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A. Tsuda · H. Saito · H. Kasai

Life histories of *Neocalanus flemingeri* and *Neocalanus plumchrus* (Calanoida: Copepoda) in the western subarctic Pacific

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Abstract Life cycles of large suspension-feeding copepods were investigated in the western subarctic gyre (Oyashio area). Two populations were recognized in *Neocalanus flemingeri* by body size, life cycle and timing of ontogenetic migration. Small forms (same size as original description; adult female ca. 3.6 mm in prosome length) have a 1-year life cycle and occurred at the surface between December and June. At least some individuals of large forms (adult female ca. 4.5 mm in prosome length) have a biennial life cycle with winter dormancy as Stage 4 copopodites (C4) and adult females. The young copepodites of the large form occur in the surface water later than the small forms, then grow to C4 with full deposition of lipid. The following year, the C4 individuals start grazing in January, and sink to deep layers at the same time as the small forms. The life cycle of *Neocalanus plumchrus* was identical to the original description made for the Alaskan gyre population, although the recruitment to the surface layer during copepodite stages occurred 2 weeks to a month later than in other areas of the subarctic Pacific. Temporal partitioning of surface habitat utilization between *N. plumchrus* and the small form of *N. flemingeri* was clearly established, but overlap was observed between *N. plumchrus* and the large form of *N. flemingeri*.

Introduction

The zooplanktonic assemblage in the subarctic Pacific is dominated by large interzonal copepods: three species of *Neocalanus* and one species of *Eucalanus*. They feed and grow in the surface layer for a few months, and reside at depth for the remaining months, with 1- or 2-year life cycles (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). *N. flemingeri* and *N. plumchrus* clearly divide the surface mixing layer seasonally, and they divide the habitat with *Neocalanus cristatus* and *Eucalanus bungii* vertically (Mackas et al. 1993). These works were mainly based on samples collected in the eastern subarctic gyre of the North Pacific. There is substantial evidence which shows physical and biological differences between eastern and western gyres of the subarctic Pacific (Sugimoto and Tadokoro 1997; Saito et al. 1998; Mackas and Tsuda 1999). *Neocalanus* species show variations in life cycle strategy, as well as in body size, depending on the local oceanographic conditions (Miller and Clemons 1988; Miller and Terazaki 1989; Miller 1993). Trophic status also differs between the open ocean and marginal seas. High grazing rates on phytoplankton were observed in *Neocalanus* species in the Bering Sea (Dagg et al. 1982; Dagg and Wyman 1983), while in the open ocean, the contribution of phytoplankton as a food source was much lower (Dagg 1993a; Tsuda and Sugisaki 1994), and microzooplankton or sinking particles were considered important food sources (Gifford 1993; Dagg 1993b).

In the area studied (Fig. 1), the first branch of the Oyashio Current (westward) usually is around Site A3 or A4, and the second branch is around A11 (Kono and Kawasaki 1997). The surface temperature ranges between near zero and 16 °C, and the minimum is observed in March. The macro-nutrients maximum is observed at the lowest temperature, and minimum concentrations are observed between July and October (Saito et al. 1998). Increased chlorophyll *a* concentration is observed April and May, but intensive blooming (>5 mg chl m^{-3}) is only observed in neritic areas and the first branch of the Oyashio (Saito et al. 1998).

The major goal of the present study was to compare the life histories of the two *Neocalanus* sibling species

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A. Tsuda (✉) · H. Saito · H. Kasai
Hokkaido National Fishery Research Institute,
116 Katsurakoi, Kushiro,
Hokkaido 085-0802, Japan

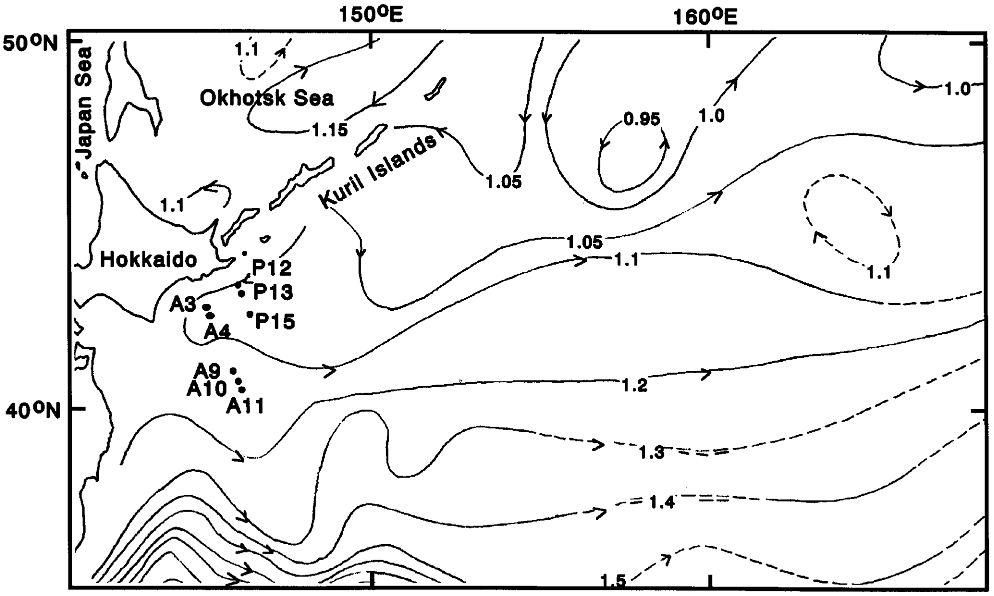


Fig. 1 Sampling locations with mean dynamic topography (dynamic meters, 0 over 1000 decibars) modified from Anonymous (1975)

between the eastern and western subarctic gyres of the North Pacific.

Materials and methods

Samplings

Sampling sites are located at the western end of the western subarctic gyre of the North Pacific (Fig. 1). More precisely, Stns A3, A4, P12, P13 and P15 are roughly located in the first branch of the Oyashio Current, while Stns A9, A10 and A11 are in its second branch. Samples were collected by the FRV "Hokkou Maru" and "Tankai Maru", Hokkaido National Fisheries Research Institute, and by the FRV "Hokushin Maru", Hokkaido Fisheries Experimental Station Kushiro, 8 to 12 times a year from July 1996 to July 1998. Copepods were collected by oblique tows with a bongo net (mouth opening 70 cm × 2, mesh opening 333 μm) from about 500 m depth during night, although maximum net depth varied between 330 and 900 m depending on the current and weather conditions (Table 1). The net was equipped with a depth meter and flow meters. Samples were preserved with neutralized formalin seawater (10% v/v).

Individuals of *Neocalanus* spp. were sorted under a dissecting microscope from appropriate aliquots of the preserved samples. Then, the number of individuals was counted for each species and developmental stage. Prosome length was measured for up to 50 individuals from each sample by an image analyzer with CCD camera attached to the microscope. Maturity stages of adult females were determined according to Miller and Clemons (1988). There was within-cruise variability in abundance and composition of copepods, which must have been caused by local heterogeneity and patchiness. In the present study, however, averaged values are used for abundance and composition.

Identification

Miller (1988) suggested characters such as body color in unpreserved specimens, morphology of mandible gnathobase and length of maxilla for the differentiation of adults and C5 of *Neocalanus flemingeri* from *N. plumchrus*. We applied width of mandible gnathobase and length of maxilla for younger copepodite stages for practical reasons. The two species were clearly distinguished by these two morphological characters, especially by maxilla length, from C2 on (Fig. 2). However, C1 individuals could not be separated reliably by these characters, or by tooth crown morphology, which was recommended by Miller (1988) for younger copepodites, because of undeveloped morphology. Because identification was not certain without dissection for individuals of C2 and C3 stages, 20 individuals from each sample were examined by dissection. Thus, the following life history analysis was mainly based on the data for Stages C2 to C6.

Results

Two forms of *Neocalanus flemingeri*

A bimodal distribution was clearly observed in the length-frequency distributions of *Neocalanus flemingeri* from C4 to adult stage (Fig. 3). The size spectra of all copepodite stages of *N. flemingeri* were wide, and overlaps in size between stages were observed. In contrast, the stages of *N. plumchrus* were sharply distinct in size (Fig. 3). Smaller individuals of *N. flemingeri* were in nearly the same size range as that reported from the eastern subarctic gyre, but larger individuals were in the same size range as *N. plumchrus*, or even larger (Fig. 3). The largest adult female was 5.2 mm in prosome length. We did not observe any morphological difference other than size between large and small forms (Fig. 2), including body pigmentation of unpreserved specimens.

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

October was the dormant season of *N. flemingeri*, during which adult females and C4 specimens constituted the population almost exclusively in both years (Fig. 4), and the C4 individuals were mostly the large form (Fig. 5). The dormancy of C4 during this period was confirmed

Table 1 Sampling data of oblique tows of bongo net in the Oyashio region from July 1996 to July 1998

Year	Date	Station	Location	Max. net depth (m)	Local time
1996	8 Jul	A10	40°45.0N; 145°52.5E	392	00:05–01:00
	8 Jul	A4	42°15.0N; 145°07.5E	508	23:40–00:31
	2 Aug	P15	42°15.0N; 146°00.0E	479	18:58–19:38
	3 Oct	A4		No data	20:12–21:03
	4 Oct	A11	40°30.0N; 146°00.0E	No data	23:27–00:15
	4 Dec	P12	40°55.0N; 145°50.0E	483	20:02–20:45
	5 Dec	P15		488	05:15–06:01
1997	13 Jan	A4		851	23:05–23:58
	13 Mar	A4		574	22:13–00:07
	14 Mar	A10		581	00:58–01:47
	14 Apr	A9	41°00.0N; 145°45.0E	482	20:45–21:45
	15 Apr	A4		521	20:25–21:30
	12 May	A10		684	01:09–01:58
	13 May	A4		734	00:13–01:00
	28 May	P15		493	18:56–19:46
	2 Jul	A9		494	23:41–00:33
	4 Jul	A4		435	01:35–02:26
	2 Aug	A3	42°30.0N; 145°00.0E	565	19:14–19:57
	22 Aug	A4		748	02:00–02:51
	22 Aug	A10		603	18:42–19:32
	3 Oct	A4		685	22:49–22:56
	4 Oct	A9		387	22:06–22:56
	5 Dec	P13	42°45.0N; 145°55.0E	493	22:48–23:39
1998	17 Jan	A4		883	18:50–20:07
	12 Mar	A9		416	21:38–22:36
	14 Mar	A3		386	23:06–00:01
	18 Apr	A9		342	22:20–23:21
	19 Apr	A4		408	20:07–21:07
	13 May	A10		793	21:43–22:10
	15 May	A4		900	18:42–19:41
	2 Jun	P15		483	02:45–03:33
	6 Jul	A11		477	00:34–01:30
	7 Jul	A4		448	02:14–03:00

by checking their mandibular gnathobases, which were in the post-molt configuration (long extension of hemocoele), a morphological character of diapause phase (Miller and Nielsen 1988). Moreover, no individuals of C4 or adult female stages had food materials in their guts. After December, both forms of C4 occurred, but large forms showed higher lipid content than small forms (Fig. 6). These results suggest that small forms have an annual life cycle like the population of the eastern subarctic gyre. In contrast, some individuals had a biennial life cycle, with dormancy as both C4 and adult female stages; these individuals were generally the large form. Table 2 shows the numerical abundance of C4 and adult females of both forms during the dormant season. The abundance of large form C4 was the same or a little higher than that of females. Thus, we could not determine whether or not all individuals of the large form have a biennial life cycle. *N. flemingeri* showed a spawning peak in January in both years, indicated by spawning females dominating the female population (Fig. 7), which agrees with the eastern population. Some difference of spawning season was observed between the two forms of *N. flemingeri*. In December, spawning females of the small form were more abundant than those of the large form, and in March the small form population was mainly spent females, while considerable numbers of spawning females of the large form were observed (Fig. 8). These facts suggest that spawning season of the large form was later and longer than that of the small form. Although the spawning peak of *N. flemingeri* was January, C4 and younger copepodites were observed at the same time (Fig. 4). Both large and small forms were found among the C4 individuals (Fig. 5), and the younger copepodite population was the small form. This suggests that copepodites of small forms derived from early spawners, because small numbers of spawning females were observed as early as October. Although the population of *N. flemingeri* increased from December to May and both forms of C4 were observed after December, C5 appeared from April to midsummer in both years (Fig. 4), which suggests that C4 lasts longer than younger copepodite stages. Although bimodal distributions in size spectra were not clear in younger copepodites (C1 to C3), seasonal variations of size were observed in C2 and C3 (C1 individuals were not analyzed because of uncertainty in identification). The sizes of C2 and C3 were stable and small between January and March, then increased in April and May in both years (Fig. 9). These variations in size of younger copepodites suggest that the large form appeared later in the season, with almost the same timing as *N. plumchrus*. Males and dormant females (according to the definition of Miller and Clemons 1988) appeared between May and August in both forms, and

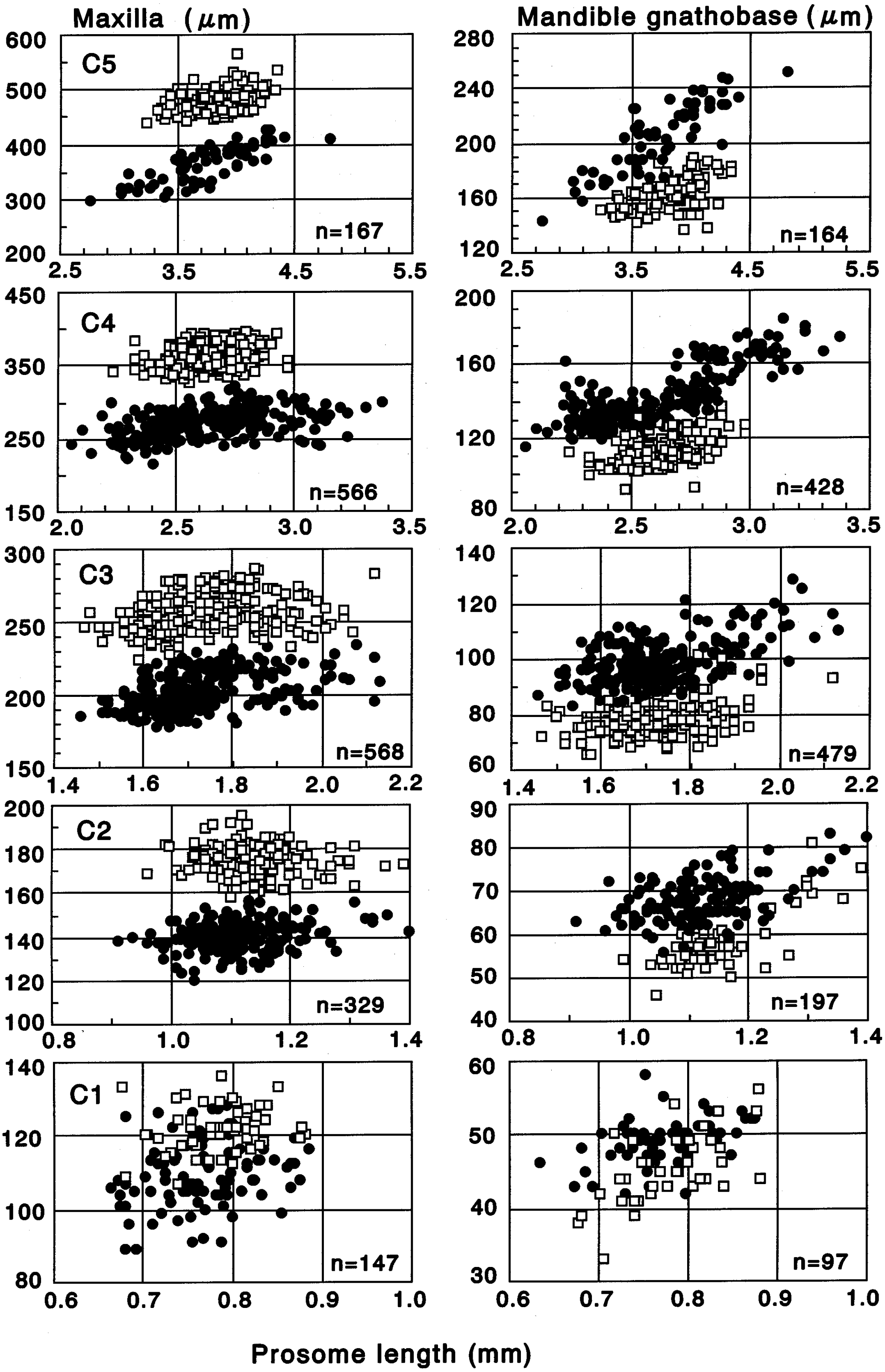


Fig. 2 *Neocalanus flemingeri*, *N. plumchrus*. Relationship between prosome length and lengths of maxilla and mandible gnathobase. *N. flemingeri* (●) and *N. plumchrus* (□). Species determination of C1 individuals were based on the season, and occurrence of C2 individuals

many dormant females with spermatophores were observed in July, indicating that the mating season of *N. flemingeri* is summer, as in the eastern gyre.

Spawning females of *Neocalanus plumchrus* were collected at all times except summer, so the spawning

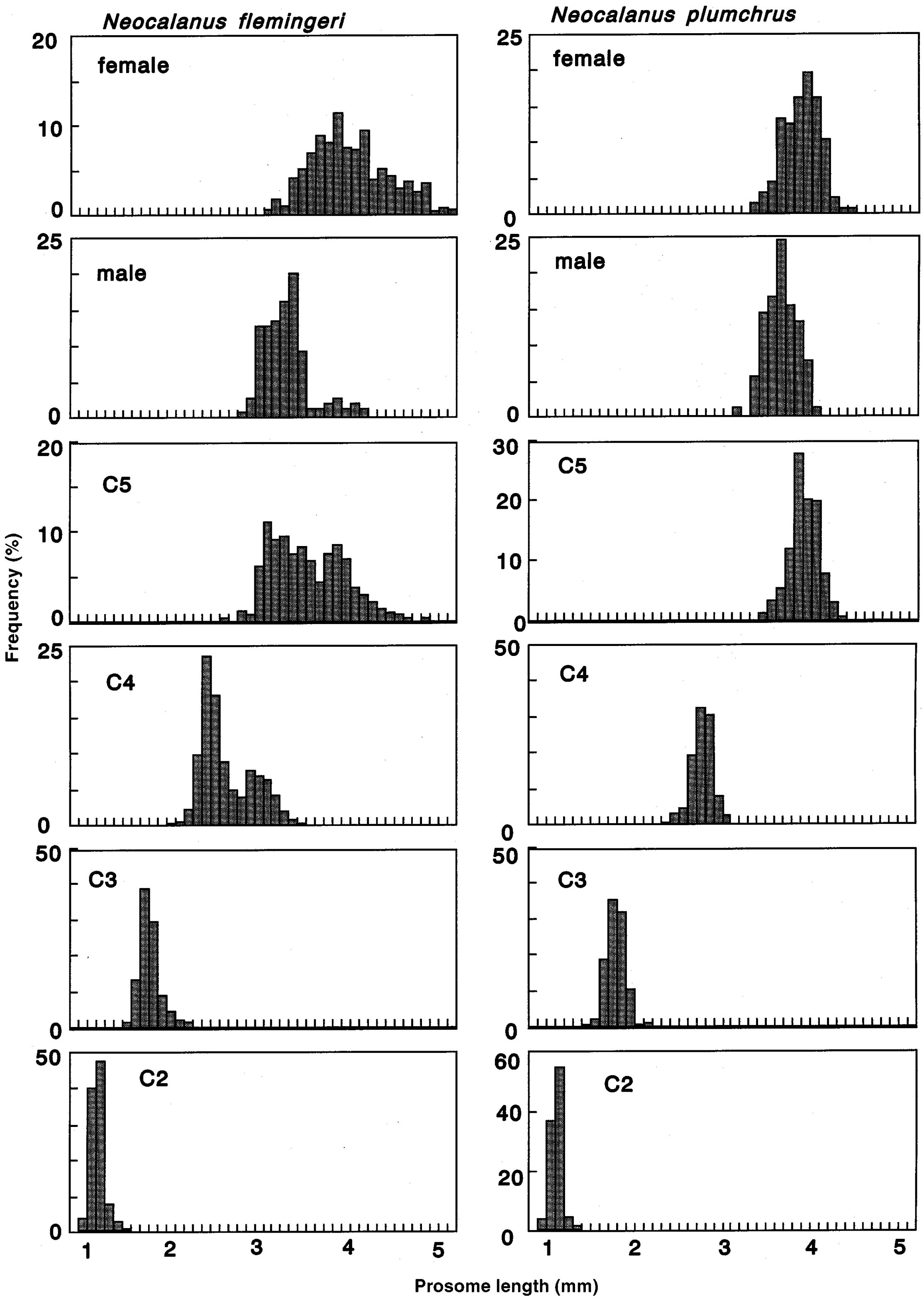


Fig. 3 *Neocalanus flemingeri*, *N. plumchrus*. Size distributions from C2 to adults. All samples in Table 1 were used

season was not clear, which was perhaps because of shallow sampling. However, it seems certain that *N. plumchrus* have a long spawning period, from fall to spring, as in the eastern gyre. Although very small numbers of younger copepodites were observed from March to May, the population suddenly increased between 12 and 28 May in 1997, and between 19 April and 14 May in 1998 (Fig. 10). The increased populations were dominated by younger copepodites (C2 to C4;

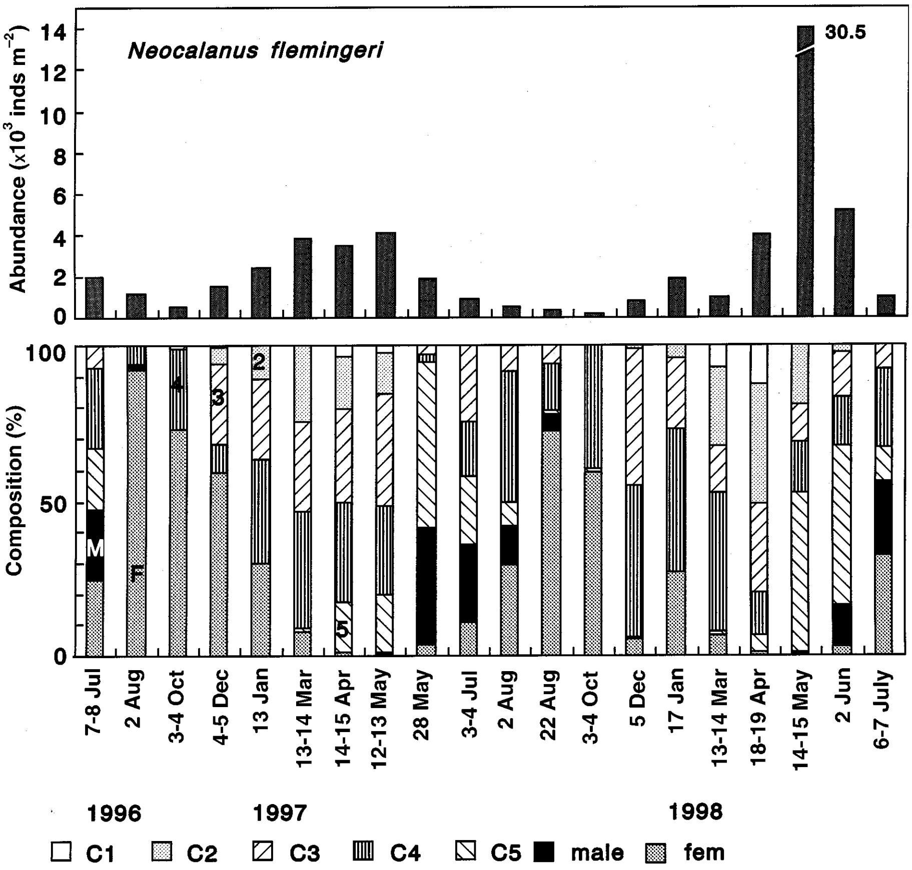


Fig. 4 *Neocalanus flemingeri*. Abundance (*upper*) and stage composition (*lower*) from July 1996 to July 1998 in the western subarctic Pacific

Fig. 10). These results strongly suggest that a major part of the population appeared in the surface layer and grew to C3 and C4 within about 2 weeks and reached C5 within 1.5 months in 1997. A part of the population reached C5 within a month at most in 1998. The population was dominated by C5 after June, and the number of individuals decreased during August (Fig. 10), suggesting that the population sank into deeper layers.

The replacement of *Neocalanus flemingeri* (small form) by *N. plumchrus* took place during May. The replacement largely depended on the timing of occurrence of *N. plumchrus*, but dormant females also started to appear, and the population gradually decreased at roughly the same time. Seasonal separation in utilization of the surface layer was not clear between the large form of *N. flemingeri* and *N. plumchrus*, because younger copepodites of both appeared from April to July (Figs. 9, 10).

Discussion

Life cycles of *Neocalanus flemingeri* and *N. plumchrus* in the western subarctic gyre (Oyashio region) are basically identical to those in other regions of the subarctic Pacific (Fulton 1973; Miller et al. 1984; Vidal and Smith 1986; Miller and Clemons 1988), except for the occurrence of a large form of *N. flemingeri*, in which at least some individuals have a biennial life cycle. Summarized life cycles are presented as Fig. 11. In this figure, only a biennial life cycle is shown for the large form of *N. flemingeri*, but this issue needs further study. The abundance of large form C4 during the dormant season was the same or a little higher than that of females (Table 2). If we assume the individuals of the large form have a biennial life cycle, we would expect a much higher abundance of C4, because of the mortality between C4 and the adult stage. Thus, it is more likely that a part of the population of the large form has an annual life cycle; this conjecture, however, has not been proven.

Neocalanus flemingeri mate mainly in July, then rest several months as dormant females. Spawning peaks in January, and newly recruited young copepodites mainly occur in the surface layer in March. Stage C5 individuals start appearing April, and molting to the adult stage occurs between June and July. On the other hand, *N. plumchrus* has a long spawning period, from fall to early spring, indicated by occurrences of spawning females and males, although the timing of the spawning peak was not clear from our shallow sampling. Newly recruited young copepodites appear in late May, and most of the population reaches C5 in June, then sinks to depth as C5 in August. In addition, numerical abundance and the ratio of the two species are similar to those of the Alaskan gyre and southeastern Bering

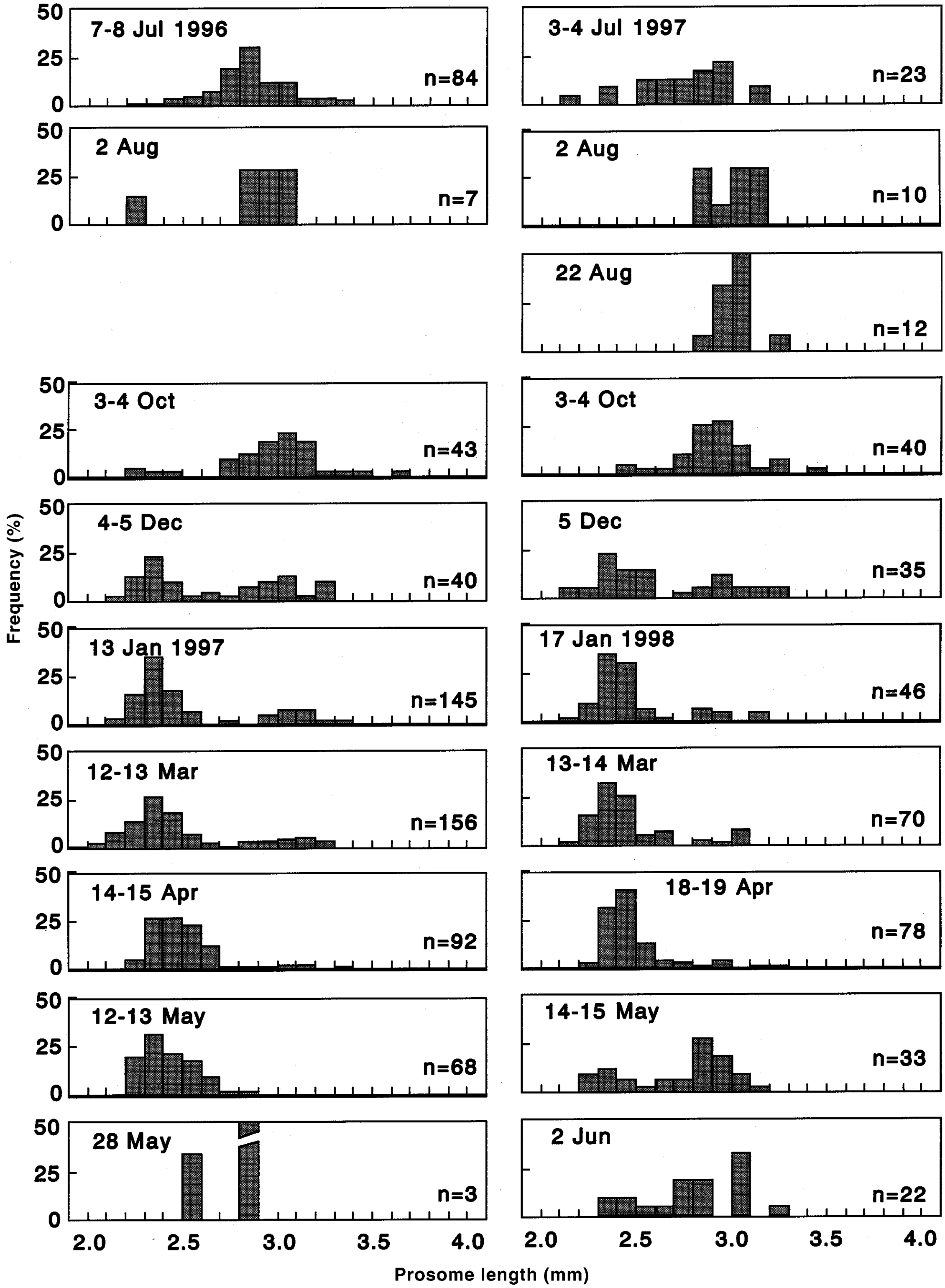


Fig. 5 *Neocalanus flemingeri.* Size distribution of C4 from July 1996 to June 1998 in the western subarctic Pacific

Sea (Vidal and Smith 1986; Miller and Clemons 1988). Peak abundances are about 2×10^4 and 4×10^3 copepods m^{-2} for *N. plumchrus* and *N. flemingeri*, respectively (Figs. 4, 10).

Seasonal segregation between *Neocalanus plumchrus* and the small form of *N. flemingeri* is also clear, as in other areas. However, replacement of small *N. flemingeri* by *N. plumchrus*, which mostly depends on the recruitment of *N. plumchrus* to the surface layer, takes place a little later in the season compared with other areas. Stages C3 and C4 of *N. plumchrus* dominate in the

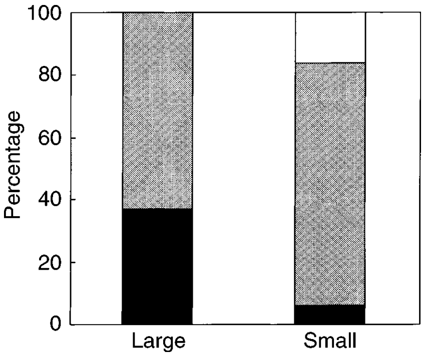


Fig. 6 *Neocalanus flemingeri*. Lipid contents of the large (>2.9 mm in prosome length) and the small (<2.6 mm) forms during winter (December and January). Oil-sac size was roughly categorized by lateral views into three classes, empty: 0 to 4% (*open column*), part: 4 to 40% (*shaded column*) and full: (*filled column*) of the prosome areas

middle of May in the Alaskan gyre (Miller 1993), C5 dominates in the middle of May in the southeastern Bering Sea (Vidal and Smith 1986), C5 dominates by April in the Japan Sea (Miller and Terazaki 1989) and C5 dominates in early May in the Strait of Georgia (Fulton 1973). In the present study, samples collected on 28 May 1997 were dominated by C3 and C4, those of 14 to 15 May 1998 by C2 to C5. Before these samplings, *N. plumchrus* was much less abundant in both years (Fig. 10). C1 and C2 individuals must be somewhat underestimated by our 333 μm sampling mesh (Miller et al. 1984). However, the order of magnitude increased between 13 May and 28 May 1997 and between 19 April and 14 May 1998 must indicate mass recruitment into the surface layer during these periods. Therefore, recruitment to copepodite stages by *N. plumchrus* in the area studied is 2 weeks to a month later than in other areas of subarctic seas. Vidal and Smith (1986) and Miller (1993) estimated a stage duration of 11 to 14 d per copepodite stage. We cannot estimate the growth rate of *N. plumchrus* because of the long sampling interval in our study compared with theirs. Their estimated growth rates or somewhat shorter stage duration can explain the stage composition of the mass occurrence in late May in the present study. Mackas et al. (1998) showed that the timing of peak abundance of *N. plumchrus* to the surface layer varies by about a month, depending on the temperature in the oceanic Stn P. Thus, late occurrence of *N. plumchrus* may be explained by the relatively low temperature (2 to 5 °C during March to April) in our study area.

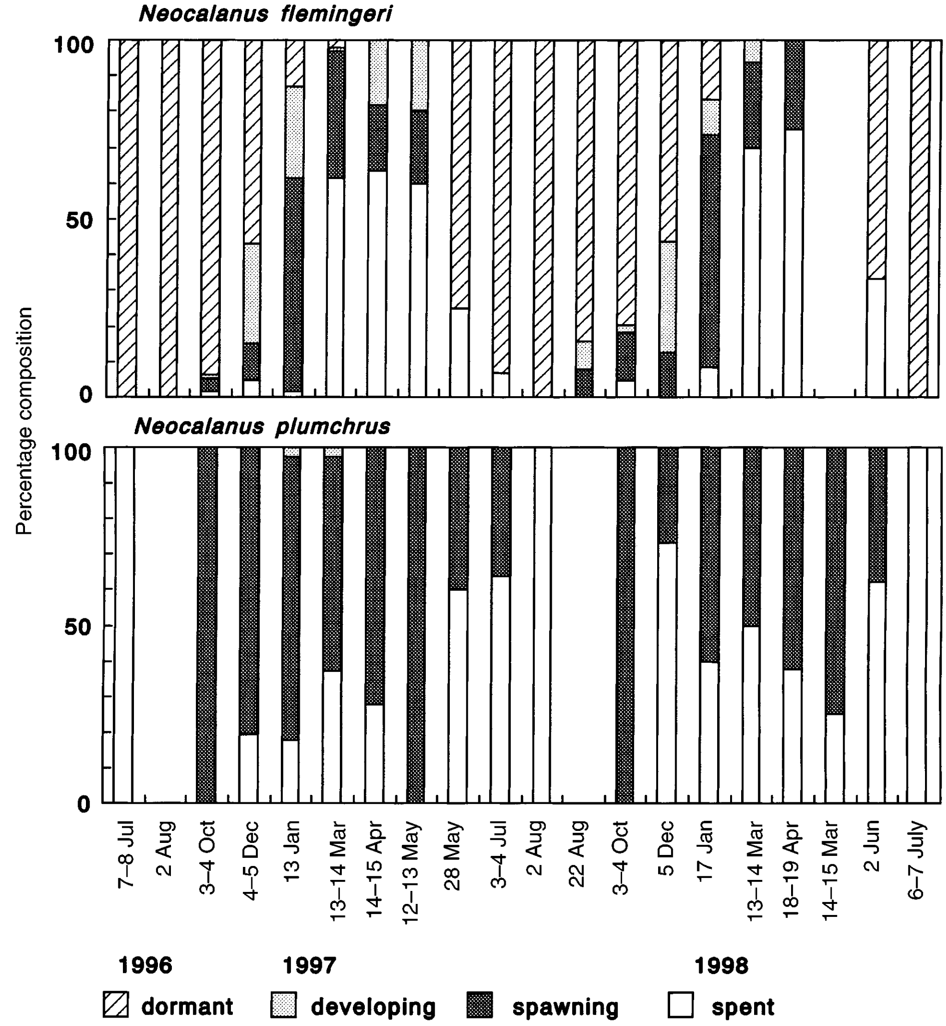
Table 2 *Neocalanus flemingeri*. Numerical abundance (ind m^{-2}) of large and small forms during the dormant season. Large and small forms were determined by prosome length (large: >4.2 mm in females, >2.8 mm in C4; small: <4.0 mm in females and <2.7 mm in C4). Numbers in parentheses denote percentage contribution of the large form

Month	Female		C4	
	Small	Large	Small	Large
1996 Jul	431	58 (12)		
Aug	1041	47 (4)		
Oct	284	83 (22)	12	118 (91)
Dec	697	182 (20)	72	59 (45)
Seasonal avg.	613	93 (13)		
1997 Jan			637	165 (21)
Mar			1355	112 (8)
Apr			1126	17 (1)
Seasonal avg.			640	94 (12)
Jul	57	40 (41)		
Aug	96	51 (35)		
Oct	44	64 (59)	8	64 (89)
Dec	3	43 (93)	263	143 (35)
Seasonal avg.	50	50 (50)		
1998 Jan			755	135 (15)
Mar			403	59 (13)
Apr			492	42 (8)
Seasonal avg.			384	89 (19)

Neocalanus species have been thought to be spring grazers. However, abundant species (in biomass), like *N. plumchrus*, migrate to the surface layer, graze and grow from late May to August in the area studied. 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. Food sources other than phytoplankton should be important to sustain the fast growth of *N. plumchrus*, as has been suggested for the open ocean area of the North Pacific (Dagg 1993a; Gifford 1993; Tsuda and Sugisaki 1994), because phytoplankton biomass is usually low (<0.5 mg m^{-3}) during this period (Saito et al. 1998). It is also curious that *Neocalanus* species succession and phytoplankton community succession take place at the same time.

Synchronism is one of the key words in the life cycle strategies of *Neocalanus* species, as suggested by Vidal and Smith (1986) and Miller and Clemons (1988). *Neocalanus* species show growth closely synchronized to seasonal variation of the environment (Jillett 1968; Miller et al. 1984). Synchronism has also been observed in summer mating and midwinter spawning of *N. flemingeri* (Miller and Clemons 1988). In the present study, C5 individuals appeared mainly in May, although considerable numbers of C4 were present beginning in midwinter, and the occurrence of adult males was observed in restricted periods (Fig. 4), suggesting synchronism in molting to C5 and the adult stage, which may facilitate mating success (Miller and Clemons 1988). However in our sampling area, more synchronized and more rapid copepodite development was observed in *N. plumchrus* than in *N. flemingeri*. Considerable numbers of C4 and younger copepodites were observed at the spawning peak (January). Although they included dormant C4 (large form), newly

Fig. 7 *Neocalanus flemingeri, N. plumchrus*. Percentage composition of females in four categories of reproductive conditions from July 1996 to July 1998 in the western subarctic Pacific



recruited individuals were a major portion of the population. If we compared the number of copepods in January (peak of spawning) and April (end of major recruitment), at least one-third of the population must derive from early spawners (Fig. 4; Table 2). This may suggest that bet hedging in the spawning period of *N. flemingeri* works in part to sustain their population. January might be the best time to synchronize copepodite development with the increase of primary production during spring, but spring weather is less predictable than summer conditions, when *N. plumchrus* appear, so the delay in development may increase competition with *N. plumchrus*. Thus, *N. flemingeri* may need early spawners to sustain their population. On the other hand, *N. plumchrus* showed tightly synchronized development during middle to late May (Fig. 10), although the spawning period was long compared with *N. flemingeri*. Moreover, individual females of *N. plumchrus* spawn for longer than those of *N. flemingeri* (Tsuda unpublished data). The spawning peak of *N. plumchrus* is October in the Alaskan gyre (Miller and Clemons 1988). Although that of our area was not clear because of shallow sampling, actively spawning females were collected abundantly by vertical tows from 1000 m in October (Tsuda unpublished data). However, most young copepodites collected during winter were *N. flemingeri* (Fig. 4), as reported in the Alaskan gyre (Miller and Clemons 1988). Thus, the long lag between spawning and C1 recruitment and the contrast between prolonged spawning and synchronized C1 recruitment seem to be a unique phenological feature of this species. Because egg dormancy was not observed in either species (Tsuda unpublished data), there must be some mechanisms during naupliar stages, such as dormancy, to create the synchronism in copepodite development.

Two distinct forms of *Neocalanus flemingeri* were observed in the present study. The large form showed a different life history from the original report of *N. flemingeri* (Miller and Clemons 1988), while an essentially identical life history was observed in the small form. At least some individuals of the large form have a biennial life cycle with dormancy at both C4 and adult female stages. Its spawning season is a little later than the smaller form and prolonged (January to March),

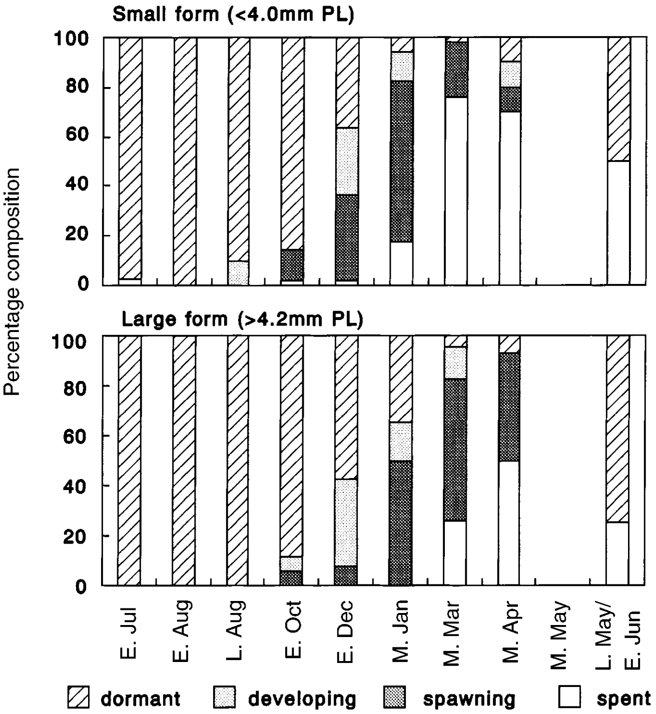


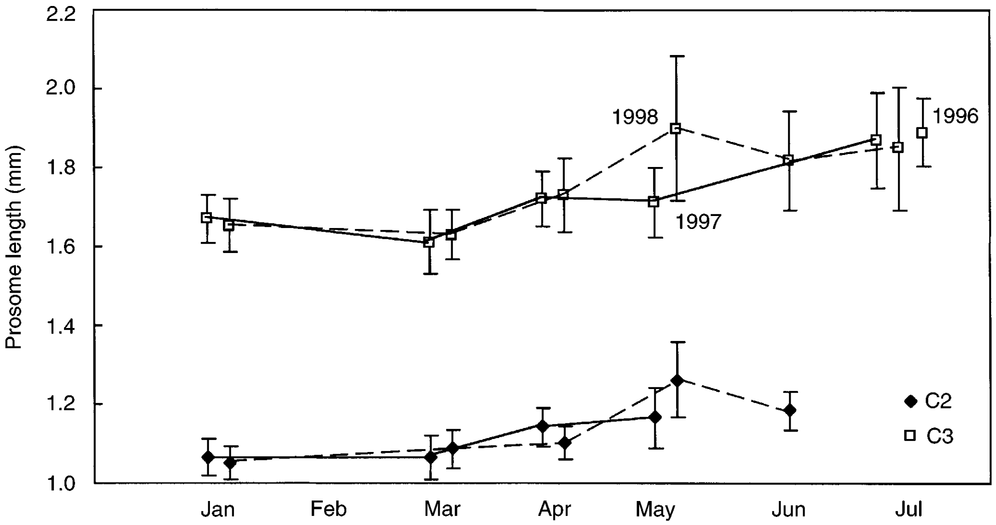
Fig. 8 *Neocalanus flemingeri*. Percentage composition of two forms of females in four categories of reproductive conditions. Values are averages of 2 years except late August (*PL* prosome length; *E* early; *L* late)

and recruitment to C1 is later (May). Therefore, the large form was not seasonally segregated in the growing season from *N. plumchrus*.

Adult males are generally smaller than females in copepods (e.g. *Neocalanus plumchrus*, Fig. 3). However, the bimodal distribution in size observed for *N. flemingeri* can not be regarded as sexual dimorphism, because bimodal distributions were observed for both adult males and females, and each form showed its own life cycle. Moreover, there is a significant difference in mtDNA sequences below the interspecific level between the two forms (A. Bucklin personal communication). However, mating isolation between the two forms could not be detected by our sampling methods (no vertical profile and rough seasonal resolution), because for both forms adult males and dormant females carrying spermatophores were observed in the same period. We have not yet been able to determine whether the two forms are sympatric populations or whether they came from different geographical origins. However, it is possible to speculate on the origin of the large form. A biennial life cycle in subarctic copepods was firstly reported in *Eucalanus bungii* (Miller et al. 1984), and then in *N. flemingeri* from the Japan Sea and the western subarctic Pacific (Miller and Terazaki 1989). These large forms are least likely to come from the Japan Sea, since there is no inflow to the studied area from Japan Sea. They are more likely to come from the Okhotsk Sea. Characteristics of the Oyashio water (cold and less saline) are generated by extensive vertical mixing by tidal currents passing through the strait between the Kuril Islands (Ohtani 1991), thus modifying the waters of our sampling area by exchange with the Okhotsk Sea (Kono and Kawasaki 1997). Therefore, the Okhotsk Sea is considered to be the most plausible origin of the large form. On the other hand, the small form seems to be an oceanic population, because body size and life history are quite similar to those of the eastern subarctic gyre.

Neocalanus species have a unique life history characterized by winter dormancy with lipid storage and ontogenetic vertical migration (Conover 1988), but the pattern of growth and reproduction is flexible according to species and to the habitat environments (Ohman 1987; Miller and Terazaki 1989). Especially, *N. flemingeri* shows flexibility in spawning period, life span and body size. The body size varied considerably with locality (Table 4 in Miller 1988). The body sizes are smallest in the oceanic gyre and relatively large in marginal seas and on edges of gyres (Miller 1988; present study). These body size variations should partly reflect the nutritional condition of the habitat (Miller et al.

Fig. 9 *Neocalanus flemingeri*. Seasonal variations of prosome length of C2 and C3 from January to July (*solid lines* 1997; *broken lines* 1998; *error bars* ±1 SD)



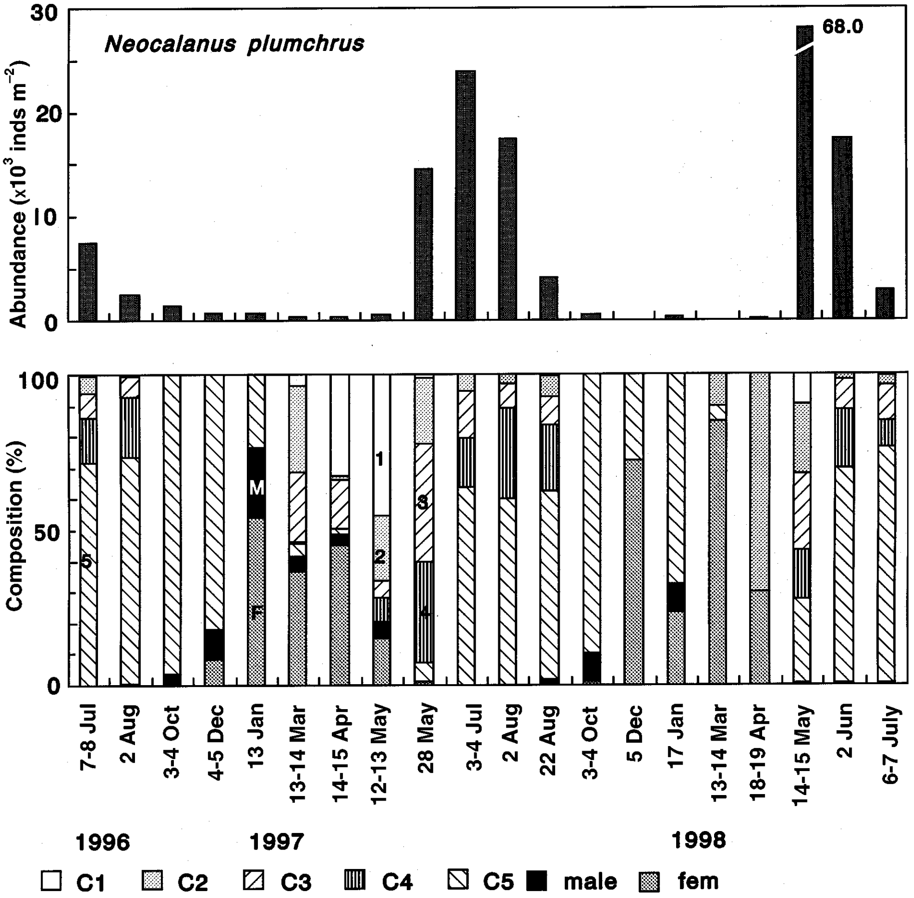


Fig. 10 *Neocalanus plumchrus.* Abundance (*upper*) and stage composition (*lower*) from July 1996 to July 1998 in the western subarctic Pacific

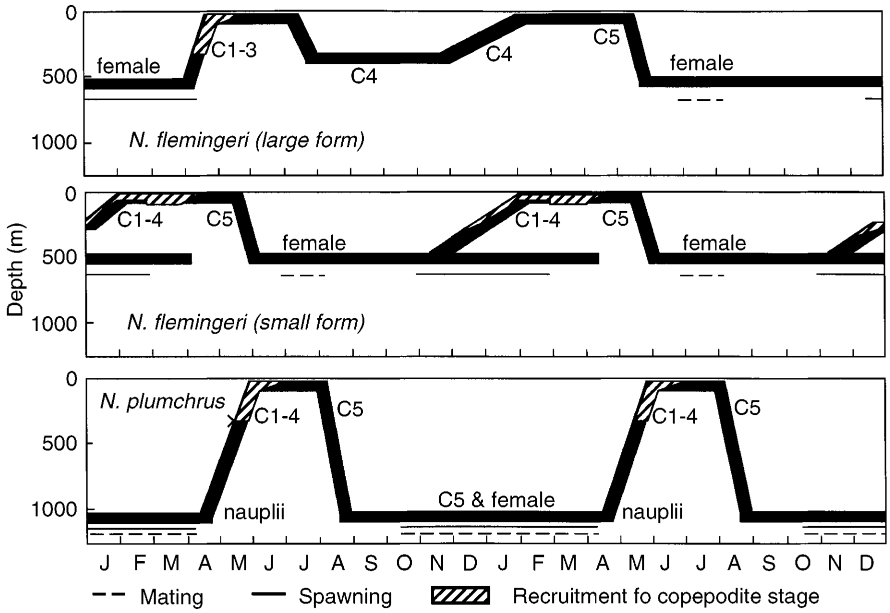


Fig. 11 *Neocalanus flemingeri, N. plumchrus.* Schematic illustration of life histories in the western subarctic Pacific. Vertical distribution of both species and mating/spawning period of *N. plumchrus* are tentatively assumed from Miller et al. (1984), Miller and Clemons (1988) and Miller and Terazaki (1989). Only biennial life cycle is illustrated for the large *form N. flemingeri* in this figure, although it is provable that a part of the population has a annual life cycle (see "Results")

1992), but may suggest local isolation of the populations. *N. flemingeri* have a very short mating season compared with that of its sibling species *N. plumchrus*. Thus, genetic isolation may be easier to establish than in *N. plumchrus*.

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