Ontogenetic vertical migration and life cycle of *Neocalanus plumchrus* (Crustacea: Copepoda) in the Oyashio region, with notes on regional variations in body sizes

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The ontogenetic vertical migration and life cycle of Neocalanus plumchrus were investigated by analyzing monthly population structure at Site H in the Oyashio region from September 1996 through October 1997. Additional sampling was also done at several stations covering the entire subarctic Pacific, Okhotsk Sea and Japan Sea as a basis for regional comparison of life cycles and body sizes. At Site H, N. plumchrus spawned October to April below 250 m depth. Young copepodite stages (C1–C5) occurred during June late in the phytoplankton bloom. The C5 migrated to the deeper layers in July–August where they molted to adults. Development time of C5 to C6 was highly variable. The ontogenetic vertical migration of N. plumchrus ranged from the surface to 1000–2000 m depth, and the life cycle was annual. Temporal data on population structure and vertical distribution suggested the annual life cycle was generally synchronized throughout the subarctic Pacific and its marginal seas. Geographical comparison of C5 prosome length indicated the occurrence of significantly large specimens in the Oyashio region and Okhotsk Sea but small specimens in the Japan Sea. Possible causes for regional variability in body sizes are discussed.

INTRODUCTION

Neocalanus plumchrus is one of the large grazing copepods occurring in the subarctic Pacific and its marginal seas (Zenkevitch, 1963; Motoda and Minoda, 1974). Together with the other large grazing copepods (*N. cristatus*, *N. flemingeri* and *Eucalanus bungii*), *N. plumchrus* often accounts for 80–95% of the summer zooplankton biomass in the surface layer (Vinogradov, 1970; Vidal and Smith, 1986). In the Alaskan Gyre, *N. plumchrus* alone occupies about half of the mesozooplankton biomass (Mackas *et al.*, 1998). *Neocalanus plumchrus* is an important prey of mesopelagic fishes (Gordon *et al.*, 1985), salmon (Burgner, 1991), Pacific saury (Odate, 1994), baleen whales (Kawamura, 1982) and seabirds (Hunt *et al.*, 1993), thereby acting as a vital link between primary production and higher trophic production in the subarctic marine ecosystems of the North Pacific.

Neocalanus plumchrus was described by Marukawa in 1921, and *N. flemingeri* may have been confused with *N. plumchrus* until the revision of the two species in 1988 by Miller (Miller, 1988). Subsequent studies have shown that both *N. plumchrus* and *N. flemingeri* undergo large-scale ontogenetic vertical migrations, but their seasonal patterns are different (Miller and Clemons, 1988; Miller and Terazaki, 1989). Because of these results, information published before 1988 about *N. plumchrus* from the Bering Sea (Heinrich, 1962) and Oyashio and Oyashio/Kuroshio transitional zone (Omori and Tanaka, 1967; Sekiguchi, 1975a, b) needs re-examination.

Recently, Tsuda *et al.* (Tsuda *et al.*, 1999) reported the life cycle of *N. plumchrus* (separating it from *N. femingeri*) in the Oyashio region, western subarctic Pacific, based on specimens collected with oblique hauls from the surface to 900 m depth at the maximum. Because of their sampling design, part of the population distributed below 900 m depth was not collected [premature and mature adults of *N. plumchrus* are distributed down to 1000–2000 m depth, cf. (Miller *et al.*, 1984; Miller and Clemons, 1988; this study)], and ontogenetic vertical distribution patterns were left unresolved.

In this study, we evaluated ontogenetic vertical migration of *N. plumchrus* in the Oyashio region, and re-examined the life cycle proposed by Tsuda *et al.* (Tsuda *et al.*, 1999), based on specimens collected year-round from five discrete depths between the surface and ≤2000 m. Further, we discuss regional variations in life cycles and body sizes of *N. plumchrus* in the subarctic Pacific and its marginal seas.

METHOD

Monthly depth-stratified sampling was done in the Oyashio region (41°30′–42°30′N latitude,

145°00′–146°00′E longitude) off southeastern Hokkaido (referred to hereafter as Site 'H'). We also obtained occasional samples from three additional stations in the western, one station in the central and two stations in the eastern subarctic Pacific, four stations in the Japan Sea, two stations in the Okhotsk Sea and one station in the Bering Sea (Figure 1, Table I). Except for the sampling in the Bering Sea (February, 1993), all other samples were collected September 1996–October 1997.

Zooplankton were collected with a closing net [60 cm mouth diameter, 100 mm mesh size (Kawamura, 1968, 1989)] equipped with a Rigosha flow-meter in its mouth
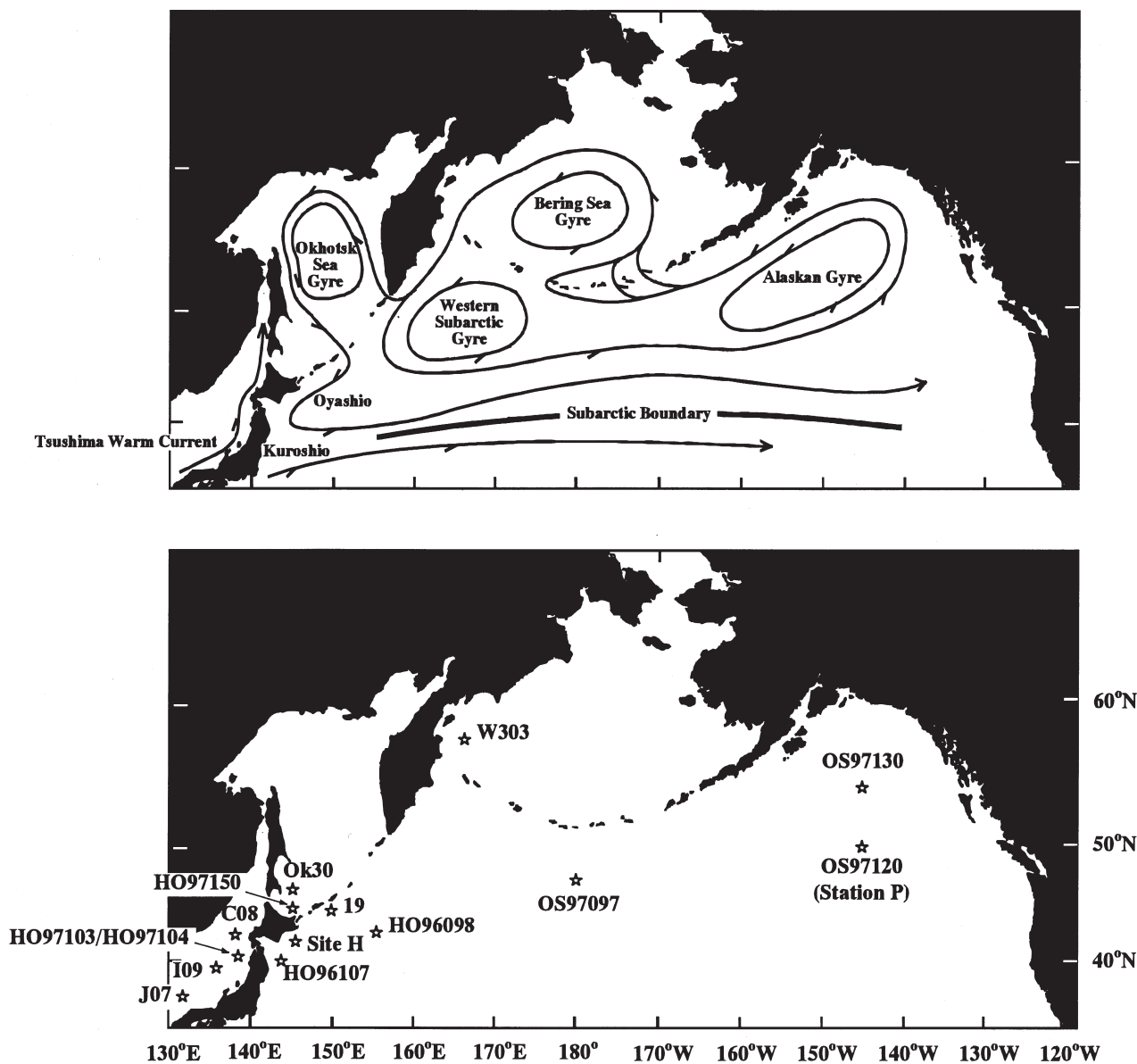

Fig. 1. Schematic diagrams of current systems (**top**, redrawn from Favorite *et al.*, 1976) and sampling stations in the subarctic Pacific Ocean and its neighboring waters (**bottom**).

Table I: Zooplankton sampling data in the northwest (NW), northcentral (NC) and northeast (NE) subarctic Pacific and its neighboring waters

Area Station code	Position	Sampling date	Time	Ship	Net	Discrete sampling depth (m)
NW Pacific						
Site H	42°00′N, 145°00′E	4 Sep. 1996	NT	Os	G	0–30, 30–250, 250–500, 500–1000, 1000–1800
	41°30′N, 145°47′E	19 Sep. 1996	NT	Ho	G	0–30, 30–250, 250–500, 500–1000, 1000–1500
	41°30′N, 145°47′E	2 Oct. 1996	DT	Ho	G	0–30, 30–250, 250–500, 500–1000, 1000–1500
	41°30′N, 146°00′E	8 Dec. 1996	NT	Hs	G	0–80, 80–250, 250–500, 500–1000, 1000–1700
	42°30′N, 145°00′E	13 Jan. 1997	DT	Hk	G	0–50, 10–500, 300–1700
	41°30′N, 146°00′E	20 Feb. 1997	NT	Hs	G	0–100, 100–250, 250–500
	41°45′N, 145°22′E	17 Mar. 1997	NT	Hk	G	0–100, 100–250, 250–500, 500–1000, 1000–2000
	41°30′N, 145°47′E	11 Apr. 1997	NT	Ho	G	0–150, 150–250, 250–500, 500–1000, 1000–1500
	42°01′N, 145°21′E	7 May. 1997	NT	Hk	G	0–150, 500–1000, 1000–2000
	41°30′N, 145°47′E	4 Jun. 1997	NT	Os	G	0–80, 80–250, 250–500, 500–1000
	41°30′N, 145°47′E	23 Jun. 1997	NT	Ho	G	0–20, 20–250, 250–500, 500–1000
	41°30′N, 145°47′E	2 Jul. 1997	NT	Ho	G	0–40, 40–250, 250–500, 500–1000, 1000–2000
	41°30′N, 145°47′E	17 Aug. 1997	NT	Os	G	0–80, 80–250, 250–500, 500–1000, 1000–2000
	41°29′N, 145°47′E	26 Aug. 1997	DT	Ts	G	0–20, 20–250, 250–500, 500–1000, 1000–2000
	41°30′N, 145°47′E	5 Oct. 1997	NT	Ho	G	0–75, 75–250, 250–500, 500–1000, 1000–2000
HO96098	42°30′N, 155°00′E	27 Sep. 1996	BT	Ho	G	0–40, 40–250, 250–500, 500–1000, 1000–1500
HO96107	40°32′N, 144°29′E	3 Oct. 1996	DT	Ho	G	0–30, 30–250, 250–500, 500–1000, 1000–1500
19	44°26′N, 149°40′E	16 Oct,. 1996	DT	Ky	G	0–50, 50–250, 250–500, 500–1000, 1000–2000
NC Pacific						
OS97097	47°00′N, 180°00′E	18 Jun. 1997	NT	Os	G	0–100, 100–250, 250–500, 500–1000, 1000–2000
NE Pacific						
OS97120 (= Stn P)	50°00′N, 145°00′W	5 Jul. 1997	NT	Os	G	0–40, 40–250, 250–500, 500–1000, 1000–2000
OS97130	55°00′N, 145°00′W	10 Jul. 1997	NT	Os	G	0–40, 40–250, 250–500, 500–1000, 1000–2000
Bering Sea						
W302	56°12′N, 167°59′E	8 Feb. 1993	DT	Ky	WP-2	0–500
Japan Sea						
C08	42°30′N, 137°30′E	11 Jan. 1997	NT	Ky	G	0–100, 100–500, 500–1000, 1000–2000, 2000–3000
I09	39°00′N, 135°00′E	24 Jan. 1997	NT	Ky	G	0–100, 100–500, 500–1000
J07	37°00′N, 131°30′E	26 Jan. 1997	NT	Ky	G	0–200, 200–500, 500–1000, 1000–2000
HO97103	40°48′N, 138°19′E	19 Sep. 1997	DT	Ho	G	0–100, 100–250, 250–500, 500–1000, 1000–2000
HO97104	40°48′N, 138°19′E	19 Sep. 1997	NT	Ho	G	0–100, 100–250, 250–500, 500–1000, 1000–2000
Okhotsk Sea						
Ok30	46°00′N, 1454°00′E	9 Nov. 1996	DT	Ky	G	0–50, 50–250, 250–500, 500–1000, 1000–2000
HO97150	44°40′N, 145°20′E	1 Oct. 1997	NT	Ho	G	0–50, 50–250, 250–500, 500–1000, 1000–2000

NT: nighttime; DT: day time; Os: TS 'Oshoro Maru'; Ho: TS 'Hokusei Maru'; Hs: RV 'Hokushin Maru'; Hk: RV 'Hokko Maru'; Ts: RV 'Tansei Maru'; KRV 'Kaiyo Maru'. Wp-2: WP-2 net, G: Closing type net.

ring and a TSK Depth-Distance Recorder or RMD Depth Meter on its suspension cable. The net was towed vertically at a speed of 1 m s⁻¹, usually through five discrete strata: 0 m–the bottom of thermocline, the bottom of thermocline–250, 250–500, 500–1000, 1000–≤2000 m (Table I). When we failed to obtain this complete discrete depth series in monthly samplings, missing depth stratum data were time-interpolated from the previous and subsequent sampling date. Since the samplings were made without standardizing the time of the day, diel vertical migration of *N. plumchrus* could be a potential source of error in estimating its vertical distribution pattern.

However, *N. plumchrus* is known to carry out little or no diel vertical migration (Mackas *et al.*, 1993; Tsuda and Sugisaki, 1994; Kobari and Ikeda, unpublished data). For the isolated samplings in the Bering Sea, where the specimens were used for prosome length measurements only, a WP-2 net [57 cm mouth diameter, 200 μm mesh size (UNESCO, 1968)] was used. After collection, zooplankton samples were preserved immediately in 5% formalin–seawater buffered with borax.

Temperature and salinity profiles were determined with a CTD system at each sampling of zooplankton. Chlorophyll *a* concentration data at Site H were supplied by H. Kasai of Hokkaido National Fisheries Research Institute.

In the land laboratory, *N. plumchrus* was sorted from the zooplankton samples, then separated into five copepodite stages (C2–C6) under a dissecting microscope. The C1 of *N. plumchrus* could not be distinguished from *N. flemingeri* due to undeveloped second maxilla and the mandibular gnathobase. C6 specimens were separated into males and females. *Neocalanus plumchrus* was distinguished from *N. flemingeri* by the smaller proportion of second maxilla to prosome (Tsuda *et al.*, 1999), the wider tooth row on the mandibular gnathobase for C2–C5, the lesser head/prosome ratio for the C6 male and the lesser width of the first urosome segment for the C6 female (Miller, 1988). The maturity conditions of the C6 females were classified into the following four categories depending on their gonad conditions: 'dormant', 'developing', 'actively spawning' and 'spent', following the criteria of Miller and Clemons (Miller and Clemons, 1988). The body structure of all C5 specimens from Site H was examined under the dissecting microscope and classified into three types depending on the musculature development and lipid storage after Ikeda *et al.* (Ikeda *et al.*, 1990): a 'solid' type with well developed musculature and conspicuous lipids, a 'transparent' type with poorly developed musculature and no lipids, and an 'intermediate' type with characters between the 'solid' and 'transparent' types. As an index of body size, the prosome length was measured under the dissecting microscope to the nearest 0.05 mm.

RESULTS

Hydrography

Site H

The western boundary current of the subarctic circulation in the North Pacific is called the 'Oyashio'. It flows southwestward along the Kuril Islands and reaches the east coast of northern Honshu, Japan, then turns east at about 40°N [cf. (Reid, 1973)]. During this journey, the properties of the Oyashio Water are modified as a result of exchange with the Okhotsk Sea Water, Tsugaru Warm Current Water and Kuroshio Water (Kono, 1996). Because of the meandering flow pattern, isolated loops of Kuroshio extension are often entrapped between the downstream, and return flows of the Oyashio and are called 'Warm Core Rings'.

Site H of this study is near the southern end of the alongshore flow of the Oyashio. Over the study period, the extreme range of the surface temperatures was from 2°C (March-April 1997) to 18°C (September–October 1996 and 1997) (Figure 2). Oyashio Water, characterized by salinities from 33.0 to 33.3 and temperature below 3°C (Ohtani, 1971), occurred in the upper 150 m from February to April 1997. After April, less saline, seasonally-warmed water (possibly originating in the Okhotsk Sea; Kono, personal communication) covered the upper 50 m. Surface temperatures above 10°C were observed in September–November 1996 and in June–October 1997 when the thermocline was well established at 20–50 m in the water column. The effects of the Warm Core Rings originating from the Kuroshio extension were seen in September in both 1996 and 1997, and from December 1996 to January 1997, as judged by temperature at 200 m (>4°C) and salinity in the 0–200 m layer (>33.5 psu). The temperature and salinity in the 200–1500 m layer were stable at 2–3°C and 33.5–34.5 psu throughout the year.

Phytoplankton biomass determined as chlorophyll *a* showed a marked seasonality (Figure 2). Chlorophyll *a* at the surface was around 0.4 mg m^{-3} from August 1996 to the end of February 1997, then increased rapidly to >9 mg m^{-3} in May 1997. During this chlorophyll peak season, concentrations above 2 mg m^{-3} extended down to 50 m. The surface chlorophyll *a* concentration decreased to 2 mg m^{-3} by the end of June and to 0.4 mg m^{-3} towards the end of 1997. Chlorophyll *a* was consistently <0.4 mg m^{-3} below 100 m depth throughout the year.

Other areas

Among three stations in the western subarctic Pacific, temperatures of the top 500 m increased in the order of stations 19, HO96098 and HO96107 (Figure 3). Compared with Site H, the upper 500 m of stations 19 and HO96107 were colder and warmer, respectively, and HO96098 was similar to Site H (except for higher temperatures near the surface layer). The colder temperatures at station 19 reflect the influence of cold Okhotsk Sea Water, and warmer temperatures at HO96107 are due to the influence of the warm Kuroshio Water [cf. (Kono and Kawasaki, 1997; Kono, 1997)]. Taking sampling season into account, the temperature profiles at station OS97097 in the central subarctic Pacific, OS97120 (=Station P) and OS97130 in the eastern subarctic Pacific were closely comparable with that at Site H, except those in the top 500 m
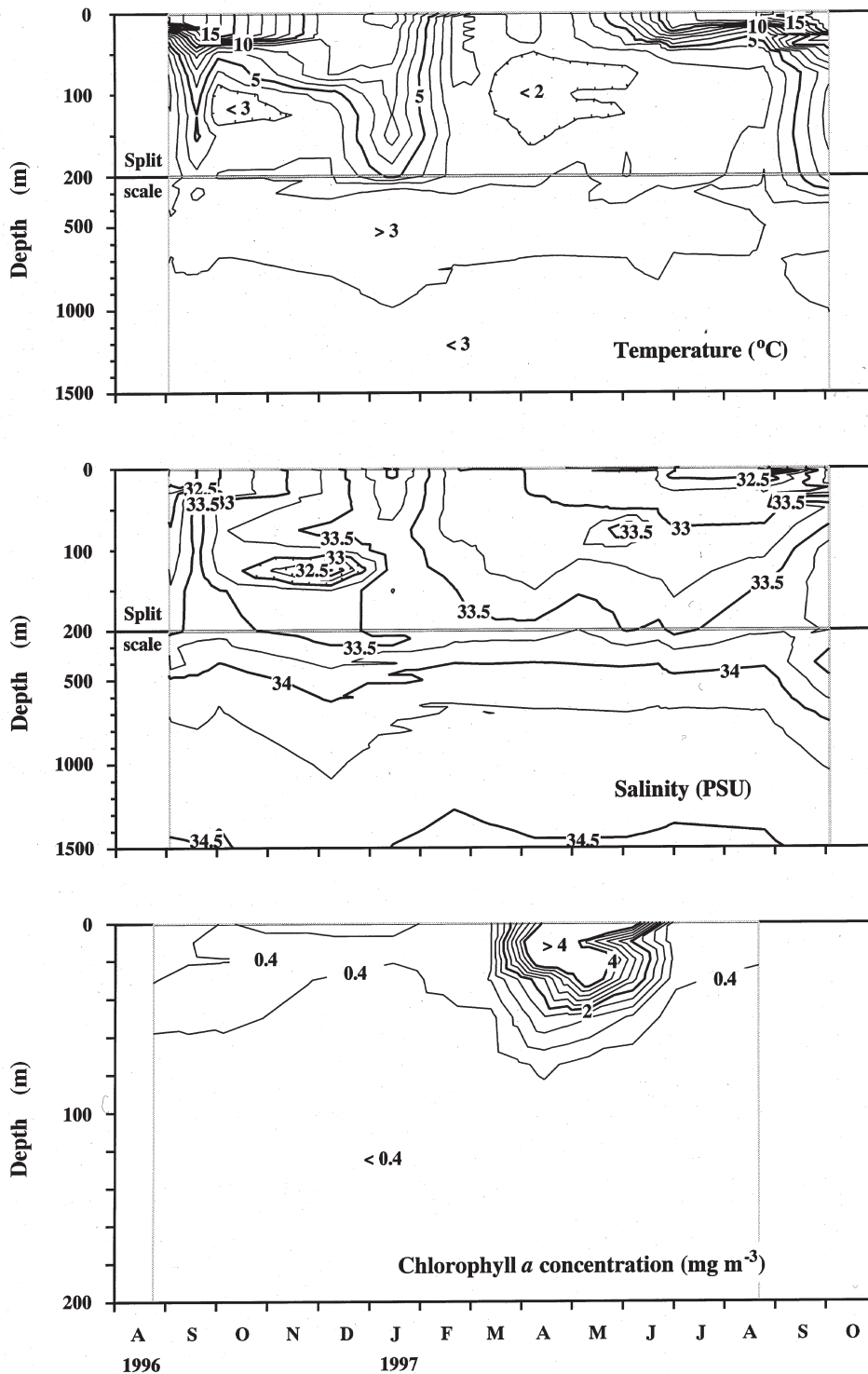
Fig. 2. Seasonal changes in vertical structures of temperature (°C, **top**), salinity (psu, **middle**) and chlorophyll *a* concentration (mg m^{-3}, **bottom**) at Site H from August 1996 to October 1997. Note that depth scale of the bottom panel is not the same as those of the top two panels.
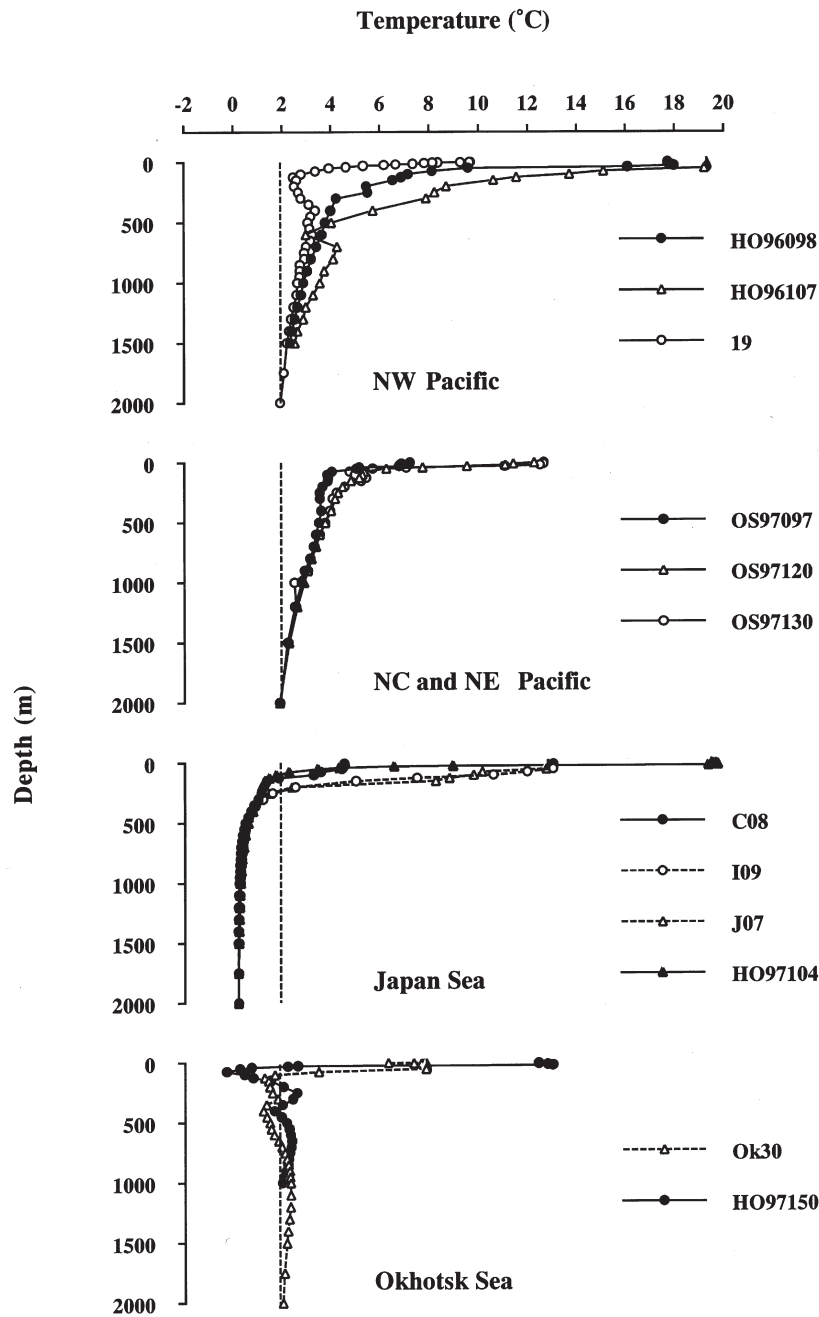
Fig. 3. Vertical structure of temperature (°C) at stations in the western (NW), central (NC) and eastern (NE) subarctic Pacific, and Japan and Okhotsk Seas. Vertical dashed lines (2°C) are superimposed to facilitate comparison.

were slightly warmer at the latter two stations. Comparison of annual temperature variations of the top 500 m at Site H (Figure 2) and Station P (Miller *et al.*, 1984) showed that Site H was characterized by a wider temperature range in the surface layer (2–18°C versus 6–14°C) and lower temperatures in the 200–500 m stratum (2–3°C versus 4–5°C).

The thermal regimes in the marginal seas (Japan Sea

Fig. 4. Seasonal changes in standing stock of each development stage (C1–C6) of *Neocalanus plumchrus* and relative percentage of actively spawning and spent of C6 females in 0–2000 m at Site H from September 1996 to October 1997. Annual means are shown in parentheses. Shaded area denotes high chlorophyll period. Open symbols = no occurrence.
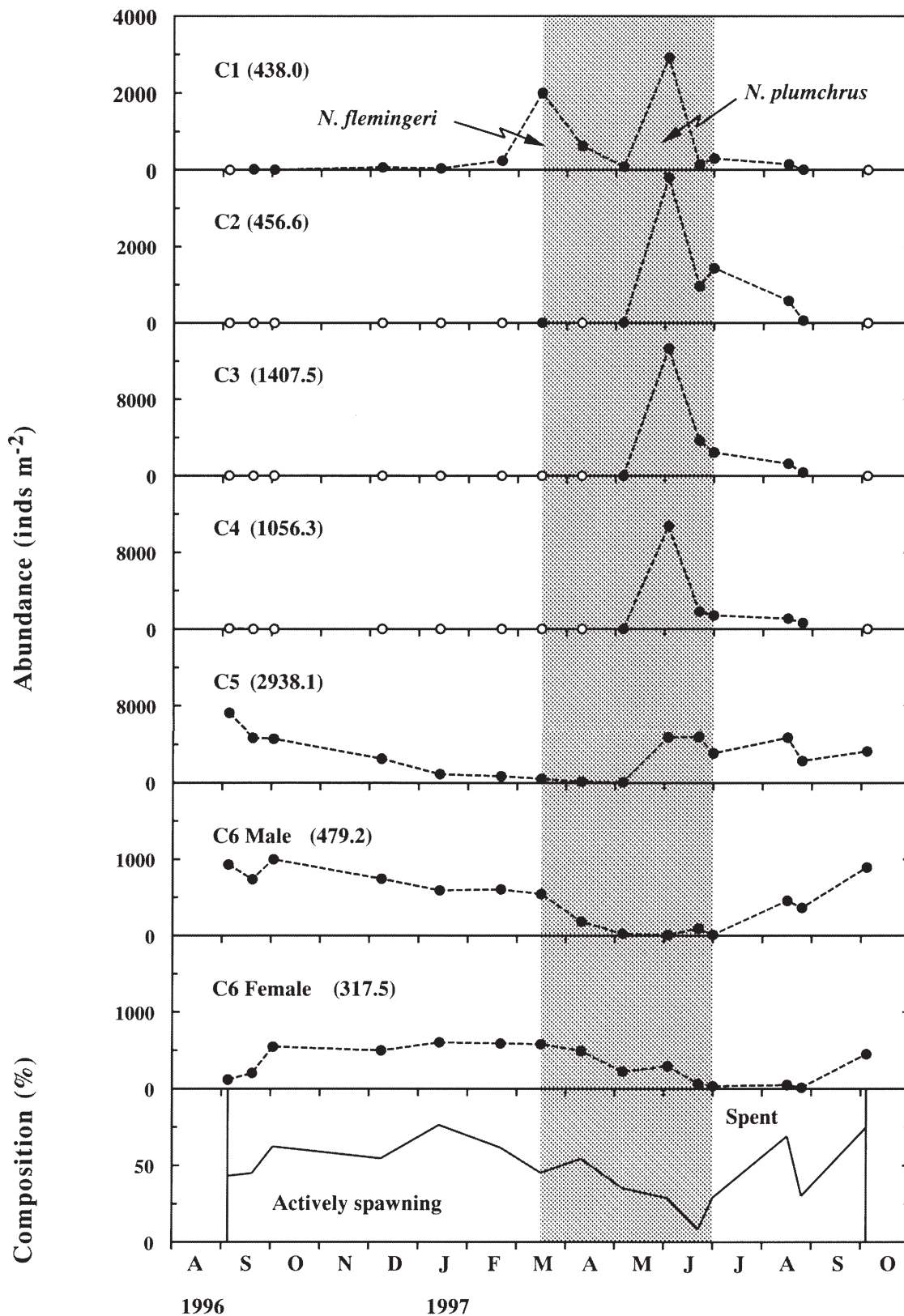
and Okhotsk Sea) differed from those in the subarctic Pacific by the occurrence of near-zero temperature (Zenkevitch, 1963). This very cold water is termed 'Deep-Water' in the Japan Sea, and 'Cold Intermediate Water' in the Okhotsk Sea. At all four stations in the Japan Sea, the Deep-Water was below 500 m. At stations I09 and J07 in the southern Japan Sea, water temperature in the top 300 m was higher than at stations C08 and HO97104 in the northern Japan Sea, perhaps due to the effect of the Tsushima Warm Current [a branch of Kuroshio carrying warm water from the south (Nishimura, 1969)]. Nishimura classified Japan Sea regions as 'subtropical', 'subarctic' and 'arctic' based on biological features (Nishimura, 1969). According to his classification, stations C08 and HO97103/HO97104 in the northern Japan Sea are in the subarctic region, and stations I09 and J07 in the southern Japan Sea are in the subtropical region. At two stations in the Okhotsk Sea, the 'Cold Intermediate Water' was at 30–200 m depth, shallower than in the Japan Sea. This was especially evident at southern station HO97150.

Population structure

Site H

Prominent abundance peaks of the mixed C1s of *N. plumchrus/flemingeri* were observed in March and June 1997 (Figure 4). After tracing back C2–C5 abundance peaks in June, and C6 male and female in October, it is evident that the later C1 peak is *N. plumchrus*. Abundance peaks of C1–C5 were seen in the later half of the high chlorophyll period. Based on the persistence of C5s in June–October and the occurrence of adults throughout the year, the C5 development time was long and variable, while those of C1–C4 were short. The C6 males and females were abundant from September 1996 to April 1997.

In adult females, actively-spawning and spent specimens were observed throughout the year. A large fraction of actively-spawning specimens was seen between October 1996 and April 1997. Spent females were most common in June 1997. Based on all these seasonal features of female structure and maturity conditions, the life cycle of *N. plumchrus* at Site H appears to be annual.

Table II: Standing stock (ind. m⁻² in 0–2000 m depth) and stage composition (%) of each developmental stage (C2–C6) of Neocalanus plumchrus in the subarctic North Pacific and its neighboring waters

| Area | Standing stock | Composition (%) | | |
Station code		C2–C4	C5	C6
NW Pacific				
Site H	6655.2 (±4412.7)	18.6	48.9	32.5
HO96098	2304.5	0.0	87.1	12.9
HO96107	3015.1	0.0	85.6	14.4
19	5260.2	0.5	91.5	8.0
NC Pacific				
OS97097	7821.9	60.5	39.1	0.4
NE Pacific				
OS97120 (= Stn P)	2076.0	4.8	77.8	17.4
OS97130	1236.1	45.4	54.6	0.0
Japan Sea				
C08	1875.8	0.0	50.8	49.2
I09	128.6*	0.0	15.2	84.8
J07	8.2	0.0	0.0	100.0
HO97103	8150.7	2.6	94.0	3.4
HO97104	5198.0	4.9	88.0	7.1
Okhotsk Sea				
Ok30	2935.4	0.0	87.9	12.1
HO97150	5806.5	0.0	94.4	5.6

Standing stock and stage composition at Site H are annual means (±95% CI for the former is in parentheses). *: 0–1000 m depth.

Other areas

At most stations, population sizes of the C2–C6 in the 0–2000 m water column were closely comparable with those at Site H (Table II). In the eastern subarctic Pacific (OS97120 and OS97130) and the Japan Sea (C08, I09 and J07), the population sizes were significantly less than that at Site H.

The predominant stage was C5 at most stations, although C2–C4 were abundant in the central subarctic Pacific (OS97097) and northern Gulf of Alaska (OS97130), and C6 in the southern Japan Sea (I09, J07) where population sizes were markedly less. However, these differences between stations may be attributed to dissimilar sampling seasons and explained if the life cycle of *N. plumchrus* (cf. Figure 4) is taken into account.

Vertical distribution

Site H

C2–C4 occurred mainly in the top 250 m throughout the year (Figure 5). C5 showed the widest vertical distribution and their distribution patterns varied markedly with

season. A large part of the C5 population was found below 500 m from September 1996 to April 1997 and October 1997. In June–July 1997 when chlorophyll *a* concentrations were high (Figure 2), the C5 were concentrated in the surface layer, after which they sank gradually to great depth. Both adult males and females resided at depths below 250 m throughout the year, and no appreciable differences were evident between the sexes.

Other areas

C2–C4 occurred mainly in the upper 250 m (Figure 6) as at Site H. Most C5 were below 250 m in the western subarctic Pacific (HO96098, 19 and HO96107), Okhotsk Sea (Ok30 and HO97150) and Japan Sea (C08 and I09). C5 showed a surface or bimodal depth distribution in the central (OS97097) and eastern (OS97120 and OS97130) subarctic Pacific and part of the Japan Sea (HO97103/97104) where C2–C4 co-occurred. All these vertical distribution patterns of C5 were observed in summer–winter at Site H. Adult males and females were restricted to deeper waters below 250 m at all these stations.
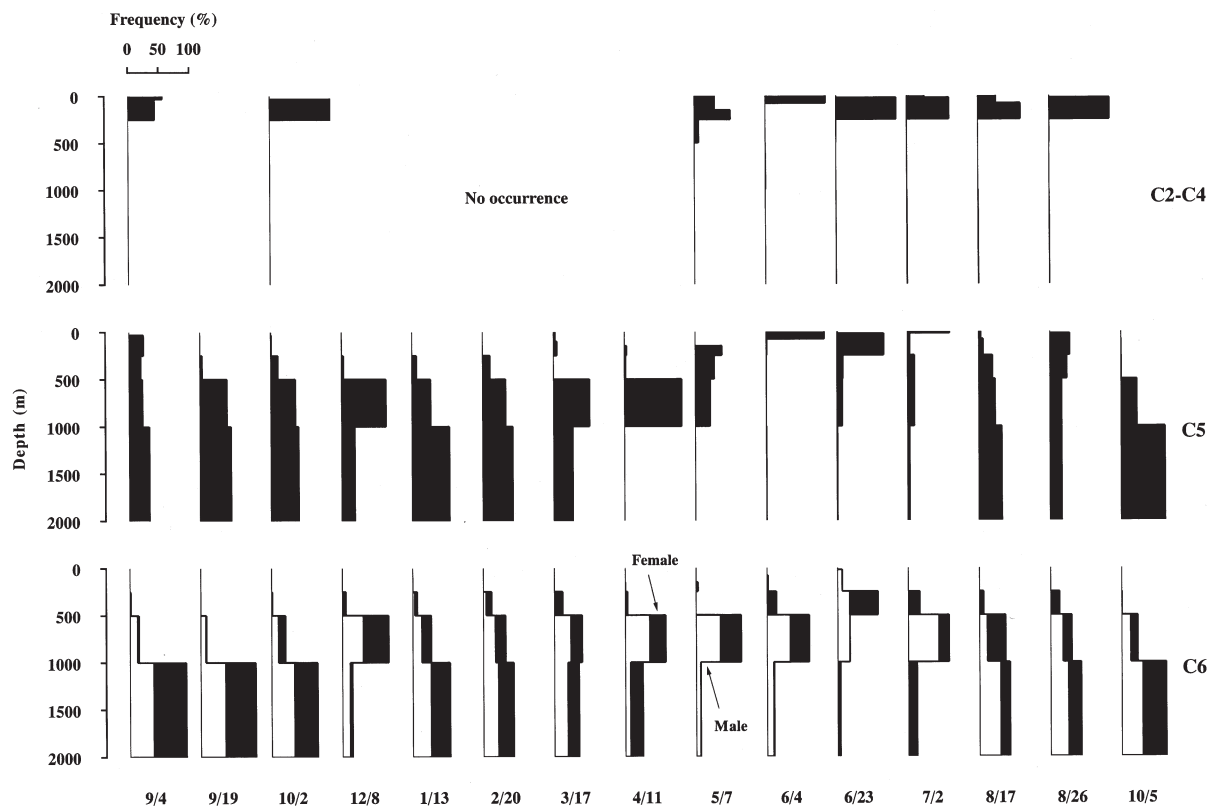

Fig. 5. Seasonal changes in vertical distribution of C2–C4 (**top**), C5 (**middle**) and C6 (**bottom**) of *Neocalanus plumchrus* at Site H from September 1996 to October 1997. Date (month/day) of sampling is on the bottom of each panel.
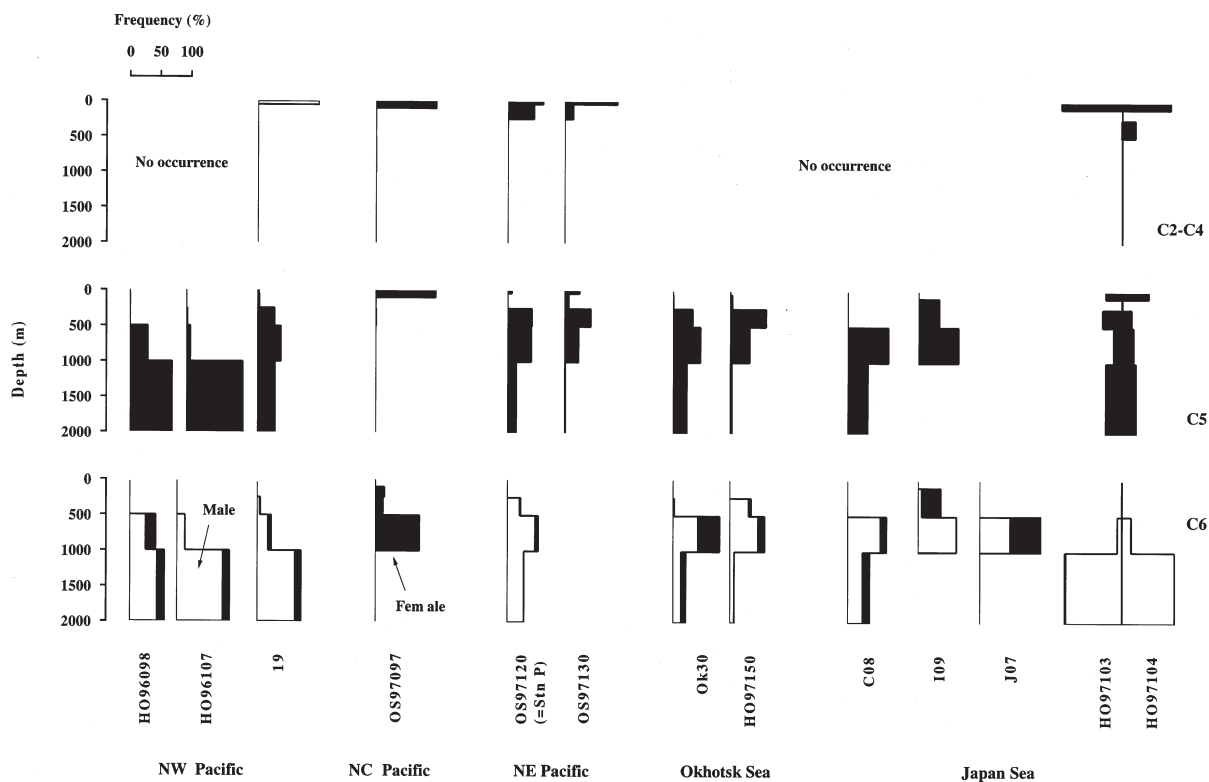
Fig. 6. Regional variations in vertical distribution of C2–C4 (**top**), C5 (**middle**) and C6 (**bottom**) of *Neocalanus plumchrus* at additional stations in the northwest (NW), northcentral (NC) and northeast (NE) Pacific, and Okhotsk and Japan Seas.

Prosome length

Site H

The prosome length distributions of C2–C6 were all uni-modal, with small standard deviations around means (coefficient of variation; C2: 8.3%, C3: 4.8%, C4: 3.5%, C5: 3.7%, C6 male: 3.5%, C6 female: 4.4%) (Figure 7). Prosome length increased 1.4–1.6 times at each molt during development of C2–C5. Compared with C5 prosome length, C6 females were identical (1.0 times; Mann-Whitney *U*-test, $P = 0.0945$), but C6 males were smaller (0.9 times; Mann-Whitney *U*-test, $P < 0.0001$). The prosome lengths of C5, C6 males and females, which occurred throughout the year, were constant over the year. 'Runs'-tests (Tate, 1957) revealed no significant seasonal patterns (i.e. variations were random, $P > 0.05$).

Well-nourished, solid type C5s were predominant throughout the year and increased gradually in May–August 1997 (Figure 8). Poorly-nourished, transparent type C5s and the intermediate type C5s were relatively abundant only in May–June 1997 when early copepodites developed into C5.

Other areas

Since *N. plumchrus* do not feed in the adult stage (Miller *et al.*, 1984), no additional growth occurs in the adults. Therefore, C5 prosome lengths are accurate measures of *N. plumchrus* body size. According to the statistical tests (one-way ANOVA and Scheffe's *F*), specimens from the Oyashio region (Site H and 19) and Okhotsk Sea (Ok30 and HO97150) were significantly larger than those from other regions (Table III). Specimens in the Japan Sea (C08 and HO97103/HO97104) had the smallest prosome lengths. Because of fewer specimens, a similar statistical comparison was not possible for adult males and females, but their regional size patterns were similar to those of the C5s (Table III).

DISCUSSION

Life cycle

Adult females spawn at Site H below 250 m depth largely from October to April of the next year and form the marked C1 abundance peak in early June (Figures 4, 5 and 8). The development of C1 through C5 occurs in the
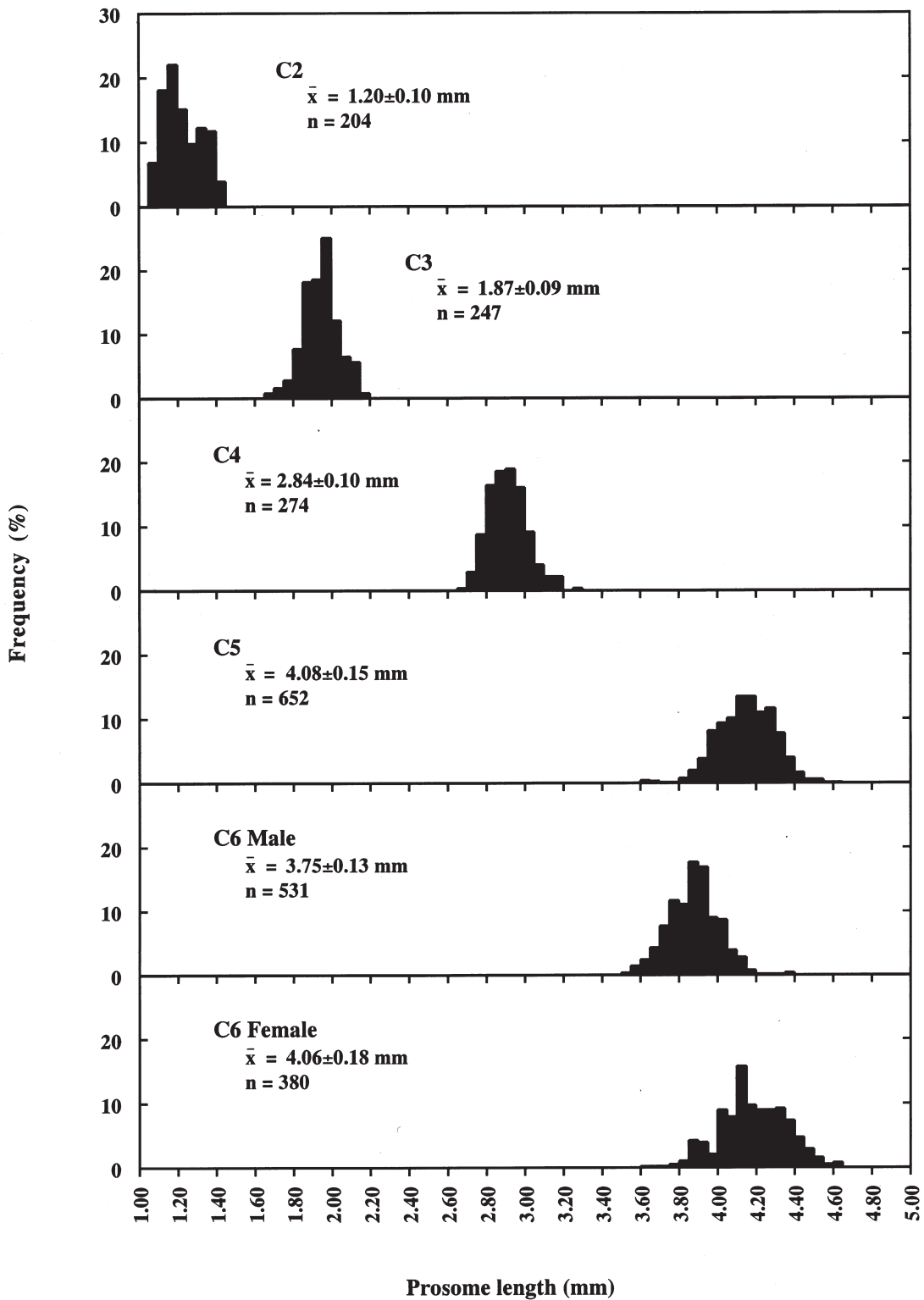
Fig. 7. Frequency distribution histograms of prosome length of each copepodite stage (C2–C6) of *Neocalanus plumchrus* at Site H from September 1996 to October 1997. x̄: annual mean, n: number of specimens measured.
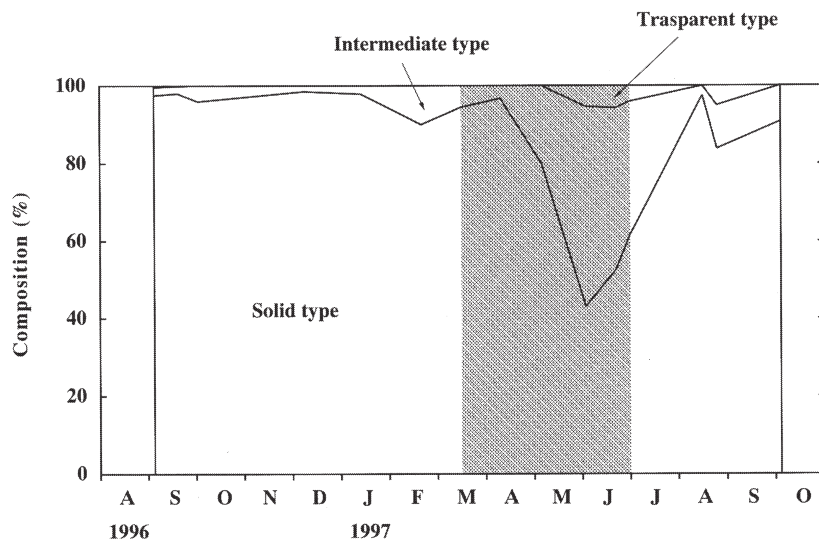
Fig. 8. Seasonal changes in composition of three nutritional states (solid, intermediate and transparent) of the C5 of *Neocalanus plumchrus* at Site H in 0–2000 m depth from September 1996 to October 1997, as judged by the development of musculature and lipid storage after Ikeda *et al.* (Ikeda *et al.*, 1990). Shaded area denotes high chlorophyll period. See text for details.

surface layer late in the phytoplankton bloom. Co-occurrence of C1–C5 abundance peaks in early June suggests that the development of C1–C5 proceeds too fast to resolve intermolt duration with the approximately one-month sampling intervals. The C5 specimens with no or little lipid and undeveloped musculature (transparent and intermediate types, cf. Figure 8) which occurred near the end of phytoplankton bloom had probably just molted. They fill up with lipid and are eventually equipped with full musculature (solid type). They then descend to deep layers after late July and disappear from the surface layer by September. In deep layers, the C5 gradually molt to adulthood, and C6 females commence spawning immediately. The entire range of depths for the ontogenetic vertical migration of *N. plumchrus* is from the surface to 1000–2000 m (a few below 2000 m, Ikeda unpublished data), and their life cycle is annual. These results of the life cycle scenario in the Oyashio region are consistent with the previous study by Tsuda *et al.* (Tsuda *et al.*, 1999) in the same region. However, that study lacked information about stage-specific vertical distribution patterns.

The life cycle of *N. plumchrus* at Station P in the eastern subarctic Pacific studied by Miller and Clemons (Miller and Clemons, 1988) is similar to that of the same species in the Oyashio region. *Neocalanus plumchrus* at Station P spawns in September–February (October–April in the Oyashio region) and the C5 migrate down to depth in late June–August (July–August in the Oyashio region), but these reported differences may be not significant when the

monthly sampling intervals of the present study are taken into account.

There is increasing evidence for regional variations in the life cycle patterns (timing of reproduction, generation length, with/without resting stage, etc.) in various marine planktonic grazing copepods, i.e. *Metridia pacifica* (Hirakawa and Imamura, 1993), *Calanoides acutus* (Atkinson *et al.*, 1997), *Rhincalanus gigas* (Ward *et al.*, 1997), *Calanus finmarchicus* (Planque *et al.*, 1997), *Calanus hyperboreus* (Hirche, 1997), and regional dissimilarities in thermal regimes and phytoplankton production cycles are considered as primary causes. From this point of view, the agreement in the life cycle pattern of *N. plumchrus* in the Oyashio region with that at Station P is unexpected because of large environmental differences between these two regions. At Station P, phytoplankton biomass does not show a clear seasonality throughout the year (0.1–0.6 mg chlorophyll a m^{-3}), although primary production reaches its maximum in May–July (Parsons and Anderson, 1970; Anderson and Munson, 1972; Welschmeyer *et al.*, 1993). In contrast, the occurrence of a phytoplankton bloom (2–9 mg chlorophyll a m^{-3}) in April–May is a regular annual event in the Oyashio region (Kasai *et al.*, 1997, 1998), as was observed at Site H in this study (Figure 2). In addition, habitat temperature of *N. plumchrus* in the Oyashio region is dissimilar to that at Station P for the surface layer [2–12°C at Site H: Figure 2 versus 6–12°C at Station P: Figure 6 in (Miller *et al.*, 1984)] and 200–500 m [2–3°C at Site H: Figure 2 versus 4–5°C at Station P:

Table III: Prosome length (PL: mm) of the C5 and C6 (male and female) of Neocalanus plumchrus in the subarctic North Pacific and its neighboring waters. Regional comparison was made for the C5 only and against the means at Site H (the largest mean), OS97120 (= Stn P), HO97103/HO97104 (the smallest mean) (1-way ANOVA, Scheffe's F)

Area Station code	C5 Mean ± SD	(n)	CV	Compared with Site H	OS97120	HO97103/HO97104	C6 Male Mean ± SD	(n)	C6 Female Mean ± SD	(n)
NW Pacific										
Site H	4.08 ± 0.15	(652)	3.7		+++	+++	3.75 ± 0.13	(531)	4.06 ± 0.18	(380)
19	4.07 ± 0.10	(50)	2.5		+++	+++	3.71 ± 0.11	(50)	4.14 ± 0.15	(8)
HO96098	3.97 ± 0.12	(50)	3.0	−		+++	3.69 ± 0.15	(29)	3.90 ± 0.21	(11)
HO96107	3.91 ± 0.15	(50)	3.0	− − −		++	3.71 ± 0.15	(32)	3.95	(1)
NC Pacific										
OS97097	3.95 ± 0.12	(50)	3.0	− − −		+++	nd		3.63	(2)
NE Pacific										
OS97130	3.88 ± 0.09	(50)	2.3	− − −			nd		nd	
OS97120 (= Stn P)	3.92 ± 0.09	(50)	2.6	− − −		+++	3.57 ± 0.13	(42)	4.03 ± 0.10	(3)
Bering Sea										
W302	3.97 ± 0.11	(43)	3.0	−		+++	3.70 ± 0.14	(4)	nd	
Japan Sea										
C08	3.82 ± 0.11	(50)	2.9	− − −			3.50 ± 0.11	(50)	3.60 ± 0.15	(50)
HO97103/HO97104	3.79 ± 0.11	(100)	2.9	− − −	− − −		3.51 ± 0.12	(100)	nd	
I09	nd		nd				3.54 ± 0.09	(14)	3.85	(1)
J07	nd		nd				3.45	(1)	nd	
Okhotsk Sea										
Ok30	4.03 ± 0.13	(50)	3.2			+++	3.70 ± 0.14	(50)	3.94 ± 0.18	(40)
HO97150	4.01 ± 0.11	(50)	2.7			+++	3.76 ± 0.14	(50)	4.13 ± 0.14	(7)

Number of specimens in parentheses. +, −: significantly greater or smaller, respectively, at $p < 0.05$ (+, −), $p < 0.01$ (++, − −) and $p < 0.001$ (+++, − − −). nd: no data. CV: Coefficient of variation.

Figure 6 in (Miller *et al.*, 1984)]. Considering that temperature and food availability are the major factors affecting developmental time of marine copepods (Mullin and Brooks, 1970; Vidal, 1980a, b), life cycle patterns of *N. plumchrus* should be different between Site H and Station P.

A plausible explanation for the similar life cycle patterns seen for *N. plumchrus* at Site H and Station P is that temperature and food abundance act oppositely at the two sites. Perhaps the negative effect of lower temperature on the development of *N. plumchrus* at Site H is compensated for by the positive effect of higher food concentrations. Such compensatory effects of temperature and food supply have been reported for *Calanoides acutus* in the Southern Ocean (Atkinson *et al.*, 1997). No significant regional differences in ontogenetic vertical migration and life cycle pattern between Site H and Station P populations were noted on another sympatric copepod, *N. cristatus*, by Kobari and Ikeda (Kobari and Ikeda, 1999).

While the matched life cycle schedule of *N. plumchrus* at remote regions (Site H and Station P) in the oceanic subarctic Pacific is confirmed in the present study, somewhat divergent life cycles of the same species have been noted for the populations in the Japan Sea (Miller and Terazaki, 1989) and in the Strait of Georgia [(Fulton, 1973), reanalyzed by (Miller and Clemons, 1988)]. The life cycles of the Japan Sea and Strait of Georgia populations are characterized by reproduction occurring in late December–January (Japan Sea population) or February–March (Strait of Georgia population), and near-surface dominance of late copepodites in April (Japan Sea population) or April–June (Strait of Georgia population). Recently, Mackas *et al.* (Mackas *et al.*, 1998) noted that the dates of surface growth of *N. plumchrus* at Station P vary with the year (from early May to late July, as judged by the date of 50% C5 in the population), and considered interannual ocean climate fluctuations and interannual differences in survival among early versus late copepodites of cohorts as possible underlying mechanisms. Bearing in mind the sampling seasons, life cycle and possible interannual variabilities, the temporal data on vertical distribution (Figure 6) and stage composition (Table II) indicate a wide spatial synchrony in ontogenetic vertical migration/life cycle patterns similar to Site H and Station P populations. At the southern stations in the Japan Sea (I09 and J07), the population size is very small (Table II) and therefore, considered to be expatriated specimens transported from the northern Japan Sea. In the study of Kobari and Ikeda (Kobari and Ikeda ,1999), *N. cristatus* also occurred at these stations in the southern Japan Sea, but its population sizes were markedly smaller than those at Site H.

Body size

Body size of marine planktonic copepods is influenced by water temperature and quality/quantity of food in the laboratory (Vidal, 1980a, b; Escribano and McLaren, 1992) and field (Digby, 1954; Deevey, 1960; Geiger, 1966). In general, lower temperature and higher food supply yield a larger body size of copepods.

The regional comparison of C5 prosome length of *N. plumchrus* revealed the largest specimens in the Oyashio region and the Okhotsk Sea, and the smallest specimens in the northern Japan Sea (Table III). The present results for *N. plumchrus* are different from a similar regional comparison made for *N.cristatus* (Kobari and Ikeda, 1999). For *N. cristatus*, larger specimens were found in the Okhotsk Sea and northern Japan Sea, and smaller specimens from the southern stations in the subarctic Pacific (OS97120 = Station P and HO96107). Kobari and Ikeda (Kobari and Ikeda, 1999) related these regional size variations to temperature and phytoplankton abundance; the larger specimens were due to the lower temperature (Kitani and Shimazaki, 1972; Nishimura, 1969) and higher phytoplankton abundance (Saitoh *et al.*, 1996; Kim *et al.*, 2000), the smaller specimens to the higher temperature (Figure 2) and lower phytoplankton abundance. However, such simple differences in environmental conditions (temperature, phytoplankton abundance) between regions do not explain the regional prosome length variations of *N. plumchrus* in this study. Smaller *N. plumchrus* in the northern Japan Sea may be caused by the shallower distribution of *N. plumchrus* compared with *N. cristatus* [cf. (Mackas *et al.*, 1993)], thereby receiving the widespread influence of the Tsushima Warm Current more effectively than *N. cristatus* in the cold Deep Water during the course of copepodite development. Likewise, copepodite development of *N. plumchrus* in the Okhotsk Sea occurs in the warmer surface layer, rather than in the Cold Intermediate Water, yielding not larger (as in *N. cristatus*) but similar-sized specimens to those at Site H.

Miller *et al.* analyzed interannual size variations in *N. plumchrus* based on a 20-year sample series at Station P, and indicated a negative correlation with year-to-year primary production (new production), but the correlation with year-to-year temperature was insignificant (Miller *et al.*, 1992). Kobari and Ikeda (unpublished) analyzed latitudinal size variations using a 20-year sample series in the central subarctic Pacific, and their regression analysis indicated that the progressive southward reduction in the prosome length of *N. plumchrus* was correlated significantly with southward increase in habitat temperature. With regard to the effect of temperature on the prosome length of *N. plumchrus*, the differences in conclusions between Miller *et al.* (Miller *et al.*, 1992) and Kobari and Ikeda

(unpublished) may be due to the difference in the variations range of each parameter. A narrow range as seen by Miller *et al.* (Miller *et al.*, 1992) may mask the relationship between prosome length and temperature in *N.plumchrus* [prosome length and temperature are 3.58–3.84 mm and 5.7–9.5°C in (Miller *et al.*, 1992) and 3.06–4.12 mm and 3.4–15.2°C in Kobari and Ikeda, unpublished].

The present results on regional size variations of *N. plumchrus* can be compared with similar analyses made at the same stations shown in Figure 1 on other sympatric *Neocalanus* copepods, i.e. *N.cristatus* (Kobari and Ikeda, 1999) and *N. flemingeri* (Kobari and Ikeda, in press). Despite the fact that all these *Neocalanus* spp. are grazers having similar life cycle patterns, they exhibit not only dissimilar regional patterns of prosome length variation but also, different amplitudes, i.e. the ratio between the largest and smallest specimens is only 1.08 (4.08 mm/3.79 mm; Table III) for *N. plumchrus* C5 compared with 1.22 [8.35 mm/6.84 mm; Table III, (Kobari and Ikeda, 1999)] for *N. cristatus* C5 and 1.31 (4.57 mm/3.50 mm; Table III, (Kobari and Ikeda, in press)] for *N. flemingeri* C6 females. In a within-station comparison, the variation of *N. plumchrus* (CV: 2.3–3.8%, Table III) is less than that (2.6–8.7%) for *N. cristatus* and that (3.6–10.1%) for *N. flemingeri*. Thus, among the three co-occurring *Neocalanus* species in the subarctic Pacific and its marginal seas, fluctuations in body size are most marked in *N. flemingeri*, followed by *N.cristatus* and *N. plumchrus*. In the analysis of size variations of *N. plumchrus* and *N. flemingeri* over 20 years at Station P, Miller *et al.* (Miller *et al.*, 1992) also noted that the variation of the former is less than the latter.

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