

## Local Aggregations of Surface Zooplankton in the Pelagic Regions of the Northern North Pacific, Bering Sea and the Gulf of Alaska\*

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### Summary

In order to investigate local aggregation patterns of the surface macro-zooplankton, a total of ten consecutive series of samples were collected using a submerged pump in the northern North Pacific, Bering Sea and the Gulf of Alaska during the summers of 1985-1987. The consecutive samples comprised 21-36 segmental catches and each segment covered a horizontal sampling distance of 220-400 m. The total wet weight zooplankton biomass for a segmental catch varied from 20 upto 3700 mg/m<sup>3</sup>. Local peaks of the biomass were mainly composed of *Neocalanus plumchrus* of the C<sub>5</sub> stage and *Metridia pacifica* of varying copepodite stages. The highest individual density of the C<sub>5</sub> of *N. plumchrus* and adult *M. pacifica* including the two sexes were 1002 and 1577 inds/m<sup>3</sup>, respectively. These species formed local peaks independently from each other. Number of peaks detected was five in *M. pacifica* and six in *N. plumchrus* over the whole series. The spatial scales of these aggregations were estimated as 220-3700 m for *N. plumchrus* and 320-2900 m for *M. pacifica*. The average spacing distance between the two adjacent aggregations was approximately 8 km. The individual density at the local peaks indicates that all the swarm-like aggregations detected in this survey are supposed to be of precursory gatherings at a stage of forming or fading out from the so-called surface swarms.

### 1. Introduction

Since the studies by Hardy (1935, 1936) the uneven and/or patchy distribution of zooplankton in the horizontal plane has been an interesting study area in the field of marine ecology in relation to both distribution ecology and ecodynamics of zooplankton with respect to fishing and feeding grounds for the planktivorous animals. The zooplankton, when aggregated at an extremely high density, forms a swarm to discolor the surface of seawater. Studying the feeding grounds of the southern sei whales, Kawamura (1974) observed and illustrated the surface swarms of *Calanus tonsus* Brady that aggregated as high as  $\times 10^3$ - $\times 10^4$  inds/m<sup>3</sup> in the waters south of Western Australia while the background density of *C. tonsus* in the same region was less than 1.0 ind/m<sup>3</sup>.

The baleen whales and many other filter feeders rely on their forage mostly from these kinds of zooplankton swarms and/or schools of micronektonic animals. Due to the enormous biomass of aggregating planktons

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together with large number of predatory animals that feed on them, a large part of secondary production is transferred to the animals of higher trophic levels through the local aggregations of zooplankters. Through studies on the food habits of baleen whales in the world oceans (Kawamura, 1980a), it became clear that stomach content of baleen whales is usually composed of a single species as a result of feeding on aggregating zooplankton and such aggregations in relatively shallow layers were composed of a limited number of plankton species. Most of these animals were crustaceans such as copepods and euphausiids in their advanced developmental stages, and they were mainly represented by the herbivorous and omnivorous species. Geographically, the occurrence of surface swarms of zooplankton has been found in the so-called productive boreal seas as well as in the tropical seas such as the Coral Sea, South Pacific, eastern and southwestern Indian oceans (Kawamura, 1980b). Swarms of planktonic crustaceans in the latter was mainly represented by euphausiids (see Roger, 1973a, b). In the northern North Pacific swarms of planktonic crustaceans, such as *Neocalanus plumchrus*, *N. cristatus*, *C. pacificus*, *Metridia pacifica*, several species of euphausiids, amphipods and decapods have been detected (Nemoto, 1963; Omori *et al.* 1972; Parsons, 1972; Kawamura, 1982). However, in the pelagic waters of the north Pacific neither the ambient aspects of occurrence and the status of swarming copepods by the conventional zooplankton tow net nor any discolored water patches due to aggregating zooplankton have been detected except an observation on *Calanus helgolandicus* (= *C. pacificus*) (Kitou, 1956). Omori and Hamner (1982) did not include those copepod species mentioned above in their review on the patchy distribution of marine zooplankton.

The consecutive surface plankton sampling was carried out for four years to estimate the spatial scale and frequency of the occurrence of surface zooplankton aggregations, especially copepods. Among planktonic crustaceans, *N. plumchrus*, *N. cristatus* and *C. pacificus* were the major target species since they were the possible key species from the ecological point of view together with some euphausiid species in the North Pacific Ocean, Okhotsk Sea and Kurile regions (Zenkevitch, 1963; Kos, 1977). One of the consecutive samples collected with a modified Norpac net in 1981 were already published (Kawamura and Hirano, 1985), and their findings corresponded to 'fine' or 'coarse' scaled patches proposed by Haury *et al.* (1978). In the present report, the unevenness of surface zooplankton distributions in relation to spatial scale based on the consecutive samples in the northern North Pacific, Bering Sea and the Gulf of Alaska in the summer from 1985 through 1987 will be discussed.

### Material and Methods

The material was collected during the three cruises on the training ships, 'Oshoro Maru' and 'Hokusei Maru' of Hokkaido University, covering a total of thirteen stations (Fig. 1). The data on sampling are given in Table 1.

The consecutive plankton sampling was conducted using a vortex/semi-vortex submerged pump (Ebara 50DVS6.4S, see Omori, 1985) which has a delivering rate of ca. 200 l/min and a spindle-shaped iso-flow rate distribution as measured in still water tank (Fig. 2). In practice, the pump provided with an additional lead weight was hung into the sea and was fixed a towing rope from the upstream side to keep the pump at a depth of 1–5 m. The ship trawled at a speed of ca. 1.5–2.0 kt. The sampling was started at 1 hr or more after the sunset. The location of sampling was determined simply by checking the occurrence of *N. plumchrus* in the catches with a Norpac net. The water being delivered onto the ship's deck was allowed for a 5-min filtration (ca. 1.0 m<sup>3</sup> of water filtered) with a small sampling conical net of pylon #60 netting (0.3 mm apertures). The

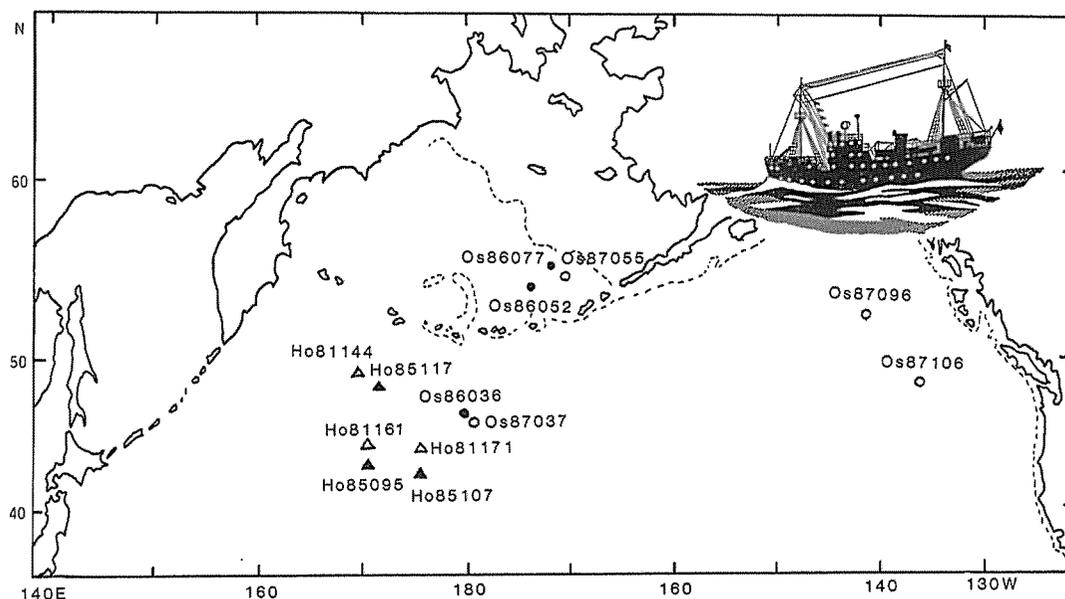


Fig. 1. Map showing the stations for consecutive plankton samplings. Results for the catches in 1981 (Ho81144, 81161 and Ho81171) were previously reported (see Kawamura and Hirano, 1985).

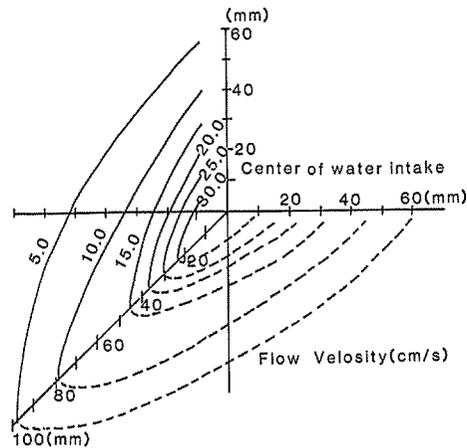
Table 1. Data on Consecutive Plankton Sampling

No.	Year	Date	Sta.*	Time	Total distance sampled (km)	Average distance per sample (m)	Depth (m)	No. of segment samples
1	1985	July 19	Ho85095	2037-2230	6.74	321	2.0	21
2	1985	July 27	Ho85107	2000-2206	7.30	332	1.0-1.5	22
3	1985	August 2	Ho85117	1959-2203	7.82	326	1.5	24
4	1986	June 18	Os86036	2127-0032	8.15	220	1.0-2.0	37
5	1986	June 26	Os86052	2247-0147	8.91	247	1.0-1.5	36
6	1986	July 6	Os86077	2149-0049	8.96	249	3.0	36
7	1987	June 18	Os87037	2315-0120	9.30	372	3.0-4.0	25
8	1987	June 26	Os87055	2035-2250	10.0	400	4.0	25
9	1987	July 17	Os87096	2028-2232	8.87	355	5.0	25
10	1987	July 22	Os87106	2159-0028	12.04**	502	5.0	24

\*) For location of sampling station, see Fac. Fish. Hokkaido Univ. (1988).

\*\*) Over estimation due to trouble during sampling.

number of consecutive sampling series in each year was 3, but 4 in 1987. Each consecutive sampling series consisted of 22-37 segmental catches, each of which covered a horizontal distance of 220-500 m. The sampling depth varied between 1.0-5.0 m. Samples retained on the filter cone were fixed by a 10% buffered formalin solution. The wet weight and individual number of selected species were obtained without sub-sampling.



**Fig. 2.** Distribution of the velocity magnitude for pumping water across the two sections around the water intake of vortex/semi-vortex submerged pump (Ebara 50DVS6.4S). Contour interval is 5.0 cm/sec.

Surface temperature and salinity were monitored during the course of consecutive samplings and no notable fluctuation that may explain the variations of zooplankton concentration were found.

## Results

### 1. Biomass Distributions

Zooplankton biomass (wet weight  $\text{mg}/\text{m}^3$ ) for segmental catch was at a level of several hundreds  $\text{mg}/\text{m}^3$  in most series of catches (Table 2), but it showed considerable degree of variations from year-to-year and from one consecutive sample series to another within a short distance (Fig. 3). In several samples, i.e., Ho85117 and Os87096, a small fluctuation was found throughout the segments in a range of less than 2–3 fold between upper and lower extremes, while in a pronounced unevenness of more than 80 fold was recorded. It was interesting to

**Table 2.** The Coefficient of Variation (CV) and Lloyd Index (LI) in Total Wet Weight Biomass of Zooplankton through the Consecutive Catch Series in the Surface Waters ( $\text{mg}/\text{m}^3$ )

No.	Sta.	SD	$\bar{x}$	CV	LI
1	Ho85095	553	590	0.94	1.88
2	85107	1170	670	1.75	4.05
3	85117	193	870	0.22	1.05
4	Os86036	155	303	0.51	1.26
5	86052	125	130	0.96	1.92
6	86077	87	68	1.28	2.62
7	Os87037	972	1889	0.52	1.24
8	87055	472	479	0.98	1.97
9	87096	110	427	0.26	1.06
10	87106	53	89	0.60	1.34

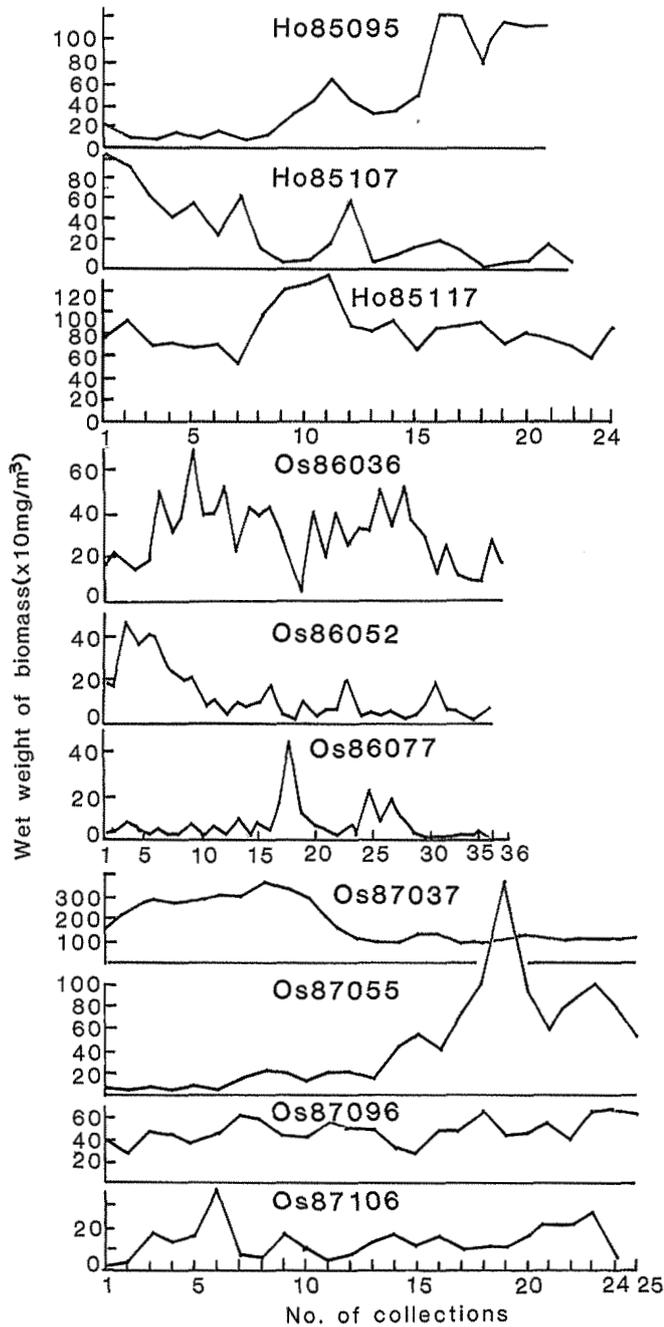


Fig. 3. Horizontal changes in the total zooplankton wet weight biomass in consecutive plankton samplings. Note changed scale in the collection segments for the 1986 catches.

note that many less prominent local peaks occurred, each of which was usually isolated and rarely encompassed over the sequential catches. The coefficient of variation (CV:  $S.D./\bar{x}$ ) of the total biomass was in a range of 0.22 and 1.75, meaning that the biomass of surface zooplankton in terms of wet weight distribute evenly in the study

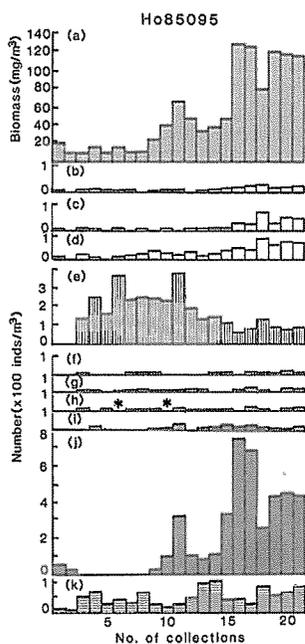


Fig. 4.

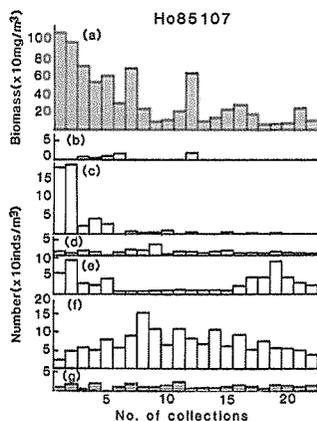


Fig. 5.

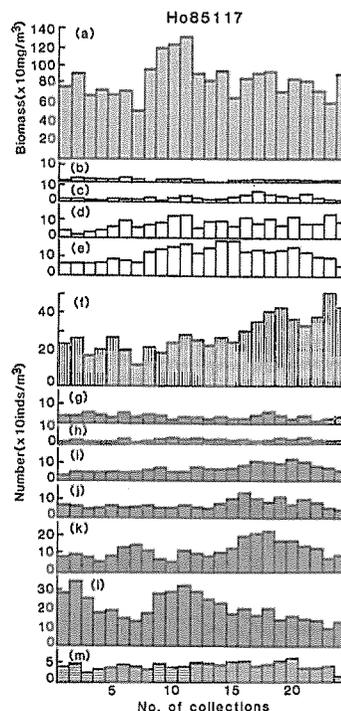


Fig. 6.

Fig. 4. Horizontal changes in the individual number in consecutive catches at Ho85095. Symbols in Figs. 4–13 are respectively; Total biomass (dotted), *N. plumchrus* (hatched), *M. pacifica* (vertical stripe) and *C. pacificus* (horizontal stripe).

(a) Total biomass, (b) Chaetognatha, (c) Amphipoda-hyperiid, (d) Micro-calanoids, (e) *Metridia* spp., (f)–(j) *Neocalanus plumchrus*, C<sub>1</sub>, C<sub>2</sub>, C<sub>3</sub>, C<sub>4</sub> and C<sub>5</sub>, (k) *C. pacificus* (all copepodids). \*: <1 ind./m<sup>3</sup>

Fig. 5. Horizontal changes of the individual number in consecutive catches at Ho85107. (a) Total biomass, (b) *Rhynchonellera gracilis*, (Polychaeta), (c) *Salpa*, small aggregate forms, (d) Appendicularia, (e) Amphipoda-hyperiid (f) Micro-calanoids, (g) *C. pacificus* (all copepodids).

Fig. 6. Horizontal changes in the individual number in consecutive catches at Ho85117.

(a) Total biomass, (b) Chaetognatha, (c) *Limacina*, (d) Amphipoda-hyperiid, (e) Micro-calanoids, (f) *Metridia pacifica* (all copepodids), (g) *E. bungii bungii* (all copepodids), (h)–(l) *N. plumchrus* C<sub>1</sub>–C<sub>5</sub>, (m) *C. pacificus* (all copepodids).

regions. However, the cases such as Ho85095, Ho85107, Os86052, Os86077 and Os87055 showed relatively large CV values and this fact suggested the occurrence of a localized concentration of zooplankton. As the horizontal distance covering each consecutive sampling series from 1985 through 1987 was 6.7–10.0 km (See Table 1), the local concentrations occurring at a single segment or over 2–3 consecutive segments, would be of an order of several hundreds to thousand meters.

## 2. Local Variation in Major Zooplankton Species

### 2-1. Catches in 1985

The distribution pattern in a total of 11 kinds of zooplankton groups or species were examined over the

**Table 3.** The CV and LI Values in Major Zooplankton Taxa for the Consecutive Catches in 1985

Plankton taxa	Ho85095		Ho85107		Ho85117	
	CV	LI	CV	LI	CV	LI
<i>Neocalanus plumchrus</i> C <sub>1</sub>	1.37	2.48	—	—	0.46	1.14
C <sub>2</sub>	0.65	1.31	—	—	0.37	1.12
C <sub>3</sub>	0.96	1.79	—	—	0.32	1.09
C <sub>4</sub>	0.71	1.43	—	—	0.38	1.14
C <sub>5</sub>	1.14	2.29	—	—	0.34	1.11
<i>Calanus pacificus</i> C <sub>2</sub> -C <sub>5</sub>	0.48	1.21	0.45	1.10	0.23	1.03
<i>Metridia pacifica</i> *	0.64	1.40	—	—	0.33	1.11
<i>Eucalanus bungii bungii</i> C <sub>5</sub>	—	—	—	—	0.38	1.11
<i>Parathemisto</i> sp. Ad	1.19	2.01	0.49	1.17	0.42	1.16
Euphausiids furcilia	—	—	—	—	1.14	1.94
<i>Limacina</i>	0.93	1.65	—	—	0.52	1.23
<i>Clione</i>	—	—	—	—	0.66	1.29
<i>Oikopleura</i>	1.22	2.34	0.53	1.19	0.88	1.27
<i>Salpa</i>	—	—	2.34	6.42	—	—
Cnidarians	—	—	0.94	1.75	—	—
Chaetognatha	0.88	1.67	—	—	0.39	1.05

\*) Adult males, females and juveniles.

three consecutive sampling series (Figs. 4-6). Of three series one notable local high concentration of the C<sub>5</sub> stage of *Neocalanus plumchrus* was found at Ho85095 where the CV was 1.14 with the highest individual density of 736 inds/m<sup>3</sup> followed by 665 inds/m<sup>3</sup> (Fig. 4, Table 3). This showed a good coincidence with the pattern of peaks in the total biomass (Fig. 4). As shown in the previous report (Kawamura and Hirano, 1985), the occurrence of C<sub>1</sub>-C<sub>4</sub> of *N. plumchrus* was very poor and their density was far from forming any local aggregation. The fluctuation pattern in *Metridia pacifica* also showed a less pronounced local concentration with a CV value of only 0.64. It must be noted that local peak of each species tends to be different in the timing of appearance within the same consecutive series. *Salpa* at Ho85107 mostly composed of a small developing aggregate forms, also demonstrated a local high concentration with a maximum density of 185 inds/m<sup>3</sup>, and its CV was 2.34 (Fig. 5). The *Salpa* was the only responsible organisms for the two local peaks in biomass distribution. Although C<sub>5</sub> of *N. plumchrus* at Ho85117 occurred at a high density as more than 300 inds/m<sup>3</sup> (max. 344 inds/m<sup>3</sup>), there observed no sign of uneven distributions (CV: 0.34), and the same was true for all copepodids of *Metridia pacifica* (CV: 0.33, max. 504 inds/m<sup>3</sup>, average, 283.2 inds/m<sup>3</sup>) (Fig. 6). All copepodid stages of *Calanus pacificus*, *Eucalanus bungii bungii*, chaetognaths, young hyperiid-amphipods, micro-calanoids and errantia polychaetes showed sporadic occurrences with little sign of unevenness.

## 2-2. Catches in 1986

Of the three consecutive sample series, pronounced local high concentrations were found in C<sub>5</sub> of *N. plumchrus* at Os86036, Os86052 and Os86077, while those of *M. pacifica* were at the latter two stations (Figs. 7-9). The CV values for the local aggregations of C<sub>5</sub> in *N. plumchrus* at three stations were 0.61, 1.42 and

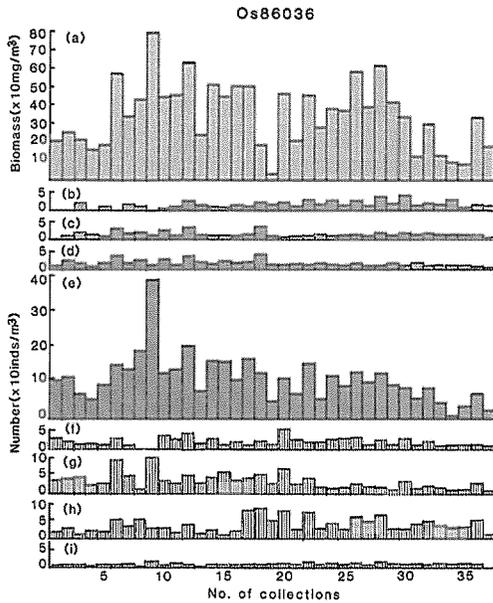


Fig. 7.

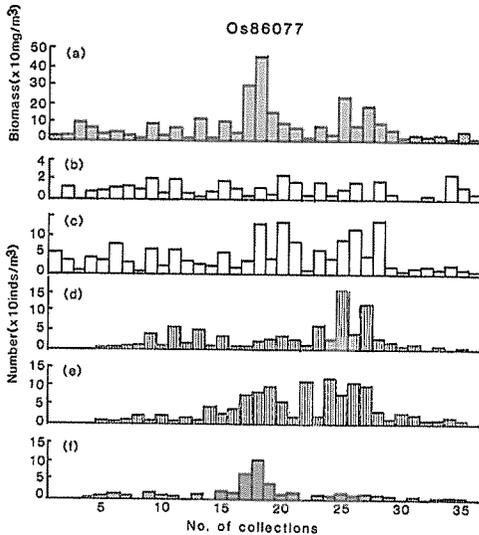


Fig. 9.

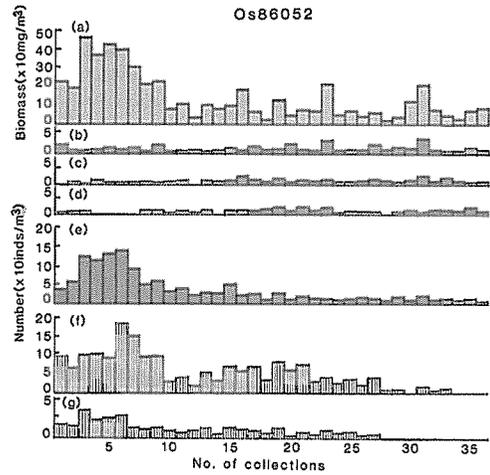


Fig. 8.

Fig. 7. Horizontal changes in the individual number in consecutive catches at Os86036.

(a) Total biomass, (b)–(e) *N. plumchrus*, ( $C_1 + C_2$ )– $C_5$ , (f)–(i) *M. pacifica*, young copepodids, immature males, adult males and females.

Fig. 8. Horizontal changes in the individual number in consecutive catches at Os86052.

(a) Total biomass, (b)–(e) *N. plumchrus* ( $C_1 + C_2$ )– $C_5$ , (f)–(g) *M. pacifica*, immature + adult males and females.

Fig. 9. Horizontal changes in the individual number in consecutive catches at Os86077.

(a) Total biomass, (b) *Acartia longiremis*, adult + copepodids, (c) *Pseudocalanus minutus* and other micro-calanooids, (d)–(e) *M. pacifica*, adult females, and immature + adult males, (f) *N. plumchrus*,  $C_5$ .

2.37, respectively, with the highest concentration of 326 inds/m<sup>3</sup> at Os86036 (Fig. 7, Table 4). Although the  $C_5$  of *N. plumchrus* at Os86036 presented an apparent local peak, the average was high resulting in a relatively low CV value (0.61). *N. plumchrus* of all or part of the developmental stages of copepodids  $C_1$ – $C_4$  occurred throughout the three sampling series, but their concentrations were low compared with  $C_5$  and showed little sign of patchy distribution as it was pointed out in the previous report (Kawamura and Hirano, 1985). Different from the catches in 1985, local peaks by each species generally coincided well with the figures of the total biomass.

**Table 4.** The CV and LI Values in Major Zooplankton Taxa for the Consecutive Catches in 1986

Plankton taxa	Os86036		Os86052		Os86077	
	CV	LI	CV	LI	CV	LI
<i>Neocalanus plumchrus</i> C <sub>1</sub>	0.76	1.48	1.25	1.90	1.19	1.93
C <sub>2</sub>	—	—	0.91	1.68	—	—
C <sub>3</sub>	0.68	1.37	0.91	1.52	—	—
C <sub>4</sub>	0.50	1.17	0.87	1.61	—	—
C <sub>5</sub>	0.61	1.36	1.42	2.99	2.37	6.51
<i>Calanus pacificus</i> C <sub>4</sub> –C <sub>5</sub>	0.71	1.29	—	—	—	—
<i>Metridia pacifica</i> Ad ♀	0.86	1.42	1.21	2.39	1.73	3.92
Ad ♂	0.55	1.28	—	—	—	—
Juv	0.69	1.44	1.36	2.83	1.20	2.40
<i>Eucalanus bungii bungii</i> C <sub>5</sub>	—	—	1.65	3.20	—	—
<i>Acartia longiremis</i>	—	—	1.19	2.13	0.77	1.47
<i>Parathemisto</i> sp.*	—	—	1.03	1.98	2.34	6.36
Euphausiid furcilia	0.56	1.16	—	—	—	—

\*) Adult and juvenile

In *M. pacifica*, the maxima of locally dense concentration were 143 inds/m<sup>3</sup> in adult females, 106 inds/m<sup>3</sup> in younger copepodids plus adult males at Os86077 and 187 inds/m<sup>3</sup> in copepodids plus adult males at Os86052 (Figs. 8–9). *Acartia longiremis* in the Bering Sea at Os86077 was low in concentrations without any sign of local aggregations (CV: 0.796). Although relatively high CV values were found in 1986, the highest concentrations of individuals were by far lower than the possible individual numbers found in such surface swarms of the copepods as in the case in *C. tonsus* (see Kawamura, 1974).

In order to monitor the environmental conditions during the course of consecutive sampling, phytoplankton in the filtrates of zooplankton was collected with a 40 µm net at intervals of once every three zooplankton catches in 1986. The phytoplankton, however, showed no notable correlation to zooplankton abundances. In Os86077 *Ceratium longipes*, *C. bucephalum* and *Rhizosolenia hebetata* dominated throughout the consecutive sampling. *Chaetoceros atlanticum* occurred in two segmental catches, between Nos. 16–18 where a small peak of *N. plumchrus* was observed. However, these phytoplankton distributions are by far unlikely to explain any local concentrations of copepods.

### 2-3. Catches in 1987

Four series of consecutive sampling were conducted (Figs. 10–13). Of these high local concentrations of C<sub>5</sub> of *N. plumchrus* were found at Os87037 where the maximal densities of 1002, 967, and 844 inds/m<sup>3</sup> were recorded and the CV value was 0.61 (Fig. 10, Table 5). C<sub>1</sub>–C<sub>4</sub> of *N. plumchrus* showed high CV values due to a sporadic occurrence at relatively low concentrations and they showed quite different spatial fluctuations from the C<sub>5</sub>, and the same was true for Os87096 (Fig. 12). *C. pacificus* and *E. bungii bungii* also occurred but the CV values were small. The fluctuation of total biomass at Os87037 was well explained by the occurrence of C<sub>5</sub> of *N. plumchrus*. Another similar case was the adult of *M. pacifica* of the two sexes where two pronounced local peaks, 1577 and 772 inds/m<sup>3</sup>, were found (Fig. 11). The CV value for this was 1.52 and 1.78 respectively,

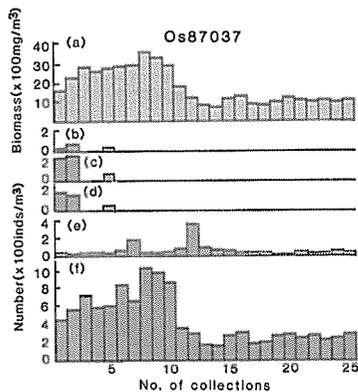


Fig. 10. Horizontal changes in the individual number in consecutive catches at Os87037.  
(a) Total biomass, (b)–(f) *N. plumchrus*, C<sub>1</sub>–C<sub>5</sub>.

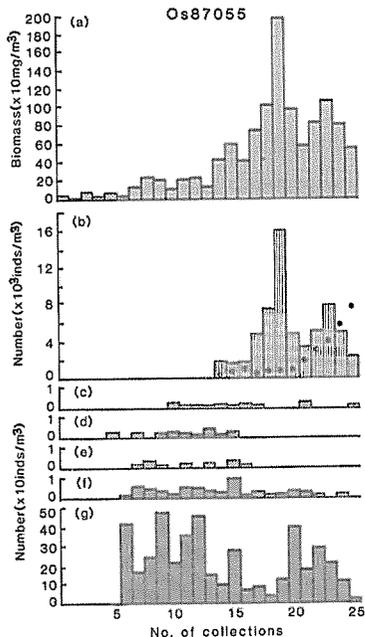


Fig. 11. Horizontal changes in the individual number in consecutive catches at Os87055.  
(a) Total biomass, (b) *M. pacifica*, adults of both sexes and copepodids (solid spots), (c)–(g) *N. plumchrus*, C<sub>1</sub>–C<sub>5</sub>.

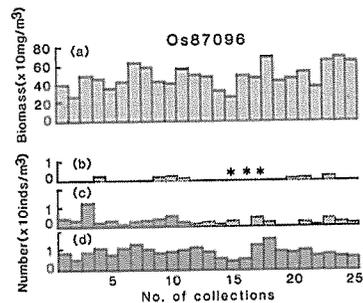


Fig. 12. Horizontal changes in the individual number in consecutive catches at Os87096.  
(a) Total biomass, (b)–(d) *N. plumchrus*, C<sub>3</sub>–C<sub>5</sub>.  
\*: <1 ind./m<sup>3</sup> with a traceable number of C<sub>2</sub>.

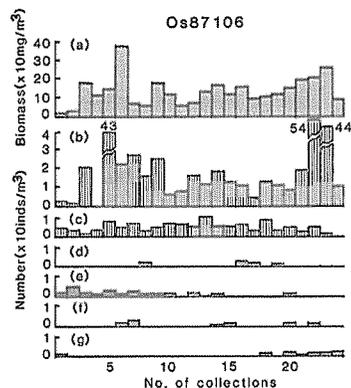


Fig. 13. Horizontal changes in the individual number in consecutive catches at Os87106.  
(a) Total biomass, (b)–(c) *M. pacifica*, adult females and copepodids, (d)–(g) *N. plumchrus*, C<sub>2</sub>–C<sub>5</sub>.

and these concentrations may indicate local aggregations or swarms. The adults of *M. pacifica* occurred in the later half of the consecutive sampling. It must be noted that their local peaks appeared in a different segmental catch from that of *N. plumchrus*. The younger copepodids of *M. pacifica* also showed possible local aggregations with the highest density of 762 inds/m<sup>3</sup> and 1.72 for the CV value at the end of the series. What is

**Table 5.** The CV and LI values in Major Zooplankton Taxa for the Consecutive Catches in 1987

Plankton taxa	Os87037		Os87055		Os87096		Os87106	
	CV	LI	CV	LI	CV	LI	CV	LI
<i>Neocalanus plumchrus</i> C <sub>1</sub>	2.97	9.69	1.42	1.45	—	—	—	—
C <sub>2</sub>	3.42	12.62	1.91	2.57	—	—	1.94	1.73
C <sub>3</sub>	3.02	10.04	1.72	2.16	—	—	1.41	1.78
C <sub>4</sub>	1.31	2.69	1.13	1.83	1.08	1.74	2.30	3.27
C <sub>5</sub>	0.60	1.36	0.94	1.83	0.29	1.07	1.66	1.76
<i>Calanus pacificus</i> C <sub>4</sub> +C <sub>5</sub>	0.33	1.07	1.74	0.91	0.71	1.21	0.59*	1.04*
<i>Metridia pacifica</i> Ad ♀	—	—	—	—	—	—	0.80	1.58
Ad ♂	—	—	1.52	3.30	—	—	—	—
Juv	—	—	1.78	4.16	—	—	0.50	1.05
<i>Eucalanus bungii bungii</i>	0.53	1.14	1.41	2.86	—	—	1.24	1.95
Euphausiid furcilia	1.04	1.56	1.26	2.53	1.20	1.87	0.78	1.22
<i>Limacina</i>	—	—	—	—	—	—	0.71	0.72
<i>Oikopleura</i>	—	—	0.54	1.26	0.83	1.17	2.30	4.14
Chaetognatha	—	—	0.52	1.21	0.76	1.27	0.94	1.66

\*) All copepodites

important here that the local peaks for both adult and copepodids of *M. pacifica* appeared in different segmental catches, that is, local peaks of the total biomass consisted of different component species or developmental stages of the same species as it was observed in the catches at Ho85107 and Ho85117. The catches at Os87106 was poor even in female *M. pacifica* (Fig. 13). However, there was also the case in which the local peak of the total biomass appeared differently from that of major component species. The maximal individual densities by adult and juvenile *M. pacifica* at Os87055 in the Bering Sea recorded  $1.6 \times 10^3$  and  $7.6 \times 10^2$  inds/m<sup>3</sup> respectively, which were perhaps at a level of a possible 'precursory' stage of aggregation before forming surface swarms.

### Discussion

The total biomass of surface zooplankton varied from 20 mg/m<sup>3</sup> upto 3700 mg/m<sup>3</sup> among the ten consecutive catch series. One of the characteristics in the horizontal distribution of zooplankton is a pronounced erratic or frequent zig-zag patterns within a small spatial scale as it was typically shown in Fig. 7. Though spacing of sampling was also variable by each consecutive sampling, it was calculated as 220–400 m. It was seldom that a local high density continued to occur extending over the successive segmental catches, that is, the local high density usually occurred with an isolated peak of one species. When the variation was less pronounced such as the case in Ho85117, Os87037 and Os87096, the coefficient of variation and Lloyd's Index of patchiness (Lloyd, 1967) were small while others marked high values of varying magnitudes (Table 2). It is of great importance that the pronounced change in zooplankton biomass may occur frequently within a fine scaled horizontal space of some hundreds to one thousand meters. Such frequent changes may also exist in a given sub-surface layer such as the case of the *Metridia* species that demonstrate two sub-surface abundance maxima (Hattori, 1989). Another case of slipping out the phase of peak abundance in the vertical distribution of zooplankton in Baffin Bay

has also been observed (Sameoto, 1984). Similar examples based on the LHPR samples may be found elsewhere (i.e., Longhurst, 1967; Wiebe, 1970; Fasham *et al.*, 1985). Of those, Haury and Wiebe (1982) demonstrated a clear horizontal variations at several different sub-surface layers. All these characteristics of distribution in both horizontal and vertical directions may cause the amount of plankton catches of vertical net hauls to vary considerably with the magnitude of upto several hundred percent in terms of the coefficient of variation. A similar fact was also observed in replicate net hauls even at a fixed sampling station (Barnes and Marshall, 1951; Motoda, 1957), which is caused by the spatially small-scale heterogenous distribution of plankton. The biomass of surface zooplankton may shows heterogeneous patterns with local peaks of varying extent (C. V.: 0.22–1.75; Lloyed Index: 1.05–4.05), and their horizontal spatial scale is an order of upto 1–2 km (see Fig. 3 and Table 1).

The local peaks by aggregating zooplanktons are composed of a single or mixed species assemblages. To see the composition of local peaks by zooplankton species throughout the ten consecutive sampling series (Figs. 4–13), a number of species that coexisted with the major component species with varying abundances was found. It seems to be unlikely that the local peaks are formed coincidentally by multiple species, but one major peak-forming species existed like in the case of *N. plumchrus* and *M. pacifica* at Ho85095 and Os87055. Between *N. plumchrus* and *Oithona similis*, it was also demonstrated that a slipping out of the phase in the forming of the local peaks in the consecutive net samples in the Sanriku waters off the northeastern Japan (Kawamura, 1979). The above evidence suggests that the major peak-forming zooplankton species may take over frequently from time to time. These aspects of the distribution pattern may become important in interpreting the local change in the abundance of plankton, particularly in the case of such data as obtained with an electronic counting system (i.e., Mackas *et al.*, 1981), which generally lack specific information. This may be critical especially in the studies of environmental conditions related to fishing and feeding grounds where the quality of feed plankton must be known as well as the total abundance of plankton.

The swarm of planktonic crustaceans in the strict meaning must be monospecific as it became clear by stomach analysis of baleen whales and by the field observations (Kawamura, 1974, 1980a, 1980b, 1982; Nemoto, 1963; Omori *et al.*, 1972). The individual density of C<sub>5</sub> stage of *Calanus tonsus* swarms was found to be in the order of between 10<sup>3</sup>–10<sup>4</sup> inds/m<sup>3</sup> (Kawamura, 1974), Taylor and Taylor (1977) demonstrated that the variance of mean density of animals became small with the increase in the mean density in log-log relationships, and the correlation between the two parameters characteristically varied according the species of the animal tested. In this sense, the density of 10<sup>4</sup> inds/m<sup>3</sup> in *C. tonsus* seems to be ordinary for the swarm of this copepod. The highest concentrations of the C<sub>5</sub> of *N. plumchrus* and mixed copepodids of *M. pacifica* were 1002 inds/m<sup>3</sup> (Os87037) and 1577 inds/m<sup>3</sup> (Os87055), respectively. These values seem to be nearly at the lower extreme of individual density for the surface swarm or swarm-like aggregation. The usual individual density of these two species estimated by the standard Norpac net hauls in the region of present study was found to be a several tenth inds/m<sup>3</sup> (Faculty of Fisheries, Hokkaido Univ., 1960–1963; Kawamura, 1978). These facts and the data by Kawamura and Hirano (1985) may lead to consideration that the concentration of copepods more than several 100 inds/m<sup>3</sup> would be a unusual high density close to a swarm-like aggregation. When a local peak of a major component species occurred, a small local peak of minor species coexisted with varying densities. No locally high and monospecific zooplankton concentrations were observed in the present study. The well established swarm is, on the other hand, monospecific composition as having been known in *Calanus tonsus* (Kawamura, 1974) and *C. finmarchicus* (Wiborg, 1976). Consequently, it is considered that all or a part of local

peaks detected in this study were not exactly a 'swarm', but probably the aggregation at a 'precursory' stage for the swarm formation or on the way of dispersal.

In the previous study through the use of a tow net, Kawamura and Hirano (1985) reported that the local concentrations of *N. plumchrus* occurred with a spatial scale of ca. 1–2 km with a separation distance of 5–6 km. In aggregation of pelagic plankton of many taxonomic groups, the density is usually higher than  $10^2$ – $10^3$  inds/m<sup>3</sup> (Omori and Hamner, 1982). Kawamura (1974) estimated the lowest density of actually swarming *C. tonsus* as  $3.3 \times 10^2$  inds/m<sup>3</sup>, and Motoda and Sato (1949) found that *N. plumchrus* in the northern Japan Sea aggregated at a density of  $5.5 \times 10^2$  inds/m<sup>3</sup>. Assuming a density of ca.  $3 \times 10^2$  inds/m<sup>3</sup> to be a sign of plausible swarm-like aggregation, six segmental catches in *N. plumchrus* and five in *M. pacifica* out of the present ten consecutive sampling series may be designated as aggregation close to what is termed a 'swarm' (see Figs. 4–13). The local peak in most cases occurred in a single segmental catch while it occurred by connecting 2–3 or more consecutive segments in Os87037, Os87055 and Ho85117. As the sampling space of segmental catch was 220 m (Os86036) to 400 m (Os87055) (see Table 1), horizontal spatial scale of an aggregation or swarm can be estimated 200–3700 m for *N. plumchrus* and 320–2900 m for *M. pacifica* (Table 6). During the Trans Pacific Investigations, the local aggregations of *N. cristatus* demonstrated spatial extension of about 200–300 m (Barrachlough *et al.*, 1969). The size of all these aggregations of copepods are categorized into a 1 m–1 km scale which Haury *et al.* (1978) named 'fine scale' patchiness, and are clearly different from the so-called micro-distributions of plankton in which the spatial scale is of an order of upto several tenth meters (i.e., Haury and Wiebe, 1982). Two cases of Os87037 and Ho85117, in which high concentrations of *N. plumchrus* extended over ten (3.7 km) and nine (2.9 km) sampling segments respectively were exceptionally large scale and should be categorized as the 'coarse' aggregations (Haury *et al.*, 1978). Even so, these spatial scales are still small with the generally known zooplankton patchiness in pelagic waters (i.e., Cushing and Tungate, 1963; Steele, 1976).

The total distance covered by the ten consecutive samplings in 1985–1987 amounts 88 km, and swarm-like aggregations numbered 5 for *M. pacifica* and 6 for *N. plumchrus*, which means that aggregation of one of the two copepod species expected to be encountered at every 8 km of sea surface. Analyzing the distribution of catch location of whales and their stomach conditions, Kawamura (1978) obtained 2–22 km as to be the spacing

**Table 6.** Estimated Scale of the Surface Aggregations in the Two Copepod Species

Distance of sampling segment (m)	No. of segments where $>300$ inds/m <sup>3</sup> were caught*	Spatial scale (m)	Frequency of occurrence	Remarks
<i>Neocalanus plumchrus</i>				
220	1	220	1	Cop. C <sub>5</sub>
321	3	963	2	∕
326	1	326	2	∕
372	10	3720	1	∕
<i>Metridia pacifica</i>				
321	1	321	2	All cop.
326	9	2934	1	∕
400	7	2800	1	Ad ♂ + ♀
400	3	1200	1	Cop. imm.

\*) Assumed this value to be the lowest individual density of the surface aggregation of copepods.

distance of *Calanus* swarms in the northwestern North Pacific. The local peaks of *C. finmarchicus* in the North Sea (Mackas *et al.*, 1985) showed very similar occurrences to above-mentioned figures. The occurrence of high concentrations of copepods (more than 100 inds/10 mile) found in the *Continuous Plankton Records* in the North Sea (Rae and Ree, 1947) was also at a spatial scale close to the present estimation. Different from the regions where various oceanic fronts exist, the present study was conducted in monotonous mid-oceanic environment. Consequently, it is unlikely that the small-scale local aggregations of zooplankton formed in the surface layer might be caused by physicochemical conditions. Haury and Wiebe (1982) are of a similar opinion due to their analyses of LHPR samples. Probably the 'fine' or 'coarse' scale aggregations or patchiness as observed in this study are at the spatial patterns of processes in biological interactions relating to mutual attraction between animals of forming aggregative gatherings which Stavn (1971) named 'coactive patterns'. The trends to aggregate, especially at the 5th copepodid stage in herbivorous members of *Neocalanus*, are noteworthy in considering possible causative reasons for the gatherings in contrast to the case in some *Calanus* species which was found in both adult and late copepodid stages. A high concentration or aggregation of *N. cristatus* of any of the copepodid stages was not detected in this study. It was perhaps due to the distribution of dense population of *N. cristatus* at 30–40 m in the northern North Pacific (Barraclough *et al.* 1969).

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## 北部北太平洋，ベーリング海及びアラスカ湾における 表層動物プランクトンの局所的集合

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海洋の表層で大型動物プランクトンが示す局所的な集合分布について、その空間規模と出現頻度の推定を試みた。北太平洋北方寒冷水域において海面下 1-5 m 深に吊下した水中ポンプを用いて合計10回の連続採集を行った。生物量（湿重量）は 20-3700 mg/m<sup>3</sup> の変動を示し、局所的な分布のピークは主として第5期ステージの *Neocalanus plumchrus* と複数の発育ステージからなる *Metridia pacifica* によって形成されていた。出現深度は特定できなかったが、両種は海表層部で高密度の集合分布をし、これによって二次生産が 'mass consumption' に曝される重要なチャンネルとなっている。*N. plumchrus* と *M. pacifica* の最高個体密度は各々1002と 1577 inds/m<sup>3</sup> であった。多くの場合、局所的ピークが連続採集標本の中で出現する位置関係は種間で異なっており、この現象が外部環境による集積ではなく生物の内在的要因によるものであると考えられた。過去のデータから 300 inds/m<sup>3</sup> 程度の個体密度をコペポータの集群状態の最低密度とすれば、今回の全採集シリーズを通じてこれを越えた例は *N. plumchrus* で計6回、*M. pacifica* で計5回であった。これらから *N. plumchrus* の局所的な高密局集合の起こっている空間規模は約 220-3700 m、*M. pacifica* では 320-2900 m 程度であり、このような局所的ピークは海表面 8 km あたり 1回程度起こっている現象と推定された。しかし、見いだされた局所的な高密度の集合は常に複数種からなっており、単一種からなるいわゆる 'swarm' ではなく、swarm の形成過程か、離散過程にあるものではないかと考えられた。