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Life history strategies of subarctic copepods *Neocalanus flemingeri* and *N. plumchrus*, especially concerning lipid accumulation patterns

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Abstract: Lipid accumulation patterns during development of *Neocalanus flemingeri* and *N. plumchrus* in the western subarctic Pacific were investigated as regards life-history strategies for overwintering and survival in an environment with highly fluctuating food availability. *Neocalanus plumchrus* accumulates lipid mainly during the copepodite-5 stage; in contrast, *N. flemingeri* starts to accumulate lipid as early as the copepodite-2 stage. The life history strategy of *N. plumchrus*, which is characterized by fast growth without lipid storage and synchronized copepodite recruitment, might be an adaptation to the predictable timing and availability of food in their environment. In contrast, the developmental strategy of *N. flemingeri* is characterized by slower growth, but with early and prolonged lipid storage, and prolonged copepodite recruitment. This strategy was regarded as an adaptation to the variable environment. The different strategies of *N. plumchrus* and *N. flemingeri* seem to be adapted for predictable food conditions in summer and for unpredictable conditions in winter–spring, respectively.

Key words: copepod, *Neocalanus*, lipid storage, life history

Introduction

"One of the key questions to be asked of Arctic zooplankton feeding at low trophic levels is how sympatric species appropriate and maximally utilize the energy provided by intense pulses of phytoplankton production during the sunlit summer months in order to survive the long winter darkness period?" (Hopkins et al. 1984). The same question can be extended to zooplankton in the subpolar region. Three species of *Neocalanus* are dominant across the subarctic Pacific and act as a trophic link between the primary production and higher trophic organisms such as pelagic fish (e.g. Mackas & Tsuda 1999). These copepods are all ontogenetic vertical migrators, residing and growing in the euphotic layer from winter to summer and descending to the meso- and bathypelagic layers from summer to winter (or fall) for maturation and spawning (Miller et al. 1984; Miller & Clemons 1988; Tsuda et al. 1999). These copepods partition the habitat vertically and seasonally (Miller & Clemons 1988; Mackas et al. 1993). *Neocalanus plumchrus* and *N. flemingeri* have similar morphology, but are sharply segregated in the timing of their seasonal utilization of the surface mixed layer (Miller & Clemons 1988; Tsuda et al. 1999).

Lipid storage is a common adaptive strategy against periods of restricted food supply for polar, subpolar and bathypelagic organisms (Lee et al. 1971; Sargent & Henderson 1986; Conover 1988). Copepods usually store neutral lipids (wax esters and triglycerides) for survival and reproduction (Lee et al. 1972). *Neocalanus* species in the subpolar oceans accumulate mainly wax esters (Lee et al. 1972; Ohman 1987), which is a better class of compounds than triglycerides for the long-term storage of energy (Tande & Henderson 1988). *Euchaeta japonica* (*E. elongata*), the dominant carnivorous copepod in the subarctic ocean, shows high wax ester content throughout all developmental stages (Lee et al. 1974). However, *Calanus* spp. generally accumulate lipid only during older copepodite stages (Hakanson 1984; Kattner & Krause 1987).

Although both *N. plumchrus* and *N. flemingeri* utilize the surface mixed layer during the growing season, *N. flemingeri* grows from midwinter to May, while *N. plumchrus* grows after the descent of *N. flemingeri* in the western subarctic gyre (Tsuda et al. 1999). The timing of the change in

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dominance between the two species is roughly the peak season of the spring phytoplankton bloom (Kasai et al. 1997; Saito et al. 1998). Thus, quantity and quality of food availability are different for the two species. We will show that the developmental timing of lipid storage as a survival strategy is also different and we will discuss the consequences of these differences in terms of their life-history strategies.

Materials and Methods

Seasonal sampling was carried out at stations located roughly in the first and second branches of the Oyashio current by the FRV *Hokkou Maru*, *Tankai Maru* and *Hokushin Maru*, 6 to 10 times a year from July 1996 to July 1998 (Fig. 1). Copepods were collected by oblique tows with a bongo net (mouth diameter, 70 cm×2; mesh aperture, 330 μm) from about 500-m depth at night. These samplings covered the depth of overwintering *Neocalanus flemingeri*, but the overwintering *N. plumchrus* mainly occurred in the deeper layers (Tsuda et al 1999). The net was equipped with a depth meter and flow meters. The samples were preserved with neutralized formalin seawater (10% v/v). Copepodites-2 (C2) to 5 of *N. flemingeri* and *N. plumchrus* were identified according to Miller (1988) and Tsuda et al. (1999) and were sorted from appropriate aliquots of the seasonal samples. Ten to over 2000 individuals of each developmental stage from each sample were used. Copepodite-1 individuals were not included in the following analysis because of uncertainty in their identification to species. However, the C1 individuals of either species rarely have oil-sacs. Pale yellow or orange oil sacs in older individuals were visible under a dissecting microscope. The sizes of the oil sacs were roughly categorized by the lateral views into three classes: sparsely stored, 0–4%; medially stored, 4–40%; and fully stored; >40% of the prosome area covered by the oil-sac. Only intact individuals were used for the analysis.

Sampling for annual variations was carried out from 1990 to 1998 southeast of Hokkaido along a transect line which crossed the Oyashio current (Fig. 1). A small bongo net (mouth diameter, 30 cm; mesh aperture, 330 μm) was towed vertically from the base of the surface mixed layer. When the surface mixed layer was deeper than 50 m, the net was towed from 50-m depth. An aliquot of each sample was preserved with neutralized formalin seawater. The net tows were conducted 4 to 6 times a year, but only samples collected in May were used for the present study because both *Neocalanus plumchrus* and *N. flemingeri* were distributed in the upper 50-m layer during this period. The data for each year contained 5 hauls, which roughly covered the first and second branches of the Oyashio current (Kono & Kawasaki 1992). The sampling date varied by less than four days interannually. All individuals of intact copepods were used for the analysis. The oil-sacs of these samples were also categorized based on the criteria mentioned above.

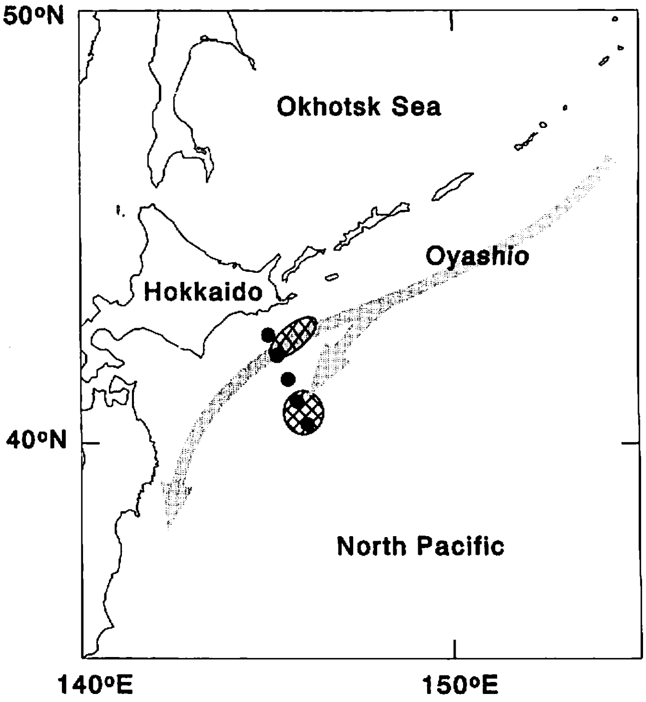

Fig. 1. Sampling locations with schematic flow pattern of the Oyashio current. The stations sampled 1990–98 for annual variations are indicated by filled circles, and those sampled 1996–98 for seasonal variation are shown as hatched areas.

Results

Two populations were recognized in *Neocalanus flemingeri* based on body size (Tsuda et al. 1999). Small forms (ca 3.6 mm in prosome length as adult female) have a one-year life cycle and occurred at the surface from winter to spring (Fig. 2). At least some individuals of the large form (ca. 4.5 mm in prosome length as adult female) have a biennial life cycle with winter dormancy as C4 and adult females. *Neocalanus plumchrus* have an annual life cycle; they occur in the surface layer after the descent of *N. flemingeri* then grow to C5 by the end of summer and descend to deeper layers for maturation and reproduction (Fig. 2). Sea surface temperature of the studied area increased from March to August and the phytoplankton bloom took place between April and May (Fig. 3). Replacement of *N. flemingeri* by *N. plumchrus* in the surface water took place between mid-May and early June (Fig. 2). This season coincides with the peak or declining season of the spring phytoplankton bloom (Fig. 3).

Lipid accumulation was observed in *N. flemingeri* as early as C2 and the fraction of C2 individuals with lipid increased later in the season of copepodite recruitment (Fig. 4). Lipid accumulation increased with developmental stage: about half of C3 were individuals with medially-stored lipid and over 80% of C4 throughout the year were individuals with medially or fully stored lipid (Fig. 4). C4 individuals occurred throughout the year because of the presence of a biennial life cycle with diapause at both C4 and C6 female

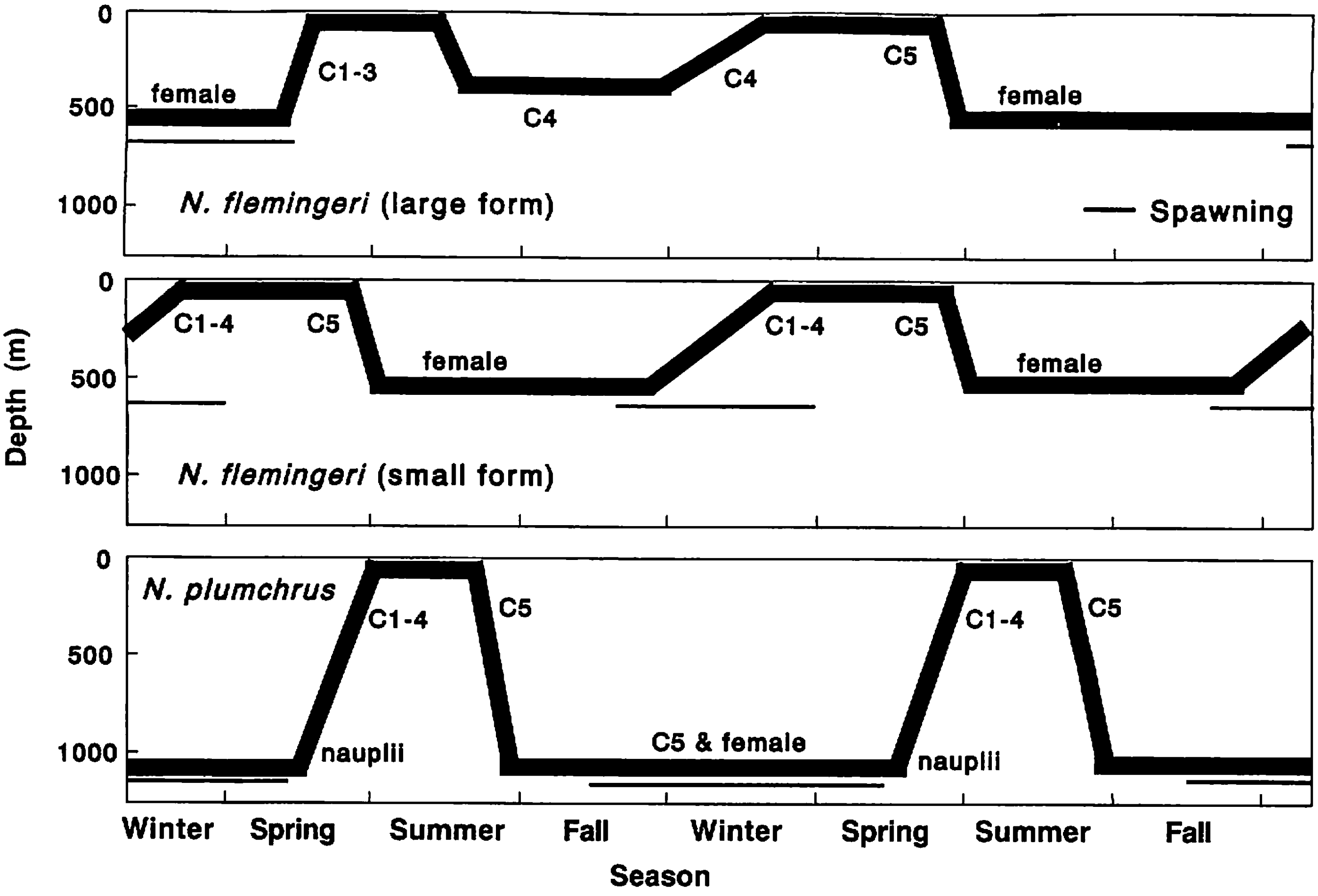

Fig. 2. Schematic illustrations of life cycles of *Neocalanus flemingeri* (large and small forms) and *N. plumchrus* in the western subarctic Pacific (modified from Tsuda et al. 1999).

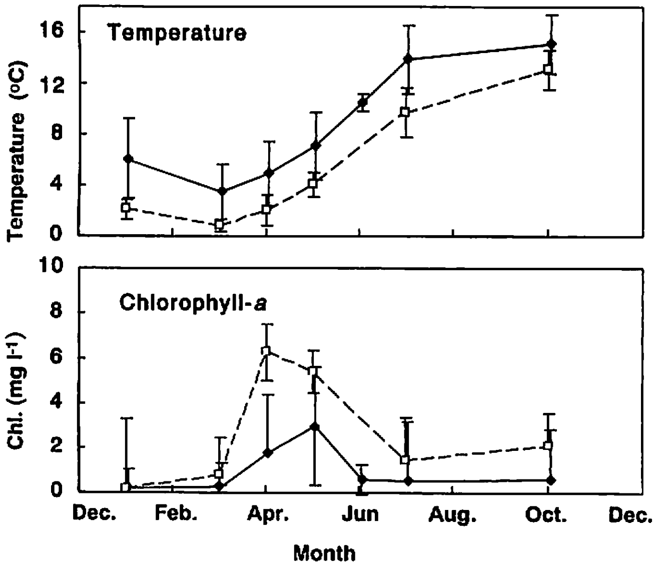

Fig. 3. Seasonal variations of temperature and chlorophyll-*a* concentration at the surface in the Oyashio area (solid lines) and in the neritic/slope area (broken lines). Average values of 5 years (1990–1994) from Saito et al. (1998). Vertical bars denote 1SD.

developmental stages (Fig. 2, Tsuda et al. 1999). Individuals of C4 with full lipid accumulation dominated during summer to fall and decreased in early spring. The spring decrease was caused by new recruitment of C4 with an annual life cycle (Tsuda et al. 1999). Most C5 showed medial or full accumulation of lipid, and the percentage of fully-stored individuals increased later in the season (Fig. 4).

The seasonal window for occurrence of young copepodites of *N. plumchrus* was shorter than that for *N. flemingeri* because of more synchronized recruitment and faster growth. In contrast to *N. flemingeri*, lipid accumulation was mainly observed in C5 for *N. plumchrus*, although some individuals showed lipid accumulation during younger copepodite stages (Fig. 5). There was no clear seasonal trend of lipid accumulation in younger copepodites but lipid accumulation in C5 progressed from spring to winter (Fig. 5). *Neocalanus flemingeri* showed significantly higher lipid accumulation than *N. plumchrus* for the all stages investigated (Table 1).

Both species showed between-year variation in lipid storage (Fig. 6). However, differences between the two species persisted throughout the sampling period. *Neocalanus flemingeri* showed constantly higher lipid content than *N. plumchrus* in both C3 and C4. The difference between the

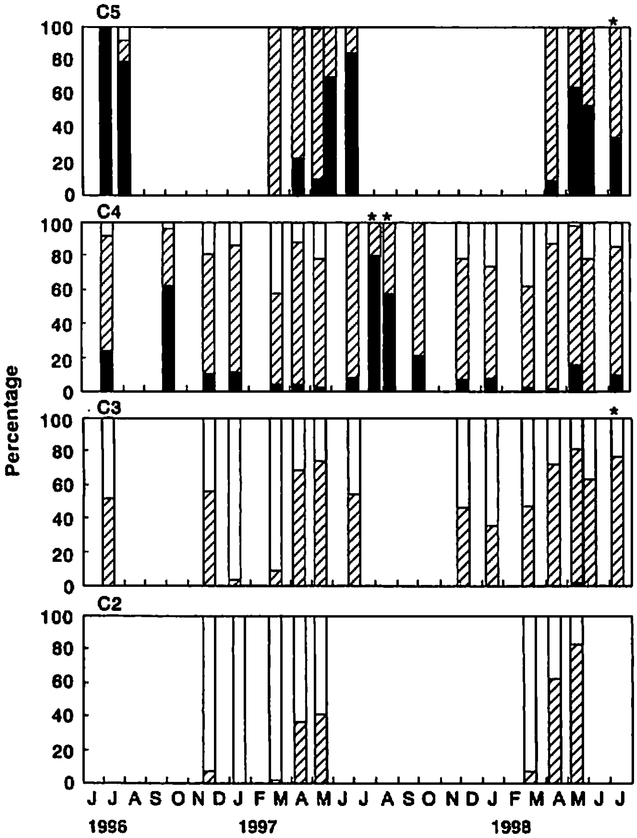

Fig. 4. Seasonal changes in lipid content for copepodite stages of *Neocalanus flemingeri* in the western subarctic Pacific. Filled bars; fully stored; shaded bars; medially stored, open bars; sparsely stored individuals. Asterisks on the top of a bar indicate that the compositions were calculated from a relatively small number of individuals (10 to 30 copepods).

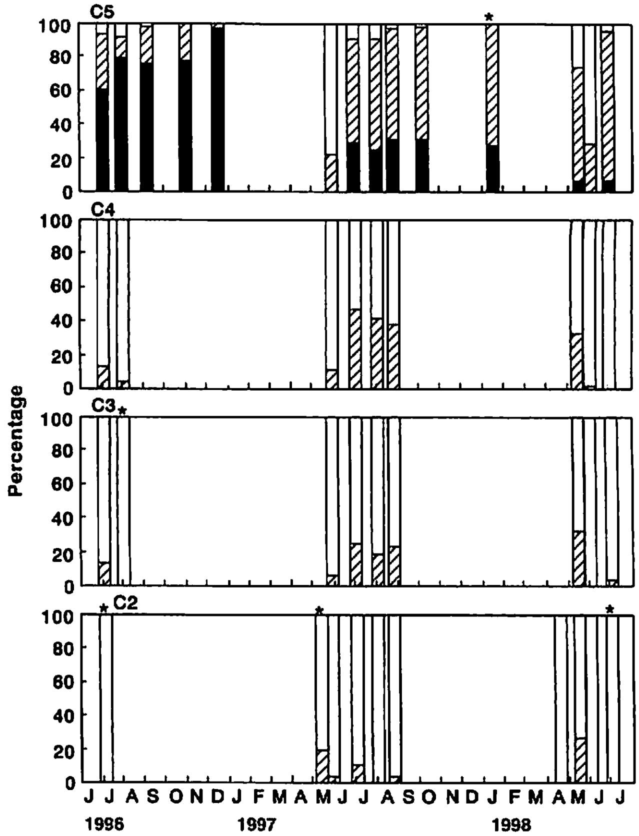

Fig. 5. Seasonal changes in lipid content for copepodite stages of *Neocalanus plumchrus* in the western subarctic Pacific. Filled bars, fully stored; shaded bars, medially stored; open bars, sparsely stored individuals. Asterisks on the top of a bar indicate that the compositions were calculated from a relatively small number of individuals (10 to 30 copepods).

Table 1. Contingency table analysis for lipid storage by *Neocalanus plumchrus* (NP) and *N. flemingeri* (NF) during the growing season (April to July). Numbers are individual number counted and categorized, the numbers in parentheses are χ^2 values and asterisks indicate significant difference ($p<0.001$) of composition between the two copepod species.

	Copepodite 5 (94.3)*		Copepodite 4 (1075)*		Copepodite 3 (92.5)*		Copepodite 2 (431)*	
	NF	NP	NF	NP	NF	NP	NF	NP
Full	571	1866	86	0	2	0	0	0
Medial	523	3016	859	504	849	21	621	149
Sparse	4	909	126	1372	341	71	416	839

two species were significant for most of the year (contingency table analysis, $p<0.05$), although the difference between the two species was smaller and statistically insignificant during the mid-nineties (Fig. 6).

Discussion

Adult females of *Neocalanus* copepods in the subarctic Pacific show reduced mouth parts and a lack of teeth on the mandibular gnathobase (Campbell 1934; Omori 1970; Miller 1988). Thus, the energy requirements for the reproduction of subarctic *Neocalanus* species are supplied entirely by their stored lipids (e.g. Conover 1988; Saito & Tsuda 2000). This contrasts with their subantarctic congener, *Neocalanus tonsus*, in which the adult females appear in the surface layer and produce eggs, while showing active grazing (Ohman 1987).

A difference in lipid accumulation strategy was observed between the two subarctic species. *Neocalanus flemingeri* showed lipid accumulation as early as C2. In contrast, *N.*

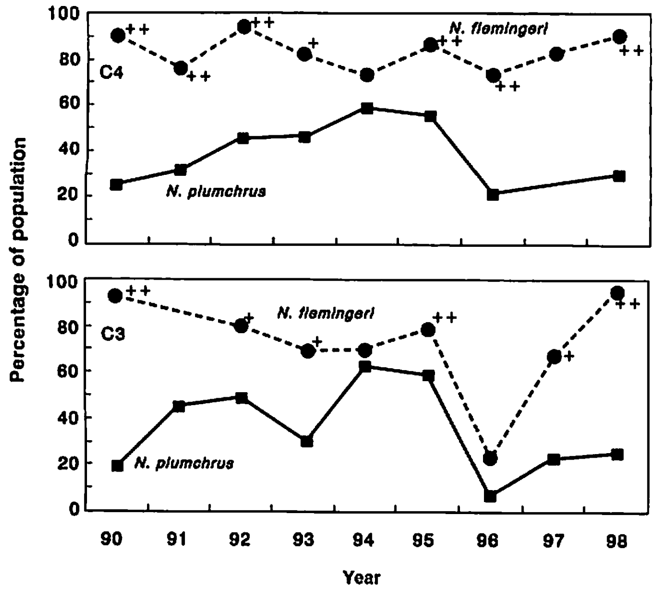

Fig. 6. Annual differences in relative percentages of medially + fully-stored individuals for *Neocalanus flemingeri* (broken lines) and *N. plumchrus* (solid lines) in the western subarctic Pacific during the second week of May. The crosses indicate a significant difference in lipid storage between the two copepods (contingency table analysis). +: $p<0.05$; ++: $p<0.01$.

plumchrus rarely showed lipid accumulation during C2 to C4 and accumulated lipid primarily during C5, the last stage before ontogenetic descent and maturation. Early lipid accumulation by *N. flemingeri* may allow flexibility in the life cycle. Some populations (Oyashio area and Japan Sea) have a biennial life cycle with dormancy during both C4 and the adult female stage (Miller & Terazaki 1989; Tsuda et al. 1999). They need lipid reserves before each diapausic stage. However, the population with an annual life cycle, recognizable by small body size (Tsuda et al. 1999), also showed lipid accumulation during younger stages. Another influence on differences in lipid accumulation may be temperature. Under food-satiated condition, development and growth can be a function of temperature (e.g. Uye 1988; Durbin & Durbin 1992). Moreover, developmental rate is more dependent on temperature than on growth rate (Vidal 1980). Hence, copepods in a lower temperature environment are more likely to accumulate lipid. *Neocalanus flemingeri* resides in a lower temperature range than *N. plumchrus* (Figs 2, 3). Thus, it is more likely to accumulate lipid and have a slower development rate. Phytoplankton biomass peaks in April and May in the study area (Fig. 3), but the chlorophyll-*a* concentration rarely exceeds the critical prey concentration for *N. plumchrus* ($4\,\mu g\,l^{-1}$, Dagg & Walser 1987). On the other hand, naked ciliates and heterotrophic flagellates as alternate food sources are relatively abundant from May to July (Shinada et al. 2000). Thus, quantitative comparison of food availability for *N. flemingeri* and *N. plumchrus* is uncertain yet and the relative quantitative contribution of temperature and food can not be determined in this study. Environmental factors such as temperature and food abundance may explain part of the difference in lipid accumulation. However, the differences may also represent different species-specific strategies for the assignment of input energy to somatic growth and/or storage, because differences were observed in samples collected in the same month (Figs 4–6). Other *Neocalanus* species seem to have the *plumchrus*-pattern of lipid accumulation. *Neocalanus tonsus* showed at least a four-fold increase in wax ester concentrations during C5 (Ohman et al. 1989), and *N. cristatus* in the western subarctic Pacific shows lipid increase mainly during C5 (Kobari & Ikeda 1999), although they always carry some lipid throughout all developmental stages (Tsuda, unpublished data). The lipid storage pattern of *N. cristatus* confirms that the copepods have some control over the assignment of energy to storage and structural growth because both *N. cristatus* and *N. flemingeri* grow over the same season, i.e. mid-winter to spring (Kobari & Ikeda 1999; Tsuda et al. 1999).

We can observe other differences in life cycle between the two species. Firstly, *N. flemingeri* utilizes the surface layer for growth during winter to early spring (December to May), while *N. plumchrus* utilizes the surface layer from late spring to summer (May to August) (Miller & Clemons 1988; Tsuda et al. 1999). In the study area, the replacement of *N. flemingeri* by *N. plumchrus* is roughly coincident with the peak or declining period of the spring bloom in the Oyashio area (Fig. 3). Secondly, *N. flemingeri* exhibited a slow developmental rate, taking several months from C1 to C5, while *N. plumchrus* developmentfrom C1 to C5 took only 1.5 months (Tsuda et al. 1999). Other differences are in the mating and egg production season (Miller & Clemons 1988; Tsuda et al. 1999). Copepodite recruitment is tightly synchronized during May for *N. plumchrus* and prolonged from December to March for *N. flemingeri* (Tsuda et al. 1999). On the other hand, spawning is prolonged for *N. plumchrus* but peaks sharply in January for *N. flemingeri*, although some spawning occurs from October to March (Miller & Clemons 1988; Tsuda et al. 1999). Although these two species are similar, there are also some morphological differences (Miller 1988). One prominent difference is that *N. plumchrus* has a relatively larger second maxillae (Miller 1988) which form the feeding basket (Marshall & Orr 1955); this difference in relative size of feeding appendages is conservative throughout the copepodite stages of both species (Tsuda et al. 1999).

Neocalanus flemingeri grows during winter and spring, in which period primary production is generally low, but includes occasional blooms of large-sized diatoms when weather conditions produce a stratified water column (Kasai et al. 1997). Therefore, *N. flemingeri* encounters occasional periods of prey abundance, but must withstand low food availability for unpredictable periods. Thus, the life-cycle strategy of *N. flemingeri*, which is characterized by slower growth with early lipid accumulation, is adaptive for variable and often low food availability from winter to spring. Prolonged copepodite recruitment for *N. flemingeri* might be another conservative or "bet-hedge" strategy. This kind of recruitment pattern would not be possible without the flexibility in energy allocation mentioned above. Although spring blooms of diatoms are only observed in the marginal areas of the subarctic Pacific (e.g. Banse & English 1999), unpredictability of food environments during winter through spring and predictability during summer might be consistent throughout the North Pacific. An arctic copepod, *Calanus glacialis* shows *flemingeri*-type lipid accumulation. They accumulate a certain amount of wax esters as early as C3 (Tande & Henderson 1988), which supports our augment because *C. glacialis* has to experience a highly fluctuating food environment and a long period of dormancy. This contrasts with *C. pacificus*, a transitional or temperate copepod, which mainly accumulates lipid during C5 (Hakanson 1984).

In contrast, high and constant primary production can be expected in late spring to summer, although phytoplankton concentration is low compared with spring. It has been shown that *N. plumchrus* in the open ocean grazes mainly on microzooplankton instead of phytoplankton (Gifford 1993), and steady growth at low algal biomass was observed at the oceanic Station Papa (Miller & Nielsen 1988; Miller 1993). Thus, we hypothesize an adaptive strategy for *N. plumchrus* characterized by large feeding appendages, rapid development without lipid accumulation and synchronized copepodite recruitment for late spring to summer conditions. The large feeding basket may additionally facilitate feeding on motile prey such as ciliates and small crustaceans.

In addition, May is a period of reliable food concentrations for both species. The phytoplankton bloom is greatest in the Oyashio area and is declining but still high in the coastal area (Fig. 3). Thus, *N. flemingeri* can depend on finishing its build-up of lipids during late copepodite stages, while *N. plumchrus* can depend upon food to carry it through the early copepodite stages during its rapid development.

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