stomach fullness of a mysid crustacean. Canadian Journal of Fisheries and Aquatic Sciences, 41, 1287-1293.


CHAPTER V

Life History and Population Dynamics of *Metridia pacifica*:

Results from Simulation Modelling.
Abstract

A numerical population dynamics model has been developed and used to investigate the functional response parameters of the copepod, *Metridia pacifica*. Equations describing growth, mortality, and reproduction are formulated and used to describe the development of individuals and to generate a population dynamics history for year-long model runs. Growth is described using an energetics-based, input-output model. Mortality is implemented as a constant daily per capita predation rate. Reproductive parameters of clutch size, clutch frequency, and total number of clutches are chosen to provide lifetime egg production similar to those previously reported for other calanoid copepods. In formulating the model I assumed that growth of *Metridia pacifica* in the subarctic Pacific is food-limited, and that temperature is unimportant.

Seasonal abundance and life history data for *Metridia pacifica* from Station P in the subarctic Pacific were used to evaluate the validity of the model. The timing of life processes, such as the time for development from egg to egg, was considered the important criterion for judging the suitability of the model and the chosen functional response parameters. A criterion of secondary importance was stage densities in the model similar to those observed in the field. "Reasonable" parameter sets provided growth rates which allowed completion of development in a generation time of approximately 100 days; the generation time observed in the field. The model was able to reproduce the population cycles in the field.
using reasonable extrapolations from the experimental physiology of copepods and seasonally constant food concentration. Development rate was very sensitive to the choice of input food stocks, specifically chlorophyll concentration, and the C:Chl ratio. This sensitivity may help to explain the large year-to-year differences in abundance of *M. pacifica* at Station P.
Introduction

During some years, *Metridia pacifica* is an abundant copepod in oceanic waters of the northeast Pacific Ocean (Batchelder, 1985). In spring and summer 1980 it was exceeded in density only by *Neocalanus plumchrus* among the larger copepods, while during autumn and winter it was the dominant large copepod. Because of their abundance, large size, and grazing activity, I (Batchelder, submitted) have suggested that *M. pacifica* may be an ecologically important grazer in the subarctic Pacific, particularly during winter. Thus, it is important to understand its population dynamics, to evaluate its trophic role, and to explain the large year-to-year differences in its abundance (Batchelder, pers. obs; Fulton, unpubl.). To these ends several studies have been completed. The seasonal abundance and life history (Batchelder, 1985) and adult female reproductive condition (Batchelder, in press) of *M. pacifica* were documented from weekly samples collected at Ocean Station P during 1980 and 1981. Per capita grazing and respiration rates of the older life stages have been measured (Batchelder, submitted). In order to couple these studies into an unified understanding of the biology of *M. pacifica* and its role in the subarctic Pacific, a numerical model has been developed of its population dynamics.

Earlier field studies suggest that *M. pacifica* completes three generations in ten to twelve months (Batchelder, 1985). The model is an attempt to reproduce this field observation using representations of individual growth, development, reproduction and mortality.
Largely it is a "fitted" model for which parameter combinations have been selected that most closely reproduce the population structure observed in 1980 to 1981. The model has been used to generate clues as to factors responsible for the large annual variations in abundance of *M. pacifica* in the subarctic Pacific.

**Criteria of Model Performance**

Output from the population dynamics model developed below is compared to the population structure observed for *M. pacifica* at Station P during 1980-1981. A specific parameter combination can be considered "possibly realistic" if it reproduces the following features:

- three generations are completed in 10.5 to 12 months
- *C₃*, *C₄*, and *C₅* densities increase from the first cohort to the third
- naupliar stages and *C₁*-*C₄* undergo marked seasonal cycles of abundance
- *C₅* and adult abundances remain relatively constant with season
- actual abundance of each life stage is comparable to field data.

The emphasis of the model is to achieve agreement with the timing of the population structure, for example the rate of development, while remaining consonant with general data on copepod physiology.

**Model Formulation and Parameter Estimation**

A metabolic input-output model for individual copepods was used to generate a time series of the population structure of *M. pacifica* from specified initial densities and parameter choices. The eggs
produced on each day are treated as separate day cohorts. Each day after hatching, individuals in a cohort become one day older, undergo one day's growth, experience predation and reproduce. The population structure reported by the model each day consists of the abundance of each copepod life stage in a 1 m² water column. Biomass (food resources, animal body size) and physio-ecological processes (ingestion, respiration, growth) in the model are expressed in carbon units. No attempt was made to model upper ocean physics such as the seasonally varying temperature and depth of the mixed layer.

The population dynamical model did not assume that *M. pacifica* is the major grazer of daily plant production, but rather that they "see" the phytoplankton standing stock as the food available for consumption. Plant standing stock is an input to the model. Throughout most of the year chlorophyll-a concentrations in the subarctic Pacific remain within a relatively narrow range, roughly from 0.15 to 0.45 ugChl liter⁻¹ (Fig. V.1). Chlorophyll rarely exceeds 1.0 ug liter⁻¹, and such events are brief. Based upon the data shown in Figure V.1, a range of chlorophyll-a concentrations was specified from which an independent, uniform variate was generated for each day of the model.

Three different ranges of chlorophyll were chosen to functionally simulate various copepod food searching behaviors. A range of 0.15 and 0.45 ugChl 1⁻¹, encompassing most of the recorded values for chlorophyll at Station P, was input to simulate
Figure V.1

Annual cycle of chlorophyll-a (ug Chl liter\(^{-1}\)) at Station P (50°N, 145°W). Data from many years summarized in Anderson, et al. (1977).
Figure V.1

Station 'P'
1959-1970
population dynamics when the copepods feed without searching for regions of higher food (random feeding). Searching behavior was modelled by restricting the range of values from which the food level was uniformly determined. A range of 0.25 to 0.45 ugChl \text{ liter}^{-1} \text{ was used as input when the copepods were assumed to move out of regions with low food. The range was narrowed further, to 0.35 to 0.45 ugChl \text{ liter}^{-1}, when the copepods were assumed to select only the richer regions for feeding. This elaboration of the model was implemented on the assumption that some vertical inhomogeneity of chlorophyll concentration exists within the mixed layer every day, and the copepods are capable of exploiting the regions of high food. The three ranges of chlorophyll used as input to the model are analogous to providing the copepods with different degrees of success in finding and securing food.

Although the chlorophyll concentration is relatively constant and low during all seasons, year-to-year variations in the seasonal pattern and magnitude of plant stocks do occur at Station P (Anderson, et. al., 1977). To evaluate the impact of a seasonal cycle of food resources on population structure, the chlorophyll-a concentrations reported by Clemons and Miller (1984) for Station P during 1980 to 1981 were used as input for several runs of the model (Fig. V.2).

Chlorophyll concentration from either of these approaches was converted to carbon units using carbon-to-chlorophyll ratios of 60 and 70 (Welshmeyer, pers. comm). Although McAllister (1969)
Figure V.2

Station P Chlorophyll concentration (ug Chl liter$^{-1}$) for the period from January 1980 to March 1981. (From Clemons and Miller, 1984).
estimated the carbon to chlorophyll ratio at Station P to vary seasonally from a low of 15 in winter to a high of 50 in summer, Welshmeyer observed relatively constant ratios during June 1983 and August 1984. Since there are no reliable measures of carbon:chlorophyll for winter in the subarctic Pacific, and to keep the model uncomplicated, the ratio was not varied seasonally. There is, because of the seasonal variation of light, reason to suppose it may vary, and the effect of that can be included in the model as data become available.

Individual growth is calculated daily as assimilation less respiration according to the equations in Table V.1. A Michaelis-Menten hyperbolic relationship was used to describe the relation between daily ingestion and food concentration. Provision was made for a threshold phytoplankton concentration below which grazing ceased, although in some simulations the threshold was set to zero. A relation between metabolism and feeding in marine zooplankton cannot be accepted with any certainty (Vidal, 1980). However, many theoretical studies of pelagic processes assume one (e.g. Steele and Mullin, 1977), and metabolism in the current model was subdivided into basal metabolism, dependent solely on animal size, and feeding metabolism, dependent on ingestion.

The parameters which must be specified to determine growth include the functional response parameters $G_m$, $T$, and $K_g$, the assimilation efficiency $AE$, the fraction of assimilated carbon that is respired $FR$, and the weight specific metabolic rate $B$. The latter
Table V.1. Equations describing growth, development, mortality and reproduction.

Growth

\[ W_{t+1} = W_t + G \]

\[ G = (AE \times I) - R \]

\[ I = \frac{G_m \times W^{0.7} \times (P-T)/(P + K_g - T)}{g} \]

\[ R = R_b + R_f \]

\[ R_b = B \times W^{0.7} \]

\[ R_f = I \times AE \times FR \]

t : day of model

G : growth (ugC animal \(^{-1}\) day \(^{-1}\))

AE : assimilation efficiency (unitless)

I : ingestion rate (ugC animal \(^{-1}\) day \(^{-1}\))

R : total metabolic rate (ugC animal \(^{-1}\) day \(^{-1}\))

G \(_m\) : maximum specific grazing rate (day \(^{-1}\))

W : body weight of animal (ugC)

P : phytoplankton concentration (ugC liter \(^{-1}\))

T : grazing threshold (ugC liter \(^{-1}\))

K \(_g\) : half maximum grazing constant (ugC liter \(^{-1}\))

R \(_b\) : basal metabolic rate (ugC animal \(^{-1}\) day \(^{-1}\))

R \(_f\) : feeding metabolic rate (ugC animal \(^{-1}\) day \(^{-1}\))

B : weight specific metabolic rate (day \(^{-1}\))

FR : fraction of food assimilated that is metabolised (unitless)

Development

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<td>0.21-0.25</td>
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<td>0.26-0.33</td>
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</table>

Mortality

\[ N_{s,t+1} = N_{s,t} \times M_x \]

s : life stage (N\(_{1+2}\) - C\(_6\))

t : day of model

M \(_x\) : mortality rate (x = naup.,cop.,adult)

Reproduction

\[ E_c = N_{s,c} \times EP \]

c : day class (cohort)

s : life stage (female only)

N : number of females in day class c

EP \(_{s,c}\) : eggs produced by one female during one reproductive event (eggs female \(^{-1}\) day \(^{-1}\))

E \(_c\) : total eggs produced by the entire day class of females for current event
three parameters were kept constant to reduce the number of simulations. The parameter $B$ was fixed at 0.10, providing a basal metabolic rate of 3% day$^{-1}$ for adult females (50 ugC) and 20% day$^{-1}$ for the youngest nauplii (0.1 ugC). The 3% day$^{-1}$ basal metabolism for adult females is less than the 7.2% day$^{-1}$ and 7.9% day$^{-1}$ total metabolic rate measured for fifth copepodites and adult females of *M. pacifica* (Batchelder, submitted). However, inclusion of a component of metabolism related to feeding activity increases the modelled rate to that measured in shipboard experiments. AE and FR were fixed at 0.70 and 0.40, respectively. An assimilation efficiency of 70% has been widely assumed for herbivorous copepods, although recent work by Landry, et al. (1984) indicates that it may be as high as 85%. The choice of 0.40 for FR, provides a gross growth efficiency of 11% for adult females with daily ingestion of 5 ugC (10% day$^{-1}$) and 34% for adult females with daily ingestion of 20 ugC (40% day$^{-1}$). These fall within the 10-40% range cited by Parsons, et al. (1977), and found for *Calanus pacificus* (30%; Paffenhöfer, 1976), and *Pseudocalanus elongatus* (18%; Paffenhöfer and Harris, 1976).

The ranges of the functional response parameters $G_m$, $T$, and $K_g$ that were investigated by model runs are shown in Table V.2. To decrease the number of simulations, $G_m$ was not varied in a systematic fashion. A maximum specific grazing rate of 2.0 was used for most of the simulations, although a value of 1.0 was tried in several runs. At saturating food levels, $G_m$ of 2.0 yields ingestion
Table V.2. Range of parameters investigated in simulation modelling.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Units</th>
<th>Range Evaluated</th>
<th>Symbol</th>
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<td>ug Chl-a L⁻¹</td>
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<td>P</td>
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<td></td>
<td>0.25–0.45 uniform</td>
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</tr>
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<td></td>
<td>0.35–0.45 uniform</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.10–0.80 seasonal</td>
<td></td>
</tr>
<tr>
<td>Carbon:Chlorophyll</td>
<td>ugC ug Chl-a⁻¹</td>
<td>60, 70</td>
<td></td>
</tr>
<tr>
<td>Ingestion Parameters</td>
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<td></td>
<td></td>
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<tr>
<td>Maximum</td>
<td>--</td>
<td>1.0, 2.0</td>
<td>Gₘ</td>
</tr>
<tr>
<td>Half Sat.</td>
<td>ug C L⁻¹</td>
<td>35–200</td>
<td>Kₛ</td>
</tr>
<tr>
<td>Threshold</td>
<td>ug C L⁻¹</td>
<td>0–25</td>
<td>Tₛ</td>
</tr>
<tr>
<td>Metabolism</td>
<td>--</td>
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<tr>
<td>Egg Production</td>
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<td></td>
</tr>
<tr>
<td>Mean</td>
<td>eggs fem⁻¹ day⁻¹</td>
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<td>X</td>
</tr>
<tr>
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<td>2–10</td>
<td>V</td>
</tr>
<tr>
<td>Frequency</td>
<td>days</td>
<td>1–6</td>
<td>IBC</td>
</tr>
<tr>
<td>Total No. Clutches</td>
<td>--</td>
<td>2–8</td>
<td>TC</td>
</tr>
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<td>Mortality Coefficient</td>
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<td></td>
<td></td>
</tr>
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<td>Naupliar</td>
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<td>Mₙ</td>
</tr>
<tr>
<td>Copepodite</td>
<td>day⁻¹</td>
<td>0.01–0.06</td>
<td>Mₖ</td>
</tr>
<tr>
<td>Adult</td>
<td>day</td>
<td>0.01–0.06</td>
<td>Mₐ</td>
</tr>
<tr>
<td>Egg Weight</td>
<td>ug C</td>
<td>0.1</td>
<td></td>
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</table>
rates equal to 324% body C day$^{-1}$ for 0.2 ugC nauplii and 62% body C day$^{-1}$ for 50 ugC adults, while $G_m$ equal to 1.0 yields ingestion rates lower by half. The adult rates are comparable to saturation feeding rates reported for *Acartia tonsa* (150% day$^{-1}$) (Kiorboe, et al., 1985), *Calanus pacificus* (85% day$^{-1}$) (Paffenhofer, 1971), *Centropages hamatus* (26% day$^{-1}$) (Kiorboe, et al., 1982), *Pseudocalanus elongatus* (140% day$^{-1}$) (Paffenhofer and Harris, 1976) and *Calanus sinicus* (47% day$^{-1}$) (S.-I. Uye, pers. comm.).

For each combination of chlorophyll range and carbon:chlorophyll the half saturation constant and threshold for grazing were adjusted until the development rate of the copepod in the model resembled that observed in the field. Growth of an individual in the model could be positive or negative. During positive growth the developmental stage of the individuals in a day class was determined from body weight according to preassigned ranges of body carbon per stage (Table V.1). Although individual growth could be negative, development could not (i.e. no backward molting). If a backward molt was indicated by the conversion from animal size to developmental stage, the individual was assigned to the oldest stage attained. If food levels and functional response parameters combined to produce extended weight loss, death ultimately occurred from starvation ($W = 0$).

Predation coefficients, as deaths per 100 individuals, were specified separately for naupliar, copepodite and adult stages as a fraction of each day class dying each day. Mortality rates for each
of the three groups remained constant throughout a complete run of
the model. Field mortality rates for copepods are poorly known and
the estimates which have been made usually encompass a wide range
(Fager, 1973). Extant data indicate that mortality, particularly of
copepodites, must be low, on the order of 0.0 to 10.0 percent per
day (Fager, 1973; Johnson, 1980; Parslow, 1980, Uye, 1982). To
maintain nearly steady state population density throughout the year,
mean survivorship to reproduction must be nearly $2/F$, where $F$ is
individual female fecundity. Using generation length for _M.
pacifica_ of roughly 100 days (Batchelder, 1985), a range of
mortality rates (2 to 6% day$^{-1}$) was derived from reasonable
estimates (20 to 500 eggs female$^{-1}$) of lifetime individual female
fecundity.

The size for transition of _C_5 copepodites to adults was set at
30 µgC and maximum adult size was 55 µgC, corresponding to the
largest females seen at Station P (Batchelder, pers. obs.). Adult
females in the model began to produce eggs the day after
maturation. The dependence of egg production on ingestion is well
documented for several copepod species (Checkley, 1980; Peterson,
1980; Durbin et al., 1983; Kiorboe, et al., 1985; Smith and Lane,
1985), however, there have been no comparable studies for _M._
pacifica. Because of this, daily egg production by an individual
dependency female in the model was generated from a random normal distribution
of prespecified mean and variance. On each day of reproduction a
clutch size was generated from the normal distribution, which
represented that day's output of eggs for each female within that day cohort. Females produced a clutch of eggs every one to four days (IBC) until death, or until a predetermined maximum number of clutches (TC) had been laid. The number of eggs produced by an individual day cohort of females was determined independently for each day of reproduction. Estimates of mean and variance for the egg production distribution were obtained from fecundity experiments with *M. pacifica* collected from Oregon coastal waters and from Station P (Batchelder, pers. obs.). Mean egg laying rates for females which produced eggs in those experiments were 1 egg day\(^{-1}\) female\(^{-1}\) and 6 eggs day\(^{-1}\) female\(^{-1}\) for females from off Oregon and Station P, respectively. For an egg weight of 0.1 ugC, this corresponds to 0.2 to 1.2 percent of body carbon per day for a female weighing 50 ugC. This is similar to the 3% day\(^{-1}\) reported for *Centropages typicus* feeding on 25 ugC liter\(^{-1}\) natural particulate matter (Smith and Lane, 1985), but substantially lower than the 30-50% day\(^{-1}\) reported for other species feeding at higher food levels (Landry, 1978; Checkley, 1980; Johnson, 1981, Ambler, 1985).

The density and stage distribution (weights) of the individuals present initially (day 0) are required as input to the model. Day 0 numbers and weights were based on the observed population structure of *M. pacifica* at Station P during February 1980, just prior to the first cohort of that year (Batchelder, 1985) (Table V.3). The effect of doubling the initial population size was investigated in several
Table V.3. Initial (day zero) abundances and weights of *Metridia pacifica*.

<table>
<thead>
<tr>
<th>Size (µg C)</th>
<th>No. m⁻²</th>
<th>Life Stage</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.5</td>
<td>1000</td>
<td>C₂</td>
</tr>
<tr>
<td>2.1</td>
<td>1000</td>
<td>C₂</td>
</tr>
<tr>
<td>4.1</td>
<td>1000</td>
<td>C₃</td>
</tr>
<tr>
<td>6.1</td>
<td>1000</td>
<td>C₄</td>
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<tr>
<td>10.1</td>
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<td>C₄</td>
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<td>14.1</td>
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<td>C₄</td>
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<tr>
<td>20.1</td>
<td>1000</td>
<td>C₅</td>
</tr>
<tr>
<td>28.1</td>
<td>1000</td>
<td>C₅</td>
</tr>
</tbody>
</table>
Several factors were not addressed in the model that may be ecologically significant to the population dynamics and life cycle of *M. pacifica* in the field. First, seasonal changes in mixed layer temperature and depth and in the temperature gradient with depth were not explicitly included. Second, except for food searching, animal behavior was ignored. Copepodite and adult female stages of *Metridia pacifica* migrate vertically several hundred meters daily, which subjects them to different predators, food sources, and temperatures. Rates of mortality, ingestion and respiration would all be affected. Third, the model is unrealistically static in that the parameters were not permitted to vary within a run. Consequently, the copepods could not modify their ingestion rate or assimilation efficiency in response to generally low or high food levels. Fourth, the model oversimplifies and generalizes some factors when data describing them are not available. Assumption of a seasonally constant carbon:chlorophyll and of a single growth relation applicable for all life stages are examples. Finally, seasonal changes in density and composition of predators and their effect upon the *M. pacifica* population were not modelled.

Random generation of the phytoplankton concentration and of eggs produced daily by each day cohort of females introduced variation into replicate runs of the model. This made interpretation of the differences among runs with different parameters difficult. Therefore, the results of five replicate
model runs for each set of parameters were averaged to produce a generalized output. That was used to compare parameter sets to each other and to the field data.
Results

The generalized output for each set of parameters was graphed as shown in Figures V.3 and V.4 for one model run. Figure V.3 shows the fraction of the *M. pacifica* population in each life stage. The lowermost portion is the fraction of the population present as N_{l+2}, while the uppermost portion is the fraction present as adult females. The fraction present as N_{l+2} increased rapidly when C_5 of the previous generation matured to adults and began to produce young. This portrayal of the data permitted easy identification of the time and duration of reproduction and determination of generation length. Figure V.4 shows the abundances of each stage for the same parameter set as in Figure V.3.

Parameters satisfying the first three criteria (p.147) of model performance were found, while the latter two criteria were difficult to satisfy. Generation time and the rate of individual growth and development were dependent primarily upon the amount of food available and the choices made for the functional response parameters. Conversely, variation of the mortality coefficients and reproduction parameters had no effect on the timing of development, but a large effect on the abundance of the life stages. Thus, generation time (the first criterion) is partially decoupled from the other four criteria in the model.

Considering the number of parameters which can be varied without control from the field data, it was decided to focus first
Life stage frequency distribution history of *Metridia pacifica* from model with chlorophyll range = 0.15-0.45; C:Chl=60; X=10 eggs day\(^{-1}\); V=10 (eggs day\(^{-1}\))^2; IBC=2 days; TC=4; G\(_m\)=2.0; K\(_g\)=70 ugC liter\(^{-1}\); T=0.0 ugC liter\(^{-1}\); B=0.1; M\(_n\)=M\(_c\)=0.02 day\(^{-1}\); M\(_a\)=0.015 day\(^{-1}\); and egg weight = 0.1 ugC.
Figure V.3
Abundance history of *M. pacifica* life stages for model run with parameters as in Figure V.3.
Figure V.4
on the parameters most significantly affecting generation time.

Table V.4 summarizes the results of varying the functional response parameters for different levels of food (i.e. copepod searching behaviors) and carbon to chlorophyll ratios. Depending on the selections for plant level and the grazing parameters the number of generations completed in 12 months ranged from less than one to eight.

Several combinations of plant concentration and functional response parameters provide development rate similar to that observed in the field. With C:Chl = 70 and a chlorophyll range of 0.15-0.45 ugChl liter\(^{-1}\) the copepods completed three generations in 12 months with functional response parameters \(K_g = 40\) ugC liter\(^{-1}\) and \(T = 10\) ugC liter\(^{-1}\), or \(K_g = 85\) ugC liter\(^{-1}\) and \(T = 0\). When \(T = 10\) ugC liter\(^{-1}\) and they could avoid water poor in food (i.e. feeding at 0.25-0.45 ugC liter\(^{-1}\)), *M. pacifica* progressed through three generations in a year with \(K_g\) as high as 55 ugC liter\(^{-1}\). When feeding only in high food patches (0.35-0.45 ugC liter\(^{-1}\)), \(K_g = 70\) ugC liter\(^{-1}\) allowed completion of three generations per year. In order to achieve the same rate of growth and development, *M. pacifica* which feed randomly must be much more efficient grazers than if they search out regions of high food.

Estimates of the half saturation constants for copepod feeding \((K_g)\) suggested by the model are substantially lower than \(K_g\) values determined in bottle incubation experiments (Batchelder, submitted). \(K_g\) from those investigations of adult female *Metridia*
Table V.4. Number of generations completed in 12 month model run.  
Grazing Parameter Set: $G_m/K/T/B$

<table>
<thead>
<tr>
<th>Grazing Parameter Set</th>
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<th>Uniform</th>
<th>Uniform</th>
<th>80-81 Chl Values</th>
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<td></td>
<td>.15-.45</td>
<td>.25-.45</td>
<td>.35-.45</td>
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<tr>
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<td>Random</td>
<td>Random</td>
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<tr>
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<td>Variate</td>
<td>Variate</td>
<td>Variate</td>
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<td></td>
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</tr>
<tr>
<td>Carbon : Chlorophyll = 70</td>
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<td>2/40/10/.1</td>
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</table>

** - model run shown in Figure V.5.
pacific feeding on *Thalassiosira weissflogii* or *Corethron hystrix* ranged from 100-200 ugC l⁻¹.

For food levels and functional response parameters producing population cycles in model runs similar to those observed in the field, mean daily growth of N₆ (0.5 ugC) and adult females (50 ugC) was 0.05 ugC ind⁻¹ day⁻¹ and 1.1 ugC ind⁻¹ day⁻¹, respectively. For adult females this corresponds to 2.2% of body carbon per day, while for N₆ growth was equivalent to 10% day⁻¹. All combinations of Kᵣ and T which allow completion of three generations per year must produce these growth rates.

Growth and development rates in models with C:Chl = 60 are much slower than in those with a ratio of 70 (Table V.4), when the ingestion and respiration parameters are equivalent. For example, with Kᵣ of 40 ugC liter⁻¹ and T of 10 ugC liter⁻¹, 3.2 generations were completed in twelve months when C:Chl was 70, but less than 2 generations with C:Chl of 60. This indicates the importance of having reliable estimates of carbon:chlorophyll for all seasons of the year.

Model runs in which the chlorophyll stocks measured in 1980-1981 specified the food available to *Metridia pacifica* yielded seasonally varying development rates and population cycles with little resemblance to the field observations (Fig. V.5). Development was slower during summer and faster during autumn in the model than in the field.
Life stage frequency distribution history of *M. pacifica* from model using measured 1980-1981 chlorophyll-a stocks; C:chl=60; X=10 eggs day\(^{-1}\); V=10 (eggs day\(^{-1}\))^2; IBC=2 days; TC=4; \(G_m=2.0\); \(K_g=60\) \(\mu g\) C liter\(^{-1}\); T=0.0 \(\mu g\) C liter\(^{-1}\); B=0.1; \(M_n=M_c=0.02\) day\(^{-1}\); \(M_a=0.015\) day\(^{-1}\); and egg weight=0.1 \(\mu g\) C.
Reproducing the stage abundances of *M. pacifica* observed in 1980-1981 was far more difficult than reproducing the development rate. Model estimates which produced stage abundances for each life stage which were within 50-200% of the field estimates throughout the year were considered reasonable. Mortality rates of 1-2% day$^{-1}$ for each group of stages (nauplii, copepodites, adults), coupled with reproductive parameters, $X = 5-8$ eggs/clutch, $V = 2-5$ (eggs/clutch)$^2$, $IBC = 2$ days, and $TC = 4-6$ clutches female$^{-1}$, produced time series of stage density most similar to the field data. Model runs in which mortality of all stages was slightly higher, for instance 3% day$^{-1}$, resulted in too few survivors to adulthood. Increasing the clutch size or the number of clutches per female, increased the number of early nauplii too much.
Discussion

According to a recent analysis, growth of zooplankton in oceanic regions is likely to be food-limited (Huntley and Boyd, 1984). Making this assumption, the population dynamical model described here provides interesting clues to factors responsible for the large inter-annual variation in abundance of M. pacifica in the subarctic Pacific. First, growth and development were much slower with C:Chl = 60 than at 70, indicating the extreme sensitivity of the population dynamics of M. pacifica to small changes in the availability of food. Individuals appear to be "poised" on the threshold of starvation. Welschmeyer's estimates of 60 to 70 for C:Chl were for spring and summer only. Measurements have not been made for other periods of the year. The model indicates that such data are crucial to understanding the population dynamics of M. pacifica, and probably of other grazers as well.

Second, the capability of the copepods to find and exploit patches of higher food has very large effects upon the dynamics of the population, particularly the rate of development (timing) and abundance. For a specific functional response curve, copepods which exploit patches have higher growth rate and more rapid development than those which do not. A consequence of the shorter generation time is a greater survivorship to reproduction and larger population size. To retain agreement with the timing of development in the field, the functional response parameter, K_g, of copepods which feed in high food patches must be higher than that of copepods which feed
Years of higher than average phytoplankton stocks may enhance individual growth, and provide for rapid development, good survival and high population density. If the sensitivity of the population structure to food resources that is evident in the model is true in nature as well, it may help to explain the large year-to-year differences in the population size of *Metridia pacifica* in the subarctic Pacific. Fulton (unpubl.) observed that the predominant autumn and winter grazer at Station P varied from year to year, with *Pseudocalanus* sp., *Calanus pacificus*, *Metridia pacifica*, and others each having been abundant during one year or another. Detailed *M. pacifica* abundance data to a depth (2000 m) encompassing most of its range are available only for the period from February 1980 to March 1981, and for May and August 1984. *Metridia pacifica* was clearly the most abundant large herbivore during autumn and winter 1980-1981 (Batchelder, 1985; Miller et al., 1984), while in 1984 it was not (Batchelder, unpubl.).

In August 1984, salps were very abundant (up to 13 ind m\(^{-3}\)), and may have been the principal large herbivore in the eastern subarctic Pacific. High salp densities occur intermittently at Station P and have been attributed to northward extension of transition water (LeBrasseur, 1965). The water column structure in August 1984 did not indicate such an extension, but nevertheless was anomalous compared to the long term record obtained from the weatherships. The halocline was shallower and sharper and the mixed
layer was 1–2°C warmer than is usual for August. Possibly these conditions are remnant from the severe 1983 El Nino which perturbed the eastern North Pacific (Tabata, 1984). Despite the anomalous physical structure of the upper water column, the biological environment, except for the prevalence of salps, appeared to be normal.

The third significant result of the model is the failure to reproduce the field population history of *M. pacifica* when chlorophyll stocks measured in the field in 1980–1981 are used as input. Poor agreement between the model and field data may result from inability of *M. pacifica* in the model to adjust to changing food conditions. Chlorophyll in 1980 ranged from 0.1 ug chl liter\(^{-1}\) in summer to 0.7–0.8 ug chl liter\(^{-1}\) during September–November. During conditions of low food the animals might increase their efficiency of assimilation to better utilize the food which is ingested (Landry et al., 1984; Giguere, 1981; but see also Tande, 1985). Alternatively, the poor fit of the model to the field data may arise from violation of the assumption of a seasonally constant C:Chl ratio. If C:Chl varies seasonally, as suggested by McAllister (1969), then the availability of food (carbon) would decrease, more so in the autumn and winter than during summer, compared to the seasonally constant 60 and 70 used here. This would lead to growth and development rates during summer approaching those of autumn.

The results of the model support the applicability to *Metridia pacifica* of physiological parameters derived from work on copepods
generally. With assimilation efficiency and the fraction of assimilated food which is metabolized fixed at values reported for other copepod species, the functional response parameters providing good fits to the field data were quite reasonable. Using plausible values for AE and FR, chlorophyll range of 0.15-0.45 ugChl liter$^{-1}$, and C:Chl = 70, functional response parameters of $K_g = 40$ ugC liter$^{-1}$ and $T = 10$ ugC liter$^{-1}$ provided a development rate similar to that observed in nature. With those parameters and $G_m = 2.0$, adult female ingestion as a fraction of body weight ranged from 0.8 to 22.6% day$^{-1}$, with mean of 14% day$^{-1}$. This compares reasonably well to the 7.2% day$^{-1}$ ingestion rate estimated by in situ gut fluorescence for females during May 1984 (Batchelder, submitted).

Similarly, mortality rates of 1 to 3% day$^{-1}$, although not perfectly reproducing the field data, are within the range expected from previous studies of copepod mortality. The fecundity required to reproduce the population history of *M. pacifica* in the field was similar to that observed in laboratory experiments (Batchelder, pers. obs.), although egg production in both laboratory experiments and the model is low compared to experimental measures for other copepod species (Landry, 1978; Checkley, 1980; Ambler, 1985).

The use of relatively simple formulations of growth, natality and mortality to simulate development and population history of *Metridia pacifica* proved to be a powerful technique, which may be applicable to zooplankton in general when growth is food-limited. In population studies of nearshore copepods, Belehradek's (1957)
function has been used successfully to predict stage-specific duration and development rates as a function of habitat temperature (McLaren, 1978; Johnson, 1981; Corkett and McLaren, 1970; Uye, 1982). That method assumes that food is always in surplus, and thus development rate is physiologically, and primarily temperature, dependent. Estuarine and nearshore zooplankton may have a surplus of food, but this is rarely the case for oceanic zooplankton (Huntley and Boyd, 1984). In oceanic zooplankton, where growth may often be food limited, the assumptions of the Belehradek function are violated. The simple model presented here may be useful in investigating development rate and population history of oceanic species where growth is food-limited. Importantly, a model of this type can draw general trophic conclusions about the adequacy of the habitat from the most readily available, non-experimental data: life cycle timing and cohort development. To be useful, however, this model requires good data for estimating the timing of the population cycle.
References


CHAPTER VI

Summary
The abundance and vertical distribution of the life stages of *Metridia pacifica* were recorded at Station P in the subarctic Pacific from February 1980 to March 1981. With the exception of naupliar stages in January, all stages were present year-round. The stage structure of the population suggested that three cohorts were completed during the study period. Generation times of the three cohorts were similar, in spite of vastly different seasonal sea surface temperatures. The effect of temperature on development rate and generation time may have been minimized by vertical migration of the older copepodites and adult females from the warmer surface waters at night to below 250 m, where water temperature remains constant seasonally, during the day.

The persistence of a coherent cycle in the population stage structure through multiple generations suggests that some process is acting to reinforce the synchrony of the population. From the orderly disappearance, youngest to oldest, of the naupliar stages in December 1980 and January 1981, it appeared that (1) either a failure of the adults to produce eggs, or (2) predatory or starvation mortality of the naupliar stages, during mid-winter might be responsible for coherent population cycles.

The possibility that conditions during early to mid-winter were inadequate for the production of eggs by *Metridia pacifica* was investigated by determining the maturation state of the adult females. A staining method, utilizing Fast Green, was developed to
selectively stain the ovaries and oviducts of calanoid copepods. No females were in "fully spawning" condition during mid-winter. The decline in the percentage of adult females actively reproducing occurred approximately 1 month before the number of nauplii began to decline, suggesting causality. Furthermore, the data indicate three major peaks in spawning activity: April, late June to early July, and late September to early October. Peaks in spawning activity were separated by periods when the percentage of females actively reproducing was significantly lower. Thus, the cycling of the population age structure is initiated by recommencement of reproduction by adult females in February and March, and reinforced by seasonal cycling of the reproductive condition of adult females.

Estimation of the grazing role of *Metridia pacifica* in maintaining the seasonally constant chlorophyll stock observed in the subarctic Pacific was one of the principal goals of this thesis. To that end, several types of experiments were conducted to evaluate the consumption of *Metridia pacifica*. Estimates of ingestion from *in situ* gut fluorescence observations, and from laboratory particle counting incubation experiments extrapolated to the low food concentrations typical of the field, indicate that daily ingestion by adult females was on the order of 5% body C day⁻¹. Metabolic rate of *C₅* and adult females was also about 5% body C day⁻¹. Thus, most of the food consumed is respired, leaving little for growth (immatures) or reproduction (females).

Using the respiration rate as a conservative estimate of energy
consumed by *M. pacifica*, the population densities observed at Station P in spring and summer 1980 provide a total grazing impact which is only a small fraction of daily primary production. During autumn and winter, however, the estimated daily consumption of the entire population was similar to total daily primary production. Two factors are responsible for the more important grazing role of *M. pacifica* at this time. First, the population size was much larger in autumn and winter than it was earlier in the year. Second, the primary productivity during autumn and winter was much lower than during spring and early summer. Nevertheless, *Metridia pacifica* may have been important in 1980 in preventing the accumulation of plant stocks in the fall after the *Neocalanus* spp. departed for diapause at depth.

It was mentioned earlier that the constancy of development rate observed in the field, may occur because *M. pacifica* migrate to cold, deep water during the day. Alternatively, *M. pacifica* generation time (i.e. development rate) may be insensitive to temperature. The field data suggest that the factor limiting growth and development must be relatively constant throughout the year. Limitation by food availability is suggested by the long known seasonal constancy of chlorophyll standing stock in the subarctic Pacific. Huntley and Boyd (1984) suggest that growth in oceanic copepods is usually food-limited rather than temperature-limited, as is common in estuarine and coastal copepods.

Since the respiration and ingestion experiments indicated that
Metridia pacifica was not a dominant grazer, I chose to investigate the nutritional adequacy of the habitat using the long-term mean chlorophyll stocks as the available food resource. Assuming that growth was food-limited, a numerical model was developed to simulate the population structure and dynamics of M. pacifica. Growth was modelled as the excess of assimilation over respiration. Individual copepod size was converted to developmental stage by specifying a range of weights corresponding to individuals of each developmental stage.

Seasonal abundance and life history data for M. pacifica from February 1980 to March 1981 were used to judge the suitability of various parameter choices. Emphasis was placed on the timing of developmental progress in evaluating the model. By using reasonable estimates for the physiological parameters of metabolism, assimilation efficiency and growth, obtained from previous laboratory experiments on copepods of other workers, and by assuming growth to be food-limited, it was possible to obtain population dynamics from the numerical model remarkably similar to those observed for Metridia pacifica in the field in 1980-1981. The concordance of the model results and the field data suggest that at food concentrations typical of the subarctic Pacific, M. pacifica growth and development may be food limited. Furthermore, development rate of M. pacifica was very sensitive to food availability. Small decreases in food availability greatly slow development rate and decrease survivorship to adulthood. The large
inter-annual variations in *M. pacifica* abundance at Station P may reflect this sensitivity to food resources.
BIBLIOGRAPHY


Peterson, W. T. and C. B. Miller. (1976). Zooplankton along the


APPENDICES
Appendix A. Sample dates and collection data. Most samples were collected between 2100 and 0100 local time. Day samples were collected between 0900 and 1300.

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