

日本海におけるNeocalanus flemingeriとNeocalanus plumchrusの生活史

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The Life Histories of *Neocalanus flemingeri* and *Neocalanus plumchrus* in the Sea of Japan^{1), 2)}

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Abstract

Plankton samples from collections at various laboratories in Japan, collected in various years, were selected to construct a "synthetic" seasonal series for the northern Sea of Japan. It was analyzed to determine the life histories of the interzonal copepods *Neocalanus plumchrus* and *Neocalanus flemingeri*. The pattern and timing of life history events for *Neocalanus plumchrus* are similar to those in Georgia Strait; the timing in the two more neritic sites differs in the same way from that in the more oceanic Gulf of Alaska. The fifth copepodite (C5) is the only resting stage. It matures in winter and spawns at depth without feeding. The young develop to the C5 stage by April, fatten and return to the resting phase at depth.

Neocalanus flemingeri has two resting stages in the Sea of Japan, the mated female with a quiescent ovary and the fourth copepodite. Fifth copepodites were never observed at depth in a resting phase. Some or all of the population in the Sea of Japan probably have a two year life cycle. At least some young spawned in a given year develop to C4, rest until the following spring, develop to C5, descend, mature, mate, and rest as females with quiescent ovaries. It is possible, but unresolvable with present data, that part of the population completes the cycle in a single year as previously observed in the Gulf of Alaska.

Introduction

Russian oceanographers have referred to the dominant copepods of the subarctic Pacific region as "interzonal" because they inhabit completely different depth zones during different parts of their life history (VINOGRADOV 1968). This terminology has recently been adopted by CONOVER (1988) in a review of life histories in the calanoid family Calanidae. MILLER et al. (1984) and MILLER and CLEMONS (1988) have shown that there are several varieties of interzonal life history in the vicinity of Station P (50°N, 145°W) in the Gulf of Alaska, essentially a separate variant for each species. Here we develop some evidence that in both *Neocalanus flemingeri* MILLER 1988 and *Neocalanus plumchrus* (MARUKAWA) 1921 the life histories vary between different subregions

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of the subarctic Pacific, while remaining of an interzonal type. We have focused particularly on the Sea of Japan, but a few observations from the Oyashio and Bering Sea will be cited.

Our approach was to examine existing collections at laboratories in Japan of plankton from various sites around the western Pacific. In an ideal approach to this problem we would have complete (or even multiple) annual sample sets from single sites. The entire water column above at least 2000 m would be included, but divided sufficiently in the vertical to distinguish between animals actively feeding at the surface and those in resting phases in the mesopelagic. MILLER and CLEMONS (1988) had the advantage of a sample set taken to such a plan, but no sampling from the western Pacific comes even close. Existing collections from the western Pacific include many samples, but they are scattered among different years and different sites, and they vary in respect to depth range sampled, depth division, mesh size, net type, degree of quantification, and haul configuration. There are parts of the year that are not represented at all. Given these limits we have examined the samples available by comparison to the models developed by MILLER and CLEMONS (1988) for the eastern Pacific. The western samples consistently suggest specific differences from the eastern pattern. Those differences should be taken as hypotheses to be tested against more nearly ideal, seasonal sample sets when those are available.

Methods

Samples from several oceanographic institutions in Japan have been assembled into a "synthetic seasonal series" by combining collections from stations in the northern Sea of Japan (Fig. 1) and representing different parts of the

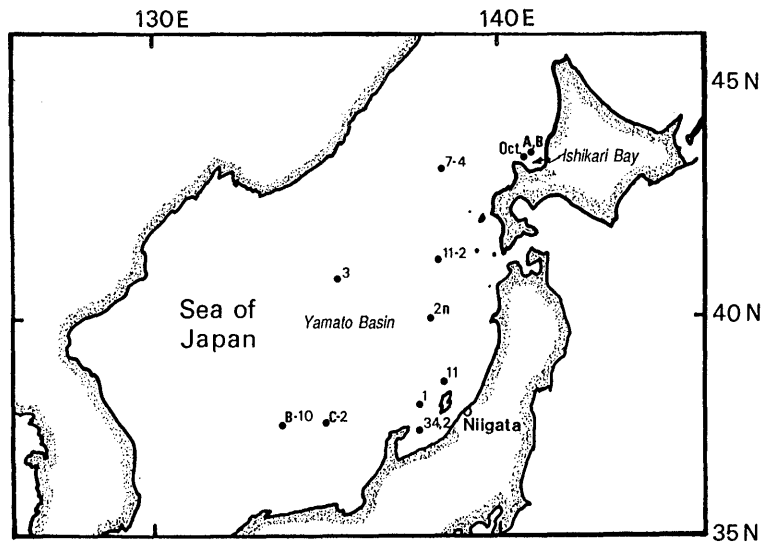


Fig. 1. Locations of stations as listed in Table 1.

synthetic year by samples from any year with a cruise in a given month. Samples examined are described in Table 1.

Samples were examined in toto or subsampled by wide-bore pipette, depending upon sample size and preliminary estimates of the number of *Neocalanus* spp. Individuals were sorted out, identified using the criteria in MILLER (1988), and counted. Ovarian stages were evaluated for females using the definitions in MILLER and CLEMONS (1988), which are repeated here for convenience:

- I. Dormant: ovary small, apparently quiescent. Oviducts not clearly defined.
- II. Developing: ova enlarging in ovary and beginning to fill the oviducts anterior to the ovary.
- III. Actively spawning: large, translucent ova fill the oviducts including diverticular pouches between the lateral muscle bundles of the thoracic segments.
- IV. Spent: expanded oviducts mostly empty. Typically there are a few ova scattered along the tract.

Illustrations of these stages are in MILLER and CLEMONS (1988).

As in the Gulf of Alaska, *N. flemingeri* has all of these stages, and *N. plumchrus* has only Stages III and IV after maturation. The equivalent of Stage II appears to occur in *N. plumchrus* at the end of the C5 stage, when there is substantial development of ovaries and some filling of oviducts in the female. A photograph of a C5 specimen undergoing this ovarian maturation is shown in Fig. 2.

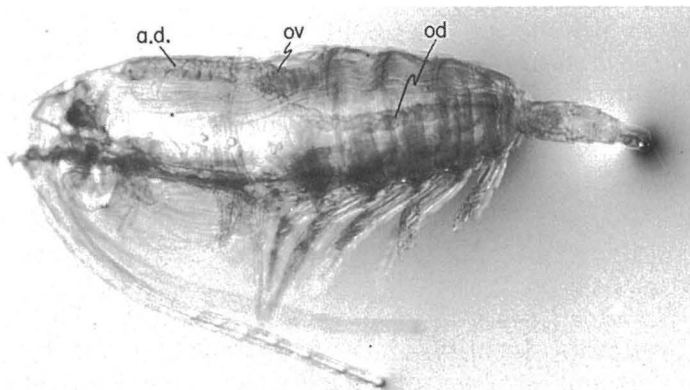


Fig. 2. Fifth copepodite of *Neocalanus plumchrus* (MARUKAWA) with maturing ovary (ov), anterior diverticulae (a.d.), and oviducts (od).

TABLE 1. SAMPLES FROM THE SEA OF JAPAN

Date	Collecting Organization	Cruise Station Designation Name	Location
11 Sept. 1984	ORI	KH-84-3 7-4	42° 50.1' N; 138° 13.0' E
13 Sept. 1984	ORI	KH-84-3 11-2	41° 22.0' N; 138° 13.0' E
11 Oct. 1987	HCFES	— *	43° 28.7' N; 140° 44.7' E
5 Dec. 1986	JSRFRL	MZ-86-19 34	37° 29.9' N; 137° 50.1' E
5 Dec. 1987	JSRFRL	MZ-87-# 2	37° 29.6' N; 137° 49.0' E
21 Dec. 1981	JSRFRL	MZ-81-09 11	38° 12' N; 138° 33' E
16 Jan. 1982	JSRFRL	MZ-82-1 11	38° 12.0' N; 138° 35.3' E
24 Feb. 1982	JSRFRL	MZ-82-9 11	38° 12.3' N; 138° 32.3' E
1 Mar. 1985	JSRFRL	MZ-85-01 1	37° 58.8' N; 137° 40.9' E
8 Mar. 1982	JSRFRL	MZ-82-03 11	38° 12.4' N; 138° 39.3' E
9 Apr. 1985	JSRFRL	MZ-85-2 B10	37° 36.2' N; 133° 54.3' E
11 Apr. 1984	JSRFRL	MZ-84-3 C2	37° 40.0' N; 134° 59.9' E
21 Apr. 1981	HCFES	M8104 A*	43° 33.0' N; 140° 56.0' E
10-11 Jun. 1987	ORI	KT-87-7 2N	39° 58.6' N; 138° 01' E
15 Jun. 1981	HCFES	M8112 B*	43° 30' N; 140° 50' E
15 Jul. 1976	ORI	KH-76-3 3	40° 56.8' N; 135° 20.4' E

*Ishikari Bay Station

Collecting Organizations: ORI—Ocean Research Institute, University of Tokyo; Tokyo.
HCFES—Hokkaido Central Fisheries Experimental Station; Yoichi. JSRFRL—Japan Sea Regional Fisheries Research Laboratory; Niigata.

Results

It is convenient to take September as a starting point, since at that season both species are in resting phases. The samples available are from stratified horizontal (as opposed to oblique) tows which cover much of the expected depth range, but which do not necessarily include the zones of maximum density. Thus, the relative proportions of stages may be misrepresented somewhat. However, the samples are numerous and cover a great range in depth. Abundance estimates are given in Table 2.

Neocalanus plumchrus in its resting phase is entirely C5. By mid-September there had been maturation of males from the resting stock amounting to about 10–15% of the total. This is not particularly different from the eastern Pacific pattern, although perhaps maturation was slightly more advanced by this date in 1980 at Station P.

Neocalanus flemingeri rests as both females and C4. The latter amount to 43–51% of the total. Identity of these C4 was checked by dissection of mandibles from subsamples of ten or so individuals at each depth. The shape of the ventral tooth, the most reliable qualitative character through the pre-adult copepodite stages (MILLER 1988), was determined by compound microscope. By contrast, virtually all resting individuals in the Gulf of Alaska were females. For both species the two stations gave close agreement in density estimates and stage composition. A single horizontal tow at 500 m from off-

Net Type	Mesh Size (mm)	Depths (m)
MTD horizontal	0.333	0, 200, 500, 700, 1000, 1500
MTD horizontal	0.333	0, 200, 500, 700, 1000, 1500, 2000, 2500
MTD horizontal	0.350	500
R80 Twin	0.925	900-0
MTD horizontal	0.333	0, 50, 100, 150, 200, 250, 300, 400, 500, 600, 700, 800
R80 Twin	0.925	500-0
R80 Twin	0.925	500-0
R80 Twin	0.925	453-0
R80 Twin	0.925	1000-0
R80 Twin	0.925	470-0
R80 Twin	0.925	1000-0 (oblique)
R80 Twin	0.925	500-0 (oblique)
MTD horizontal	0.350	20
MTD horizontal	0.333	0, 10, 25, 50, 100, 500, 600, 750, 1000, 1500
MTD horizontal	0.350	70
MTD horizontal	0.333	0, 50, 100, 200, 300, 400, 500, 600, 800, 1000

Nets: MTD is a 56 cm ring net towed from a wire clamp. It is lowered open with the ship stopped, towed mostly at a 45° wire angle, and closed by messenger (MOTODA 1971). R80 Twin is a double ring net hauled vertically.

shore of Ishikari Bay, Hokkaido, on 11 October 1987 (Table 3) shows essentially the same combination of stages for both species. None of the female *N. flemingeri* were ripening or spawning, and there were no female *N. plumchrus* at all.

For the bulk of the year in the Sea of Japan the samples available were from the Niigata area (Fig. 1), mostly close inshore but including two April samples from the Yamato Basin. Seasonal coverage was from early December through early April. All hauls were made with 0.925 mm mesh, which can be expected to pass all stages smaller than C4 and probably some C4 as well. However, significant numbers of C4 were retained. Most estimates are from vertical or oblique hauls extending from 500, 900, or 1000 m to the surface. An MTD series from 5 December 1987 was also examined, but it had too few specimen to be of much use, probably because of its inshore location. Without stratified sampling it is impossible to tell whether copepodites are feeding or resting, although reasonable inferences often can be made. A new observation helps with these assignments. Namely, C4 of *N. flemingeri* and C5 of *N. plumchrus* that are in a diapause phase may be full of oil, and thus have fed substantially and for a prolonged time, but their mandibular gnathobases retain the "post-molt figure" described by MILLER and NIELSEN (1988). Thus, most specimens with large oil sacs and a post-molt mandible can be assumed to have been in the resting phase at capture. This is an imperfect criterion, since a fatty C4 may in fact have just molted from a fatty C3. On the other hand, the criterion is very good, since few or no C3 carry

TABLE 2a. MTD SERIES ESTIMATES FOR 11 SEPTEMBER 1984

Depth	Temp. (°C)	Volume (m ³)	No. Individuals (1500m ³) ⁻¹						
			<i>N. plumchrus</i>			<i>N. flemingeri</i>			
			C5	males	females	C4	C5	males	females-I
0	17.9	153	"14"	0	0	0	0	0	0
200	0.81	476	367	0	0	1325	0	0	0
500	0.49	475	379	1*	0	539	0	2	1061
700	0.36	611	260	47	0	101	0	0	723
1000	0.23	439	427	40	1*	1*	0	0	46
1500	0.15	431	210	148	0	0	0	0	6

* Entire sample sorted

TABLE 2b. MTD SERIES ESTIMATES FOR 13 SEPTEMBER 1984

Depth	Temp. (°C)	Volume (m ³)	No. Individuals (1500m ³) ⁻¹						
			<i>N. plumchrus</i>			<i>N. flemingeri</i>			
			C5	males	females	C4	C5	males	females-I
0	19.1	33	0	0	0	0	0	0	0
200	0.77	242	975	0	0	1271	0	0	0
500	0.52	1040	1055	0	0	434	0	0	1301
700	0.36	1038	919	10	0	30	0	0	899
1000	0.22	591	999	47	0	0	0	0	55
1500	0.14	613	319	282	0	0	0	0	2
2000	0.15	691	286	3	0	0	0	0	0
2500	0.18	751	205	3	0	0	0	0	2

TABLE 3. MTD SAMPLE ESTIMATES FOR 11 OCTOBER 1987 OFF ISHIKARI BAY

Depth	Total Abundance in sample, No. Individuals					
	<i>N. plumchrus</i>			<i>N. flemingeri</i>		
	C5	males	females	C4	C5	females(I)
500m	448	48	0	352	1	528

enough lipid to have a full, resting phase oil sac immediately after molt to C4. Data for vertical hauls on 9 dates are given in Table 4.

In this entire series *N. plumchrus* was very sparsely represented. The sampling sites are at the extreme southern edge of the distribution for both species, where spring and summer surface flow (the Tsushima Warm Current) is northward along the Japan coast. It carries a southern plankton fauna dominated by *Calanus sinicus* (ITO et al. 1979, NEMOTO et al. 1979). Among subarctic copepods large *Metridia* sp. were dominant. Most of the few specimens identified as *N. plumchrus* were in the final maturation and spawning

TABLE 4. ESTIMATES FOR R 80 TWIN NET, NIIGATA SERIES

Date	Depth Range (m)	Estimated No. Individuals (haul) ⁻¹											
		<i>N. plumchrus</i>				<i>N. flemingeri</i>							
		C4	C5	males	females	C4	C5	males	females	I	II	III	IV
5 Dec. 1986	900-0	3	3	8	0	0	24	0	0	2	9	21	4
21 Dec. 1981	500-0	—*	—*	—*	4	2	—*	—*	—*	0	0	3	0
16 Jan. 1982	500-0	5	7	1	9	1	28	0	0	1	3	6	3
24 Feb. 1982	453-0	5	0	0	0	0	16	0	0	0	0	0	4
1 Mar. 1985	1000-0	12	2	1	8	20	230	4	0	0	0	4	42
9 Apr. 1985	1000-0	75	0	0	2	5	523	7	0	0	0	4	13
11 Apr. 1984	500-0	46	41	0	0	0	46	178	0	0	0	0	0

—* Stage was present, but not estimated.

phases. This suggests that spawning occurs in late December and January and is mostly complete by February. There were two inconsistencies from the general pattern in this part of the seasonal series. First, these were a few *N. plumchrus* C4 in the December to February samples. These may be from some fall spawning, as is observed in the Gulf of Alaska (MILLER and CLEMONS 1988), or they may be an alternate resting phase comparable to the diapause C4 of *N. flemingeri*. Second, there were spawning females present on 1 March 1985, but they were absent in late February 1982. However, the March sample extended much deeper, and most spawning individuals of this species are expected to be below 500 m (MILLER and CLEMONS 1988). There were six females in the 500 m MTD from close inshore on 5 December 1987 (Cruise MZ-87-#, Station 2, data not tabled here), five of them spawning, one spent. There were also 3 C5 and 3 males. However, the bulk of that MTD series was poorly preserved and of little use. All in all, the sparse data suggest mid-winter spawning. Abundant C4, and in 1984 C5, began to appear in early April samples. Estimates for C4 are crude, since a jaw dissection was required for each specimen and very small subsamples (N=20) were used to apportion the total count of C4's between the species.

Throughout the period represented from vertical hauls off Niigata, the numerically dominant stage of *N. flemingeri* was C4. In the 5 December MTD series this stage was present at 200, 250, and 300 m at densities of 41, 28, and 68 m⁻³, respectively. Female spawning was in progress with dominance of Stage III by early December in 1986, earlier by 1.5 months than the schedule for the Gulf of Alaska in 1980. There were too few females in the 5 December MTD series to evaluate the reproductive or depth distribution condition of the stock. Spawning persisted into January, but at later dates the bulk of specimens were spent. The C4 resting stage appears to have continued until April or later. Without depth-stratified samples, it is not possible to ascertain whether these were still resting phase individuals from the prior year, or were new C4 from the winter spawn. However, most retained the post-

molt mandibular figure throughout, and so it seems that most of the C4 were still the resting phase stock established the previous year. The sample for 11 April 1984 showed a majority shift to C5. This had not occurred on 9 April in 1985. Mid-April may be the time that the resting C4 begin to advance again. As a preliminary guess, it appears that the resting C4 remain at rest approximately until the C4 of the new generation are also advancing to C5.

April and June MTD samples from the shelf edge at Ishikari Bay, while not ideal in location, provide useful data (Table 5). These samples were selected from more complete vertical series. In the April series all *Neocalanus* spp. were in the surface layer, and the 20 m sample was typical. This samples was enormous, about 6 liters settled volume from a 20 minute tow (speed not precisely known, but about 1.5 knots) with a 56 cm net. While no quantitative estimate was made, April in Ishikari Bay is consistently the time of very large abundance of *Neocalanus* spp. (M. KOTORI, personal communication). In the June series the surface layer was about 14°C (KOTORI 1983), and copepods in near surface samples were mostly *Centropages* sp. and *Calanus* sp. with *Neocalanus* spp. absent. The 70 m temperature was 8°C, and the sample from that depth had some *Neocalanus* spp. mixed with larger numbers of these other genera.

On 21 April at Ishikari Bay *N. plumchrus* was present as C2 through C5 with older stage progressively more abundant. Presumably the center of the annual cohort had reached C5 with later-spawned or more slowly developing individuals scattered back to C2. Specimens in the 15 June sample were all emaciated; they clearly had not reached a condition for entering a resting phase and were isolated from food in the surface. The main stock of resting phase individuals derived from the April peak at the surface was almost certainly in deeper water.

Neocalanus flemingeri on 21 April was 85% in C4, with small numbers of C3 and C5. On 15 June only one C4 was found. This near absence of the species certainly is due to the shallow sampling.

Table 6 gives data from an MTD series in mid-June 1987. There were large number of *N. plumchrus* copepodites with the age distribution centered at C4. Mostly these copepodites were excluded from the upper samples where temperatures exceeded 12°C. There were virtually no C5 in deeper layers,

TABLE 5. PROPORTIONAL ABUNDANCE OF *N. plumchrus* AND *N. flemingeri* STAGES IN ISHIKARI BAY ON TWO DATES

Date	Depth (m)	Temp. (°C)		Estimates for a small subsample								
				<i>N. plumchrus</i>				<i>N. flemingeri</i>				
				C2	C3	C4	C5	C3	C4	C5		
21 April 1981	20	7.7	count	61	264	352	400	14	120	7		
			%	6	24	33	37	10	85	5		
15 June 1981	70	8.2	count	0	29	65	27	0	1	0		
			%	0	24	54	22	-	-	-		

although they may have been missed in the sampling gap between 100 and 500 m. Adults were represented only by some empty female exoskeletons at depth.

Neocalanus flemingeri was much less abundant than *N. plumchrus* in the mid-June series, and the most abundant stages were C4 and C5 at 500 m. The July MTD data (below) suggest that most of the C4 may have been between these levels. Males were present at 500 m in substantial numbers. The C5 mostly had mandibles prepared for the maturation molt (MILLER and NIELSEN 1988), so that maturation was certainly imminent.

The seasonal series is completed by an MTD profile from the south edge of the Japan Basin on 15 July (Table 7). At this time the summer thermal pattern typical of the Sea of Japan (ZENKEVITCH 1963) was fully established. A very thin surface layer warmed to 17 °C was underlain by a very sharp thermocline at 20 to 40 m with extremely cold and, therefore, nearly isothermal water from 80 m to the bottom. There were no *Neocalanus* spp. in the surface or at 10 m, but at 30 to 100 m there were substantial numbers. There was a large population of *N. plumchrus* between the thermocline and 75 m, certainly still in the euphotic zone. The bulk of the population was in C3 and C4, presumably still feeding and growing in preparation for a resting phase. There was also a substantial stock of C5 scattered right down the water column with a very few males at 600 m and deeper. The shallow stock of C5 had much smaller oil sacs than the deep stock, and it is reasonable to conclude that those found deep had accumulated sufficient reserves for entering the resting phase, whereas the shallow stock had not.

On 15 July *Neocalanus flemingeri* had a large stock of C4 at depths from 75 m to 300 m with a few scattered below that. These animals were mostly well stocked with lipid and had the post-molt figure in the mandible, suggestive of a resting phase. A few C5 were found in middle depths among much larger numbers of *N. plumchrus* C5. However, most of the older stock of *N. flemingeri* were males and Stage I (ovary quiescent) females. The main stocks of adults of both sexes were at 500 to 800 m.

TABLE 6. MTD SERIES ESTIMATES FOR 11 JUNE 1987

Depth	Temp. (°C)	Vol. (m ³)	No. Individuals (500m ³) ⁻¹									
			<i>N. plumchrus</i>				<i>N. flemingeri</i>					
			C2	C3	C4	C5	male	female-IV	C4	C5	male	female-IV
0	12.5	304	0	0	1229	270	0	0	0	0	0	0
10	12.5	483	0	373	4327	476	0	0	0	0	0	0
25	9.1	360	4222	61222	95528	3694	0	0	0	0	0	0
50	3.3	357	0	29244	98599	2241	0	0	0	0	0	0
100	1.5	405	0	9290	12099	648	0	0	0	130	0	0
500	0.34	357	0	423	759	0	0	0	759	654	231	0
750	0.25	352	0	48	246	0	0	170 *	0	50	0	0
1000	0.17	380	0	0	7	0	1	28 *	0	1	7	4 *
1500	0.14	334	0	0	3	0	0	7 *	1	0	1	0

* Female specimens were only exoskeletons

TABLE 7. MTD SERIES ESTIMATES FOR 15 JULY 1987

Depth	Temp. (°C)	Vol. (m ³)	Number (500m ³) ⁻¹									
			<i>N. plumchrus</i>				<i>N. flemingeri</i>					
			C2	C3	C4	C5	male	female-IV	C4	C5	male	female-IV
0	17.5	91	0	0	0	0	0	0	0	0	0	0
10	16.7	115	0	0	0	0	0	0	0	0	0	0
30	Ca. 7.0	121	112*	58	5620	48376	0	0	0	0	0	0
50	Ca. 4.0	128	2734	33141	54141	8203	0	0	0	0	0	0
75	Ca. 2.0	134	191	1261	3896	1067	0	0	12985	0	0	0
100	1.45	140	0	314	207*	104*	0	0	4189	0	0	0
150	Ca. 1.0	147	0	244*	1880*	306	0	0	28190	0	0	0
200	0.79	153	0	88*	0	588	0	0	32578	63*	0	0
300	0.50	203	0	0	1121*	820	0	0	32515	49*	0	30*
400	0.37	197	0	0	0	812	0	0	1561	0	0	30*
500	0.30	191	0	0	0	1696	0	0	403	0	325	484
600	0.26	186	0	0	0	2145	38*	0	301	0	301	1016
800	0.20	180	0	0	0	2661	81*	0	450	0	19	328
1000	0.16	174	0	0	0	1011	12*	0	445	0	0	20

* Subsample count ≤ 5

Discussion

Description of the Life Histories

Without much more complete sampling we cannot fully characterize the life histories of either *Neocalanus plumchrus* or *Neocalanus flemingeri*. We must take substantial risks in combining data from nearshore and offshore samples, in including data from the very margin of the habitat, and in accepting diverse samplers. So, the following descriptions of life histories must be taken as hypothetical. We advance them to stimulate interest in gathering new data to test their validity.

Neocalanus plumchrus (MARUKAWA)

The basic life history of *N. plumchrus* in the Sea of Japan is the same as elsewhere. It is an interzonal species in which the C5 descends to deep layers for a resting or diapause phase. That is followed by maturation, then reproduction by non-feeding adults without return to near-surface layers. The sequence takes the full year in the Sea of Japan, as elsewhere. Stage progression of *N. plumchrus* in the Sea of Japan is very like that observed by FULTON (1973) in Georgia Strait, and differs in the same way from that at Station P (MILLER and CLEMONS 1988). Specifically, reproduction seems to be more confined to the mid-winter period with faster development in the Sea of Japan and Georgia Strait than in the Gulf of Alaska. Thus, the period in which the late stages of this species dominate the near-surface plankton is April in both of these more neritic regions, on both sides of the Pacific. In the more oceanic Gulf of Alaska *N. plumchrus* is dominant much later, in June and early July.

Surface warming comes earlier in the northern Sea of Japan than in the Gulf of Alaska, but in both regions warming of the surface layer to 11°C or more excludes *N. plumchrus* from the surface (present data, MILLER et al. 1984). In the Sea of Japan this appears frequently to catch large numbers of copepodites unready for descent to the resting phase. These have thin muscles and little oil, and they remain in the cooler layer just below the seasonal thermocline. Whether or not they eventually obtain enough nutrition there to complete development and enter the resting phase is not clear from our data. IKEDA (personal communication) has a substantial data set documenting an identical phenomenon for *Neocalanus cristatus* in the Sea of Japan.

FULTON (cited in CONOVER 1988) has reexamined his samples, confirming that the Georgia Strait population is all or nearly all *N. plumchrus*. He has also sent specimens to us, and we agree with this identification.

Neocalanus flemingeri MILLER

Life history data for *Neocalanus flemingeri* in the Sea of Japan suggest that this species has several options for the warm season resting stage. In autumn a substantial group were resting as adult females with quiescent ovaries (Stage I), but there was a nearly equal number of individuals resting at C4. These C4 were located mostly between 100 to 300 m (Table 7), well above the stock resting as adults from about 500 m downward. Our winter data are few. However, they suggest that most spawning is in December and January, perhaps somewhat earlier than in the Gulf of Alaska. Development of C5 appears to be complete by mid-June, if not before. The resting stock of C4 appears to continue resting during the late winter, after the female stock has commenced to spawn, based on the C4 specimens collected in February and March vertical hauls. Given the available data, there are at least two schemes by which division of the resting population between C4 and adult could arise: 1) The life history takes two years for part of the stock. The winter spawning (early spawners in December, peak spawning in January, and late spawners until April) produces a stock which develops to C4 and C5 by April. Those that only have reached C4 by about May then diapause until roughly the following March and complete development together with the new stock of the following year. Those that reach C5 mature in their first year, in June and July. The new Stage I females from both cohorts rest until winter, then repeat the cycle. See Fig. 3a.

2) The life history consistently takes two years. Spawning peaks in January. The young develop to C4 and enter diapause. The following year they continue to C5 during spring, mature, rest again, and spawn at two years of age. See Fig. 3b.

There are arguments favoring each scheme. The first retains more of the features of the pattern at Station P (MILLER and CLEMONS 1988). If all patterns observed are variants on one inherent to the species and produced by habitat conditions, then this is the more likely explanation of the Sea of Japan data. The second scheme explains the observation that no C5 of *N. flemingeri* were ever seen in the autumn resting stock. Surely in the first scheme some individuals would reach C5 but be unable to fully prepare for matura-

tion. Of course, it is possible that maturation is obligately associated with descent by the C5 stage.

The scheme observed at Station P, where food stocks are certainly low (MILLER et al. 1988) compared to spring production in the Sea of Japan (e.g. NISHIMURA 1969), appears to be a more strict annual life cycle with reproduction in January, maturation in June, and diapause entirely as females. No C4 were observed in autumn below 100 m. It might be expected that stocks in the richer Sea of Japan should be able to complete the life history faster than at Station P, so that two years should not be required to complete development. On the other hand, the duration of development may not depend upon food availability above some limit. Rather, the shorter growing season prior to surface warming in the Sea of Japan might enforce a two year life cycle pattern for some or all of the population.

Comparisons to Previous Data

October observations by MORIOKA (1976) near the Station 1 on Fig. 1 showed a mixture of C4, C5, and C6 of "*C. plumchrus*" and he noted the difference from the observations of FULTON (1973) in Georgia Strait, where only C5 are found in autumn. Almost certainly MORIOKA was seeing the same combination of *N. flemingeri* C4 and females with *N. plumchrus* C5 that we report here. MORIOKA (1976) reported no vertical migration of any of these stages, which agrees with the comparison we have between day and night MTD hauls (Sept. 1984, KH-84-3: Stns. 7-4, noon, and 11-2, midnight). MORIOKA (1981) has examined the development rate of "*C. plumchrus*" in Toyama Bay from 17 March to 9 May. Durations of C2 and C3 were each less than 15 days, considerably less than the 24-25 days observed for C3 and C4 of *N. plumchrus* at Station P by MILLER and NIELSEN (1988). The rich food stocks of a near-shore habitat makes this a reasonable acceleration of growth, but confounding of the species makes interpretation of MORIOKA's (1981) data uncertain.

SEKIGUCHI (1975a, b) conducted an extensive study of the ontogenetic vertical migrations of boreal copepods in the region east of Japan between 35°N and 45°N. He found that "*C. plumchrus*" was present in December as C4 (200 to 500 m), C5 (below 500 m), and C6. This agrees with the pattern we present for the Sea of Japan, if in fact SEKIGUCHI's C4 and C6 were *N. flemingeri* and his C5 *N. plumchrus*. Moreover, we have examined two autumn and one December MTD series (unpublished data), which showed that this combination does indeed pertain in the Oyashio area, as well as the Sea of Japan. Thus, the pattern we observed in the Sea of Japan is not restricted to it.

A small set of June and July data (unpublished) from the western basin of the Bering Sea, where surface waters never reach 11°C, was too early in the season to show whether or not *N. flemingeri* spawns there in August and September as observed by HEINRICH (1957) for a "small phase" of "*C. plumchrus*". However, *N. flemingeri* was mostly at C4 and C5 near the surface in June, and at 200 and 400 m (the deepest samples available) a mixture of C5, males, and females indicated maturation in progress. By July females were mostly in Stage I, but they did show the earliest signs of reproductive activity—development of thin anterior oviduct diverticulae and visible oviducts pos-

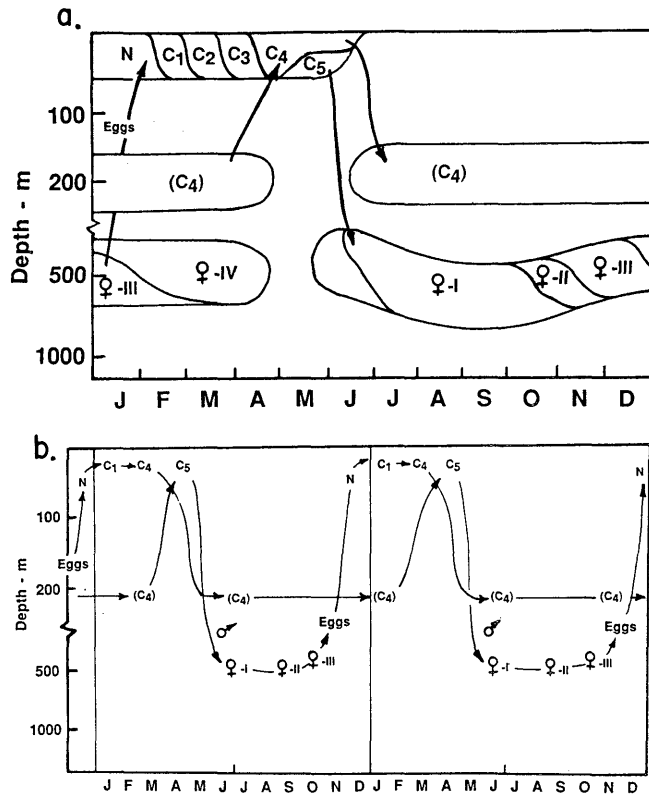


Fig. 3. Hypothetical life history patterns for *Neocalanus flemingeri* in the Sea of Japan. (C₄) designates fourth copepodite in resting phase.

- Part of each year's egg cohort complete development in one year, part in two years.
- All individuals require two years to complete development. There are nearly separate odd-year and even-year cohorts.

teriorly. About 4% were well into Stage II and 2% were spawning (Stage III). Whether this develops into a general, late summer spawning must be examined in August samples which are not at present available. There was no sign of Stage III females in our September MTD series from the Sea of Japan. It makes sense that a late summer brood could develop successfully in the Bering Sea, but not in the rest of the range, because only there does the mixed layer always remain cold enough (below 11 °C) for near-surface feeding.

General

Characters distinguishing *N. flemingeri* from *N. plumchrus* as given in MILLER (1988) held up very well during detailed examination of thousands of specimens from the Sea of Japan, the western gyre of the subarctic Pacific, and the western basin of the Bering Sea. The fifth copepodites examined by MILLER (1988) were exclusively from the Gulf of Alaska or eastern corner of the deep basin of the Bering Sea. However, almost all western specimens of C₅, as well as adults, were unambiguously identified using the morphometric

relations given in that paper. The shape of the ventral tooth proved particularly valuable as a qualitative discriminant character in stages younger than C5.

From the limited studies available, *Neocalanus plumchrus* appears to have two versions of its life history. It always rests in C5. In more coastal, more productive regions spawning is narrowly restricted to mid-winter and development is quite rapid. In the less productive Gulf of Alaska it begins to mature and spawn only a month or two after the growing season is complete and the resting stock is established. The maturation and spawning sequence extends from August until spring. Development is slower with the stock reaching a biomass peak in June or early July. The range of options is limited, but it is not clear how the differences in habitat conditions promote one extreme or the other.

Neocalanus flemingeri is more flexible, something of a life-history virtuoso. It can rest in two stages, C4 and female. It seems possible that it may have two generations per year (if there is late summer spawning in the Bering Sea; HEINRICH 1957), complete a generation in a year (MILLER and CLEMONS 1988), or take two years per generation (present data). This flexibility is reminiscent of that reported by OHMAN et al. (1989) for *Neocalanus tonsus* (BRADY) near New Zealand.

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