

# Annual Variation of Occurrence and Growth in the Life Cycles of *Neocalanus flemingeri* and *N. plumchrus* (Calanoida, Copepoda) in the Western Subarctic Pacific

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**Abstract.** Life cycles of large suspension-feeding copepods were investigated at the western subarctic Pacific gyre (Oyashio area). Two populations were recognized in *N. flemingeri* by the body size, life cycle, and timing of ontogenetic migration. Small forms (same size as original description; ~3.5 mm in prosome length at adult female) have a one-year life cycle and occur at the surface between January and June. Large forms (3.9-5.2 mm in prosome length at adult female) have a two-year life cycle with winter dormancy at C4 and adult female. The young copepodites of the large forms occur in the surface water later than the small forms, then grow to C4 with full deposition of lipid. The next year, the C4s start grazing from January and sink to a deeper layer at the same time as the small forms. The life cycle of *N. plumchrus* was identical to the original description made of the Alaskan gyre population. Temporal partitioning of the surface habitat utilization was clearly established between *N. plumchrus* and small forms of *N. flemingeri*, but overlap was observed between *N. plumchrus* and the large forms of *N. flemingeri*. Another difference in life cycle strategy among the two species of copepods was lipid deposition. *Neocalanus plumchrus* showed almost no lipid deposition until C5; in contrast, both forms of *N. flemingeri* started lipid deposition as early as C1.

Abundance, timing of occurrence, and stage composition of 3 species of *Neocalanus* were investigated from 1990 to 1997. Significant annual variations of abundance, development, and timing of occurrence were recognized. The development rates and abundance of both species were low in cold years with low chlorophyll concentration. *Neocalanus plumchrus* showed relatively high dependency on food availability.

## 1. Introduction

A zooplankton assemblage in the western subarctic Pacific was dominated by large interzonal copepods: 3 species of *Neocalanus* and 1 species of *Eucalanus*. They feed and grow at the surface layer for a few months and stay at depth for the rest of their year or more life cycle [Fulton, 1972; Miller *et al.* 1984; Miller and Clemons, 1988; Miller and Terazaki, 1989]. *Neocalanus flemingeri* was described by Miller [1988], and the life histories of the species and sibling species (*N. plumchrus*) were re-examined by Miller and Clemons (1988). These works were mainly based on the samples collected in the western subarctic gyre of the North Pacific. There is substantial evidence of the physical and biological differences between the copepod populations of the eastern and western gyres of the subarctic Pacific [Sugimoto and Tadokoro, 1997; Saito *et al.*, 1998]. *Neocalanus* species show variation of life cycle strategy depending on the local oceanographic conditions [Miller and Clemons, 1998; Miller and Terazaki, 1989]. The first goal of the present study is comparison of the life histories of the two copepods between the eastern and western subarctic gyre of the North Pacific. Secondly, annual variations of abundance, growth, and timing of occurrence were studied using an 8-year sampling series; the causes of the annual variations are discussed.

## 2. Materials and Methods

### 2.1. Sampling

Sampling for life cycle analysis was carried out at the stations located along the first and second branches of the Oyashio current by FRV *Hokkou Maru* and *Tankai Maru*, Hokkaido National Fisheries Research Institute, 6 to 10 times a year from July 1996. The sampling still continues. Copepods were collected from oblique tows with a bongo net (mouth opening 70 cm, mesh opening 330  $\mu$ m) from about 500 m depth during the night. The net was equipped with a depth meter and flow meters. Samples were preserved with neutralized formalin seawater.

Sampling for annual variations of copepod occurrences was carried out from May 1990 to July 1997 southeast of Hokkaido along a transect line which crosses the Oyashio current (Figure 1). Vertical hauls with a small bongo net (mouth diameter 30 cm; mesh opening 330  $\mu$ m) were towed from the base of the surface mixing layer. When the surface mixing layer was deeper than 50 m, the net was towed from 50 m depth. An aliquot of the samples was preserved with neutralized formalin seawater. The net samplings were conducted 4 to 6 times a year; however, only samples collected in April, May and June/July were used for the analysis of annual variations of occurrences of *Neocalanus flemingeri* and *N. plumchrus*, because these copepods are distributed at deeper layers in other seasons. The data for each month included 5 hauls, which roughly sampled the first and second branches

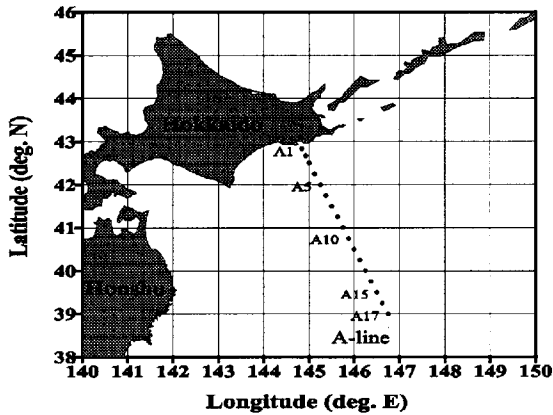


Figure 1. Sampling locations in the western subarctic Pacific gyre.

of the Oyashio current. The oceanographic data including temperature, chlorophyll-*a*, and biomass of zooplankton were summarized in Saito *et al.* [1998]. Development of *N. plumchrus* and *N. flemingeri* was indicated by the C5/C4 ratio because C5 has a relatively long duration of lipid accumulation. Development was calculated for the April and May samples of *N. flemingeri* and the May and June/July samples of *N. plumchrus*. The sampling dates in each year ranged within 4 days in May, were within 10 days in April, and within a month in June/July. However, June/July sampling was usually done in the first week of July, except in 1990 and 1994.

## 2.2 Identification

Miller [1988] suggested characters such as body color in an unpreserved specimen, morphology of mandible gnathobase, and length of maxilla to distinguish the C5 of *Neocalanus flemingeri* from *N. plumchrus*. We applied width of mandible gnathobase and length of maxilla for younger copepodite stages. The two species were clearly separated by the 2 morphological characters until C2. The following analysis of the life history was mainly based on the data of C2 to C6, and on C3 to C6 for annual variations of occurrence.

## 3. Results

### 3.1. Two populations (or forms) of *N. flemingeri*

Bimodal distribution was observed in the length frequency distribution of *Neocalanus flemingeri* for each developmental stage (Figure 2). Smaller individuals were in the same size range as those reported from the eastern subarctic gyre, but larger individuals were in the same size range as *N. plumchrus* or even larger. The largest adult female was 5.1 mm in prosome length. In the October sample, which was the dormant season of *N. flemingeri*, adult females and C4 formed the population (Figure 3), and these C4 individuals were the large forms (Figure 2). In January, both forms of C4 occurred, but large forms showed higher lipid content than small forms. These results suggest that small forms have a 1-year life cycle as does the population of the eastern subarctic gyre, and large forms have a 2-year life cycle as does the population of the Japan Sea.

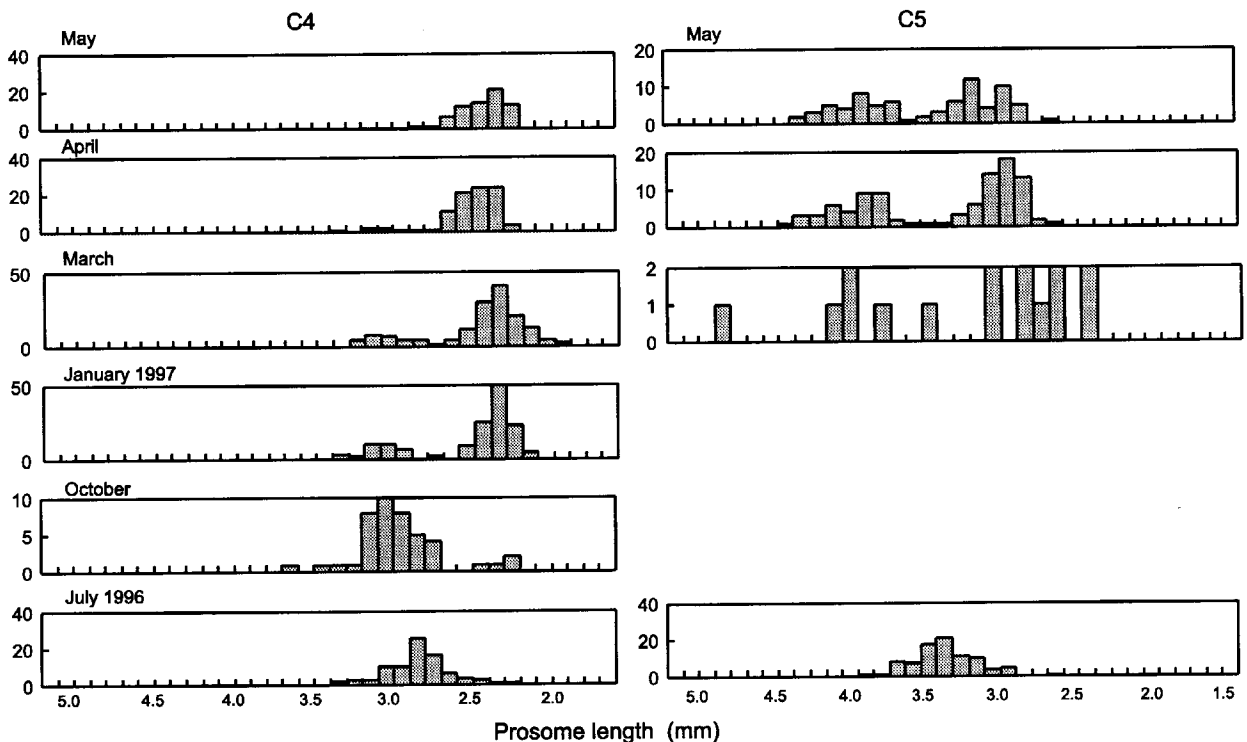


Figure 2. *Neocalanus flemingeri*. Prosome length distributions of copepodite 4 and 5.

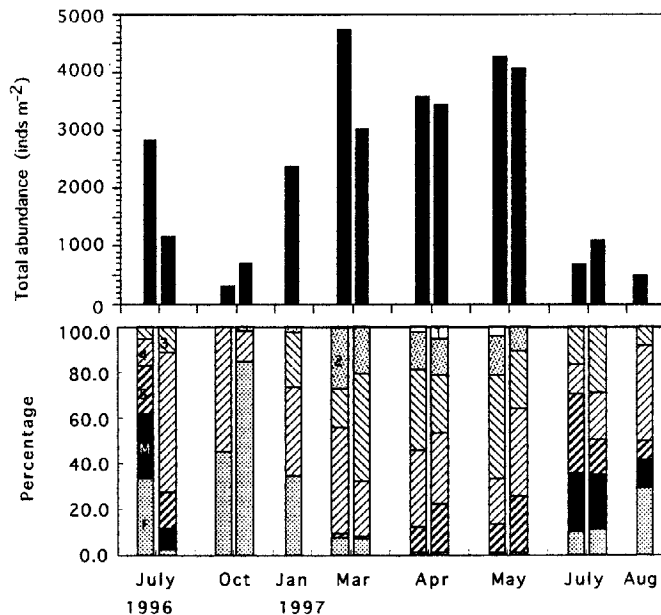
### 3.2. Life cycles of *Neocalanus flemingeri* and *N. plumchrus*

*Neocalanus flemingeri* showed the spawning peak in January, which agrees with the eastern gyre population. Difference of spawning season was not clear between the two forms of *N. flemingeri*. Although the spawning peak of *N. flemingeri* was January, C4 and younger copepodites were observed at the same time (Figure 3). As mentioned earlier, C4 individuals occurred in both the large and small forms, and younger copepodites were represented by the small forms. This suggests that the small forms of copepodites came from the early spawners, because only a few spawning females were observed in the October sample. Although the population of *N. flemingeri* increased from January to May and C4 was observed from January, C5 appeared from April, which suggests that C4 has a longer duration than younger copepodite stages. Although younger copepodite of small forms appeared from January, those of large forms appeared later in the season, which was almost at the same time as *N. plumchrus*. Dormant females and males appeared July and August in both forms, and many females with spermatophore were observed, indicating that the mating season of *N. flemingeri* is summer, as it is in the eastern gyre.

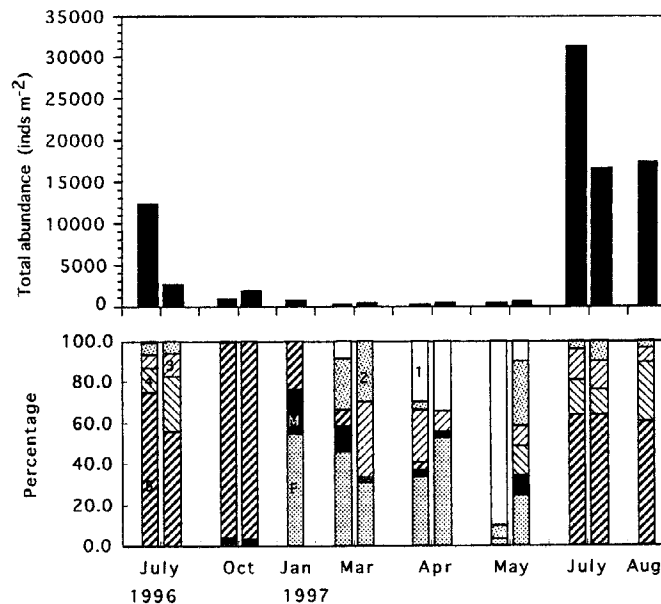
Spawning females of *N. plumchrus* were collected except in July; the spawning season could not be confirmed by our shallow sampling. However, it should be certain that *N. plumchrus* have a long spawning period, from fall to spring, as in the eastern gyre. Although a very small number of younger copepodites were observed from March to May, the population greatly increased between May (5/12) and July (7/6), and the increased population was dominated by C5 (Figure 4). These results strongly suggest that the major part of the population appeared at the surface layer and grew to C5 within one and half months at most. Then, replacement from *N. flemingeri* (small form) to *N. plumchrus* took place during June. This is about a month later in the season than that of the eastern subarctic gyre population. Separation of season for utilizing the surface layer was not clear between the large forms of *N. flemingeri* and *N. plumchrus*.

### 3.3. Lipid accumulation

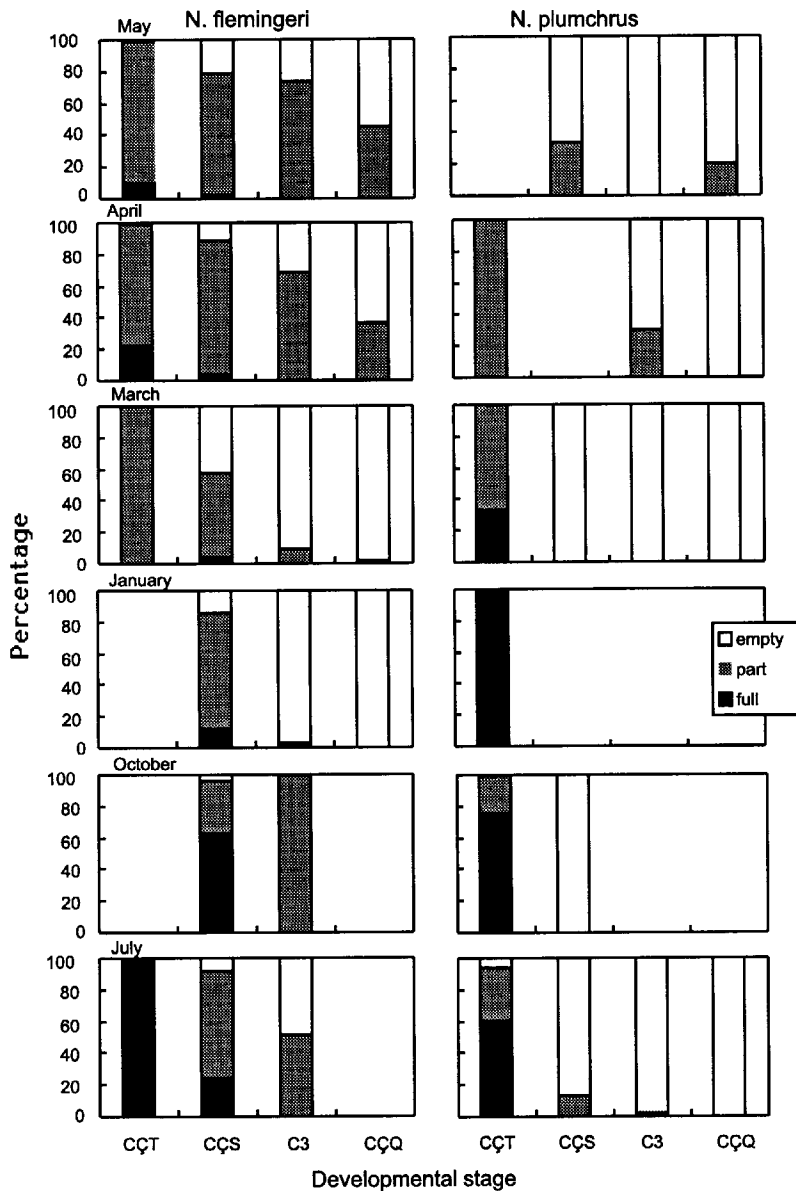
The lipid accumulation pattern was different between *N. flemingeri* and *N. plumchrus*. *N. flemingeri* showed higher lipid content throughout the year (Fig. 5). This phenomenon was most obvious at the abundant season for each species, *N. flemingeri* in May and *N. plumchrus* in July. Over 60% of C3 and C4 of *N. flemingeri* were partly filled by lipid and even C2 showed lipid accumulation; on the contrary, younger copepodites (C2 to C4) of *N. plumchrus* rarely showed lipid accumulation (Figure 5). Obvious lipid accumulation by *N. plumchrus* was observed at only C5 and the accumulation progressed from early summer to winter.



**Figure 3.** *Neocalanus flemingeri*. Seasonal variations of numerical abundance and developmental stage composition from July 1996 to August 1997.



**Figure 4.** *Neocalanus plumchrus*. Seasonal variations of numerical abundance and developmental stage composition from July 1996 to August 1997.



**Figure 5.** Lipid accumulation by copepodite stages of *Neocalanus plumchrus* and *N. flemingeri*. Lipid accumulation is categorized into 3 levels: full, part, and empty.

(Figure 8). These fluctuations were similar to those of abundance. However, high development rates of *N. plumchrus* in June/July were observed from 1992 to 1994, when the development rates and biomass were low. Moreover, the replacement of *N. flemingeri* by *N. plumchrus* occurred in June in 1994 and 1997, but in other years it took place in May (Figure 8), which shows there is a fluctuation of about a month in the timing of the replacement.

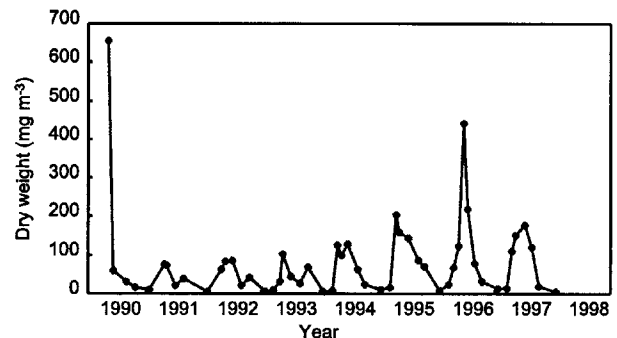
#### 4. Discussion

The large form of *Neocalanus flemingeri* has a 2-year life span, which indicates that large forms suffer roughly 2 times higher predation mortality than small forms. However, the large forms are about 1.4 times larger in length (2.7 times in volume). If we assume egg production is proportional to body volume [Fulton, 1972], we may expect 2.7 times higher egg production rate in large forms than small forms. The disadvantage of longer life span for large forms may be compensated by higher egg production rates. Younger copepodites of two forms appeared in the surface layer at different seasons, but both forms progressed from C4 to C5 and then to the adult stage mainly from May to July. Adult males were observed in July and August.

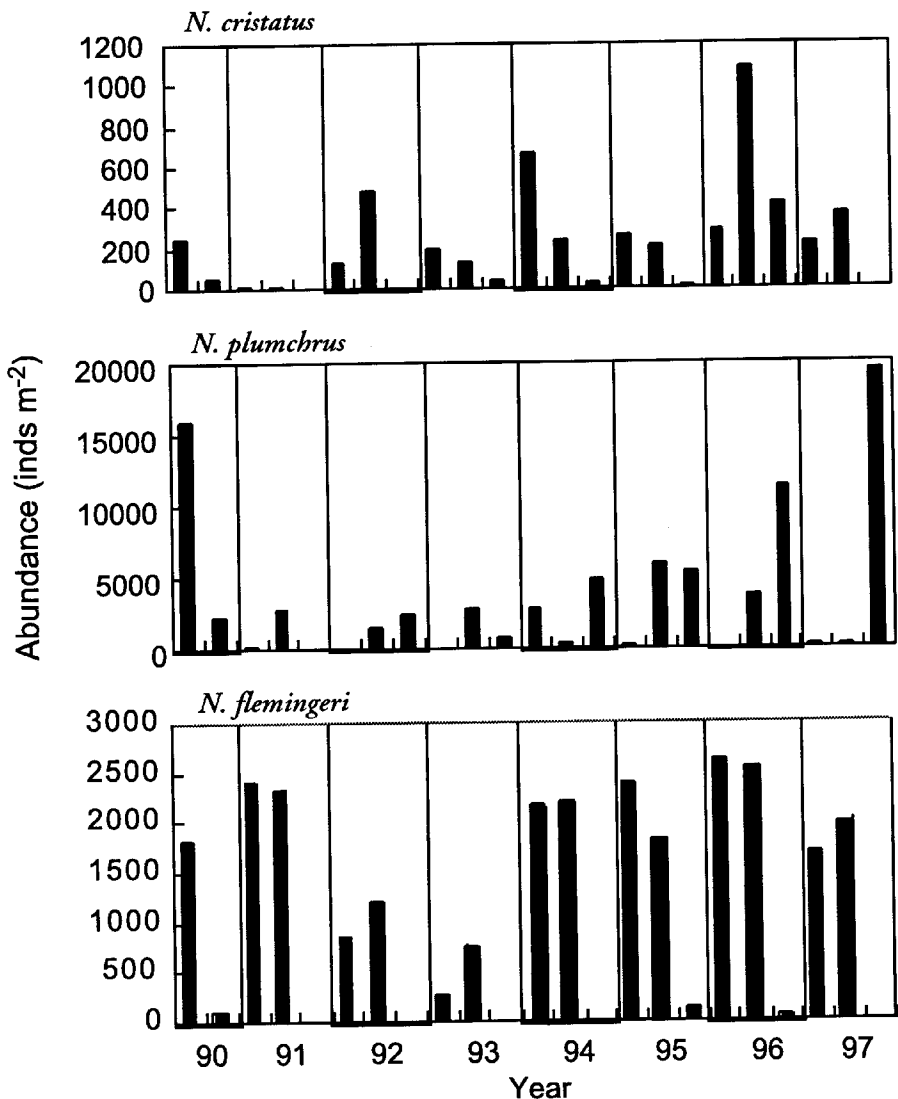
#### 3.4. Annual variations

Zooplankton biomass that contained many taxa of organisms showed clear seasonal variation with a peak at May or June and the minimum values observed during winter (Figure 6). The seasonal rises of the biomass were somewhat sudden, reflecting seasonal ontogenetic migration by *Neocalanus* spp. and *Eucalanus bungii*. Considerable annual variation over a factor of 10 was also observed. High biomass zooplankton was observed in 1990, then a decrease, and then an increase from 1994 (Figure 6). At the species level, *Neocalanus plumchrus* shows a trend similar to zooplankton biomass variation (Figure 7). *N. flemingeri* also showed decreased abundance in 1992 and 1993, but the annual variation is less than *N. plumchrus*.

Development rates in April and May of *N. flemingeri* and *N. plumchrus* showed similar variation, high in 1990, then a decrease, an increase from 1994, and again a decrease in 1997



**Figure 6.** Annual and seasonal variation of zooplankton biomass (dry weight) collected by vertical hauls from the surface mixed layer in the western subarctic Pacific, Oya-shio region.



**Figure 7.** Annual variations of abundance in *Neocalanus cristatus*, *N. plumchrus*, and *N. flemingeri* at April, May, and June/July samplings.

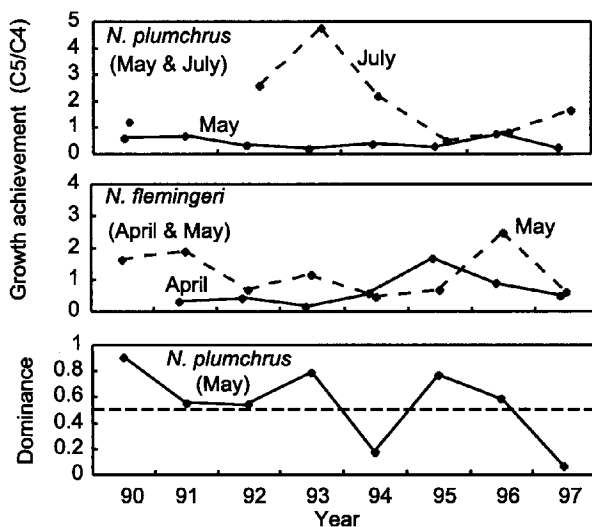
*Neocalanus* species have been thought to be spring grazers. However, the abundant species (in biomass) *N. plumchrus* migrates into the surface layer, where it grazes and grows from June to August. In our studied area, a spring bloom dominated by diatoms takes place from March to May, then the phytoplankton community changes to a non-diatom dominated community [Kasai *et al.*, 1997; Saito *et al.*, 1998]. Thus, the *N. plumchrus* population must be supported by primary production in summer. It is also curious that *Neocalanus* species succession and phytoplankton community succession take place at the same time.

Differences in lipid accumulation strategies were observed between the two species. *N. flemingeri* showed slow growth (several months to C5) with lipid accumulation, and *N. plumchrus* showed fast growth (within 1.5 month) without lipid accumulation. *N. flemingeri* grow from winter to

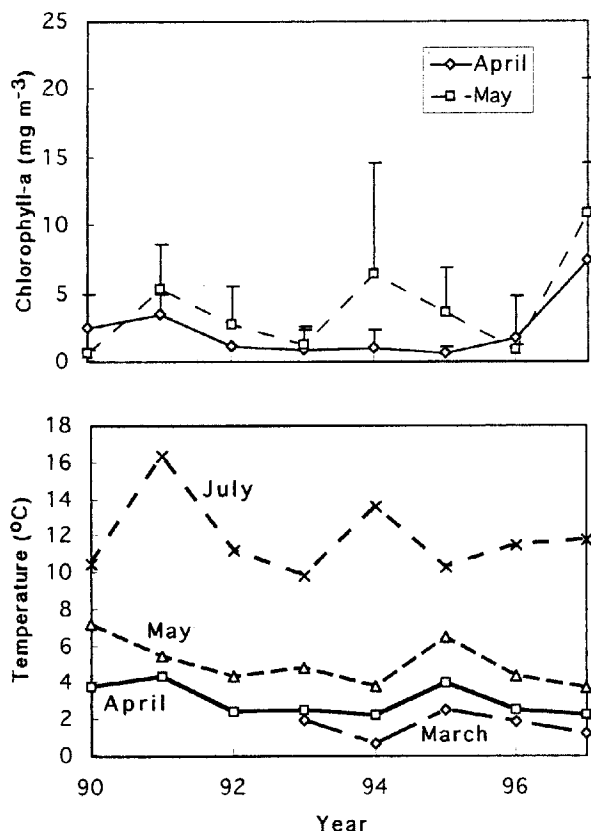
Therefore, genetic separation of the different morphs was not suggested from our sampling. Moreover, the origin of the large form of *N. flemingeri* is not clear at the present study.

spring, a period in which primary production is generally low, but some times high production occurs (spring bloom) as a result of wind and radiation inducing water column stratification [Kasai *et al.*, 1997]. Therefore, *N. flemingeri* has a good food environment some of the time but must tolerate low productivity conditions for an unpredictable period. *Neocalanus flemingeri* appears to be adapted for such spring weather conditions, with relatively coarse feeding appendages (maxillae) and slow growth with lipid accumulation. In contrast, phytoplankton in summer are smaller in size than in the spring, but primary production is expected to be high and constant in summer. The consequent adaptive strategy for summer conditions by *N. plumchrus*, with fine feeding appendages, is fast growth without lipid accumulation.

Zooplankton biomass fluctuated on a similar annual cycle with that of *Neocalanus* abundance, especially *N. plumchrus*.



**Figure 8.** Annual variations of development rates in *Neocalanus cristatus*, *N. plumchrus*, and *N. flemingeri*, and *N. plumchrus* dominance at the second week of May.



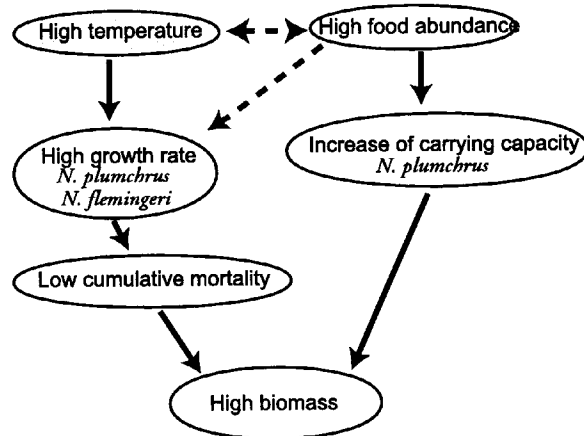
**Figure 9.** Annual variations of surface temperature and chlorophyll-*a* concentration during spring to summer. Vertical bars indicate 1 SD.

There must be two reasons: *Neocalanus plumchrus* is an abundant copepod in the zooplankton community and they stay for long periods at the surface layer as C5, large individuals. Moreover, high development rate roughly resulted in high biomass of copepods. We investigated surface temperature and chlorophyll-*a* concentration as primary causes of fluctuation of development and biomass. Figure 9 shows variations of surface temperature and chlorophyll-*a* during the *Neocalanus*-dominating season. The surface temperatures from March to May were relatively similar, low from 1992 to 1994 and from 1996 to 1997. Chlorophyll-*a* at the surface in April and May were also similar to each other, low from 1992 to 1995, but with increased chlorophyll in May 1994 and 1995. We extracted similar trends among environmental parameters and copepod production parameters. *Neocalanus flemingeri* showed relatively good correlation between temperature (April) and development rates (April and May), and between development rates and peak abundance. However, development also showed a linear relationship to chlorophyll-*a* with one exceptional year. *Neocalanus plumchrus* also showed a positive relationship to temperature and chlorophyll-*a* with one exceptional year each. In contrast to *N. flemingeri*, high development rates of *N. plumchrus* at June/July were observed in low abundance years and the abundance showed positive correlation to chlorophyll-*a* concentration (April). Roughly, development and abundance of *N. flemingeri* are more likely to depend on temperature than

food (chlorophyll), but those of *N. plumchrus* depend more on food than on temperature. This difference of dependency of growth and biomass should reflect their timing of occurrence and strategies. *Neocalanus flemingeri* come up to the surface layer in winter to spring (low temperature and spring bloom) and *N. plumchrus* rises in early summer (high temperature with low food abundance). *Neocalanus flemingeri* have the more conservative strategy for food utilization mentioned above. The magnitude of biomass variation is also caused by the difference of life cycle strategies. The pessimistic *N. flemingeri* have less annual fluctuation.

Fast growth rate caused by high temperature shortens the duration of growth (surface residence), which should decrease the cumulative mortality by predators during the growth period and finally result in high abundance. On the other hand, food abundance (chlorophyll-*a* in the present study) should be some indicator of carrying capacity of the grazing copepods and also affect the growth rate if the animals are food-limited. Food limitation is not plausible for *N. flemingeri* because they accumulate lipid as early as C2. In contrast, *N. plumchrus* shows no deposit of lipid until C5 and high growth rate is only observed at low abundance. Food limitation more likely happen in *N. plumchrus* because they are a much more abundant copepod than *N. flemingeri*, and they utilize the surface layer during periods of relatively low algal biomass.

This proposed scenario of annual variation in *Neocalanus* biomass is summarized in Figure 10. Our scenario is not cer-



**Figure 10.** Proposed scenario of annual variation of zooplankton biomass in western subarctic Pacific.

tain from only 8 years sampling. Furthermore, we could not separate the effects of temperature and food abundance in the present study, because there was positive correlation between them. However, Tomosada and Odate [1995] showed that zooplankton biomass in the Oyashio region have a positive correlation to temperature and sunshine hours on the basis of long-term record of zooplankton biomass from 1950 [Odate, 1994]. In the eastern subarctic Pacific, long-term observation revealed that wind stress during winter and some index of Aleutian low correlate to zooplankton and fish productions [Brodeur and Danware, 1992, Beamish et al., 1995]. Parsons

