

Distribution and abundance of chaetognaths along 180° longitude in the northern North Pacific Ocean during the summers of 1982 through 1989

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Abstract: The distribution and abundance of chaetognaths along 180° longitude from 37° to 51°N in the northern North Pacific Ocean were investigated using samples collected by vertical hauls from 150 m to the surface with Norpac nets (0.35-mm mesh) during the summers of 1982 through 1989. The study area was divided into 5 subareas from north to south based on seawater temperature and salinity properties: Alaska Current System (AS), Subarctic Current System (SA), Northern Transition Domain (TN), Southern Transition Domain (TS) and Subtropical Current System (ST). Eleven species belonging to 4 genera were identified and the number of species decreased from south to north. The dominant species were *Sagitta elegans* in the AS, *Eukrohnia hamata* in the SA, TN and TS, and *S. scrippsae* in the ST. All maturity stages of *S. elegans* were collected, but young stages predominated in *E. hamata* and *S. scrippsae*. Variance analysis revealed the general importance of variation between years rather than between stations for the abundance of these three species within each subarea. The mean temperature of the top 150 m was investigated as a possible cause of the interannual variation, but was significant only for *Eukrohnia hamata* in the TS and ST, and for *S. elegans* in the ST (negative correlation). Other factors influencing the interannual variations in abundance remain to be resolved. Diel vertical migration is discussed as a possible source of error in estimating catch abundance by vertical hauls from 150 m in depth.

Key words: chaetognath, interannual variation, northern North Pacific

Introduction

Chaetognatha is an exclusively marine phylum of free-living hermaphroditic animals (Pearre 1991). Chaetognaths have a world-wide distribution, and are often the second most important component of zooplankton communities (Ryther 1969; Reeve 1970; Kotori 1972). Chaetognaths prey mainly on copepods, an important component of zooplankton communities (Reeve & Water 1972; Pearre 1973), and are preyed upon by fishes and other predators (David 1955; Reeve 1966). Therefore, chaetognaths are a link in the pelagic food web between sec-

ondary producers and producers at higher trophic levels (Kotori 1976; Bone et al. 1991; Alvarez-Cadena 1993).

In addition to their important role in marine trophodynamics, chaetognaths have been used as biological indicators of water masses. Meek (1928) demonstrated that the occurrence of *Sagitta elegans* off the Northumbrian coast is associated with the intrusion of North Sea water that has mixed with oceanic water. Since then, many studies have examined the distribution of chaetognaths in relation to water masses (Russell 1935; Bieri 1959; LeBrasseur 1959; Sund 1959; Tokioka 1959; Alvaríño 1962, 1964; Kitou 1966a, b, c, 1967a, b; Kotori 1972, 1976).

Information presently available about chaetognaths inhabiting the subarctic Pacific and the Transition Domain near the subtropical North Pacific Current includes their geographical and vertical distribution patterns in relation to oceanic current systems or water masses (Alvaríño 1962; Kotori 1976), and the vertical distribution and life cycles of some species in the eastern North Pacific (Terazaki & Miller 1986). However, little is known about chaetognath populations in the Subarctic Front region of the central northern North Pacific Ocean. The oceanographic structure in the central region of the northern North Pacific (between 40°N and 50°N) in summer changes radically from north to south across the Subarctic Current System, Transition Domain and Subtropical Current System (Dodimead et al. 1963; Favorite et al. 1976) (Fig. 1). Roden et al. (1982) and Anma et al. (1990) further divided the transition domain into north and south regions.

The aim of this study is to clarify the distribution and abundance of chaetognaths in the top 150 m from the subarctic through the subtropical current systems in the North Pacific Ocean. Possible differences in life cycles are examined based on maturity stage composition, and interannual variabilities in abundance are discussed for the dominant species.

Materials and Methods

Zooplankton samplings were carried out along 180° longitude from 37° to 51°N during T/S *Oshoro Maru* cruises in the summers (June–August) of 1982 through 1989 (Fig. 1). Sampling stations were spaced at every 30' latitude (exception: every 15' latitude between 37° and 42°N in 1988), and the total number of sampling stations varied from 16 to 34 per cruise (Table 1).

At each sampling station, a vertical tow was made from 150 m to the surface with a Norpac net (45-cm mouth diameter, 180 cm long with 0.35-mm mesh; Motoda 1957) at a speed of 1 m per second. Sampling precision of this single tow was estimated by using twin-type Norpac nets with 0.35-mm mesh in the summer of 1996. The difference of chaetognath numbers between the two nets was $13.2 \pm 4.8\%$ (mean \pm 95% confidence intervals, $n=22$; Nishiuchi, unpublished data), with a maximum difference of 18%. Because of logistic difficulties, sampling time at each station was not standardized (this source of error is discussed in the "Discussion"). A flowmeter was mounted at the center of the mouth ring of the net to estimate the volume of water filtered. Zooplankton samples were fixed immediately after collection in 5% formalin-seawater buffered with borax.

The maturity stages of chaetognaths were determined following the system of Ghirardelli (1961): Stage 1, no sign of gonads; Stage 2, small ovaries present, but no sign of seminal vesicle; Stage 3, some large ova in ovaries, and seminal vesicle present; Stage 4, large number of large ova, and seminal vesicle filled with sperm.

From 1982 to 1983, hydrographic data (temperature and salinity) were determined at each station from readings of reversing thermometers and Auto-Lab salinometers on seawater samples collected with Nansen bottles. From 1984 to 1989, a CTD system (Neil Brown, Mark

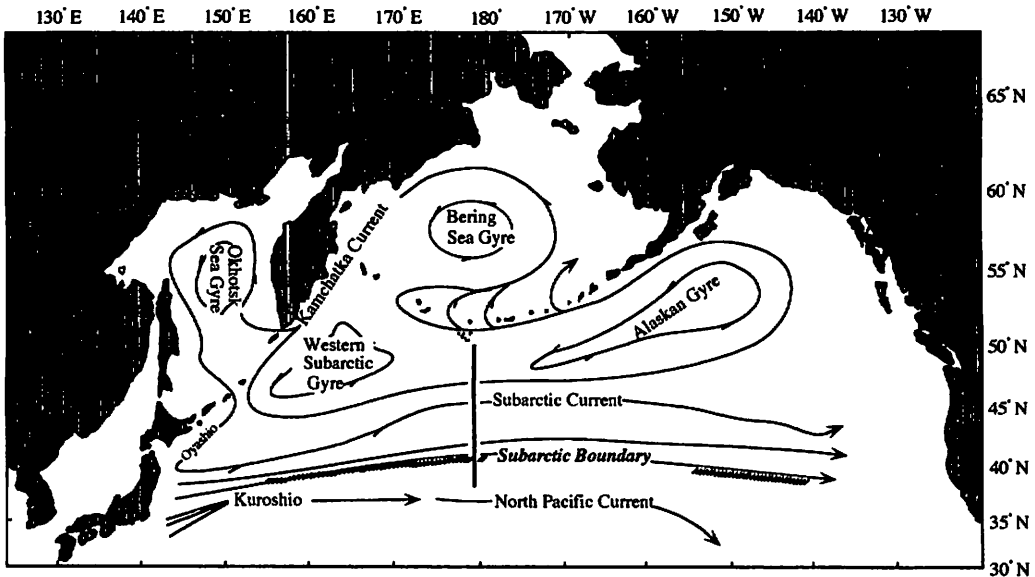


Fig. 1. Schematic representation of the current systems and gyres in the northern North Pacific Ocean (redrawn from Dodimead et al. 1963) and the transect at which the plankton saplings were carried out on the *Oshoro Maru* cruises in the summers of 1982 through 1989.

IIIB) was used. All hydrographic data have been reported in the Data Record of Oceanographic Observation and Exploratory Fisheries No. 26–33 (Hokkaido Univ. 1983–1990).

Results

Hydrography

According to Favorite et al. (1976), the boundary between the Subarctic Current System (designated as subarea SA) and the Transition Domain is clearly delineated by cold water ($<4^{\circ}\text{C}$) below 100-m depth characteristic of the Subarctic Current. The boundary between the Transition Domain and the Subtropical Current System (ST) is denoted by the vertical isohaline of 34.0 and is called the Subarctic Boundary. The Transition Domain is further divided

Table 1. Sampling data, using Norpac nets, for the present study.

Vessel, cruise number	Period	Range of sampling positions (along 180° longitude)	Number of stations
Oshoro Maru III			
90	12–22 June 1982	39°00'–51°00'N	24
95	11–19 June 1983	39°03'–47°30'N	16
Oshoro Maru IV			
3	11–15 June 1984	38°59'–49°00'N	21
8	13–18 June 1985	39°00'–49°00'N	21
13	12–20 June 1986	37°00'–50°00'N	26
18	11–19 June 1987	37°00'–48°00'N	22
23	13–20 June 1988	37°03'–49°00'N	34
28	9–20 June 1989	37°00'–48°59'N	24

into the Northern and Southern Transition Domains (TN and TS, respectively) by a frontal structure of salinity (33.6), called the Transition Front (Anma et al. 1990). These criteria were adopted to characterize the water masses at each sampling station in the present study.

Vertical profiles of temperature and salinity from surface to 600-m depth for each year are shown in Figs 2 and 3. During 1982 to 1989, the position of the boundary between subareas SA and TN was stable and located between 45°30'N and 47°00'N. The position of the Transition Front varied from 42°00'N to 45°30'N. The Transition Front was clearly identified during 1983 to 1985 and 1987 to 1989, but not in 1982 and 1986. The Subarctic Boundary, the southern boundary of the Transition Domain, fluctuated between 41°30'N and 39°00'N. The Subarctic Boundary extended from the surface to 300-m depth and convergences of isotherms and isohalines were clearly seen at depths shallower than 100–150 m.

The intrusion of low salinity water (<32.8) into the epipelagic layer and the well developed halocline seen clearly in northern stations in 1982 and 1988 reveal the influence of the Alaska Current System (AS), which flows westerly from the Gulf of Alaska along the southern edge of the Aleutian Islands (Favorite et al. 1976).

From these observations, the positions of oceanic fronts and boundaries were determined each year (Fig. 4). It is clear that while the boundary between the SA and TN was relatively stable during 1982 through 1989, the Transition Domain expanded to the south, due to the southward shift of the Subarctic Boundary.

Temperatures were integrated over the 0–150-m water column for each subarea. The mean water-mass temperatures over 1982–1989 were 4.2°C for the AS (1982 and 1988), 4.5°C for the SA, 6.4°C for the TN, 8.8°C for the TS, and 11.8°C for the ST. From the temperature anomalies recorded each year (Fig. 5), a year with a positive temperature anomaly was designated as a “warm” year and one with a negative anomaly was designated a “cold” year. From this criterion, 1982–1984 and 1986 were cold years, and 1985 and 1987–1989 were warm years for the ST and TS. Compared with the ST and TS, interannual variations of summer temperature anomalies were less pronounced in the SA and TN. Temperature anomaly data from the AS were too few to analyse its interannual variability.

Chaetognaths

A total of 11 chaetognath species belonging to 4 genera were identified, i.e. *Eukrohnia hamata* (Möbius), *Krohnitta subtilis* (Grassi), *Pterosagitta draco* (Krohn), *Sagitta hexaptera* (d'Orbigny), *S. lyra* (Krohn), *S. scrippsae* (Alvariano), *S. elegans* (Verrill), *S. pseudoserratedentata* (Tokioka), *S. minima* (Grassi), *S. neodecipiens* (Tokioka) and *S. zetesios* (Fowler). The total and mean abundances (individuals/10³ m³) of each species within the 5 designated subareas are summarized in Table 2. Of the 11 species, 2 (*E. hamata* and *S. elegans*) were recorded in the AS and SA, 6 (*E. hamata*, *S. lyra*, *S. scrippsae*, *S. elegans*, *S. neodecipiens* and *S. zetesios*) were recorded in the TN, 9 (*E. hamata*, *K. subtilis*, *S. hexaptera*, *S. lyra*, *S. scrippsae*, *S. elegans*, *S. minima*, *S. neodecipiens* and *S. zetesios*) were recorded in the TS and all species were recorded in the ST.

The most predominant chaetognath species within each subarea were *Sagitta elegans* for the AS (2,409 individuals/10³ m³), *Eukrohnia hamata* for the SA (11,020), TN (5,541), and TS (2,838), and *S. scrippsae* for the ST (1,617). These three predominant species exhibited wide distribution patterns; *E. hamata* and *S. elegans* were found in all subareas, and *S. scrippsae* occurred in three of the five subareas (TN, TS and ST) (Table 2).

Because of their wide distributions and high abundances, *Eukrohnia hamata* and *Sagitta elegans* in subareas SA, TN and TS, and *S. scrippsae* in the TS and ST were selected for analy-

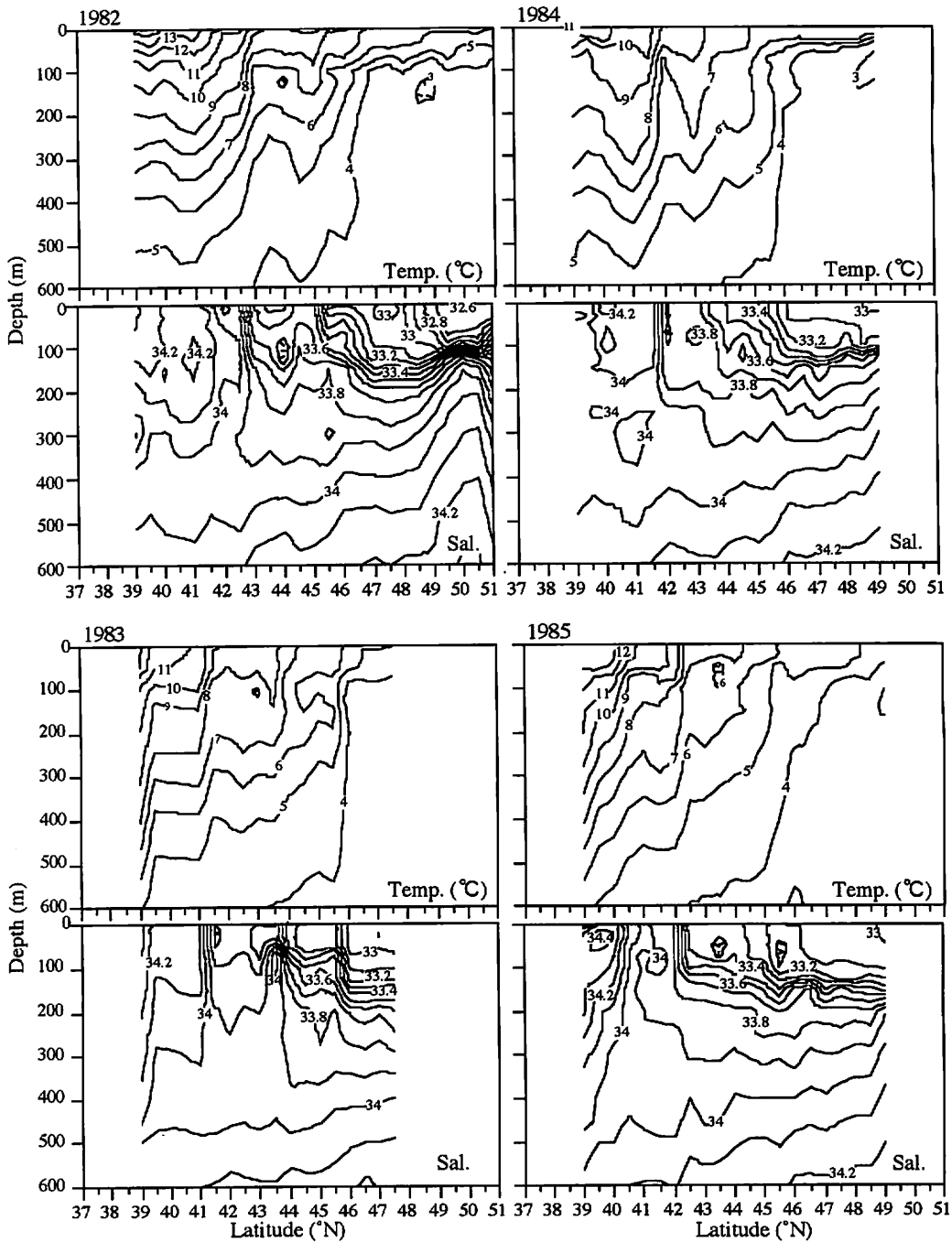


Fig. 2. Vertical sections of temperature and salinity along 180° longitude during the summers of 1982 through 1985.

sis of maturation stage (Fig. 6). The maturation stage of *E. hamata* ranged consistently from stage 1 to stage 3 with stage 2 being the most dominant in all three subareas (grand mean: 75.3%). Between subareas, stage 3 was more numerous for the SA population (mean: 10.7%) than the TN (1.7%) and TS (3.8%) populations. The populations of *S. elegans* included all

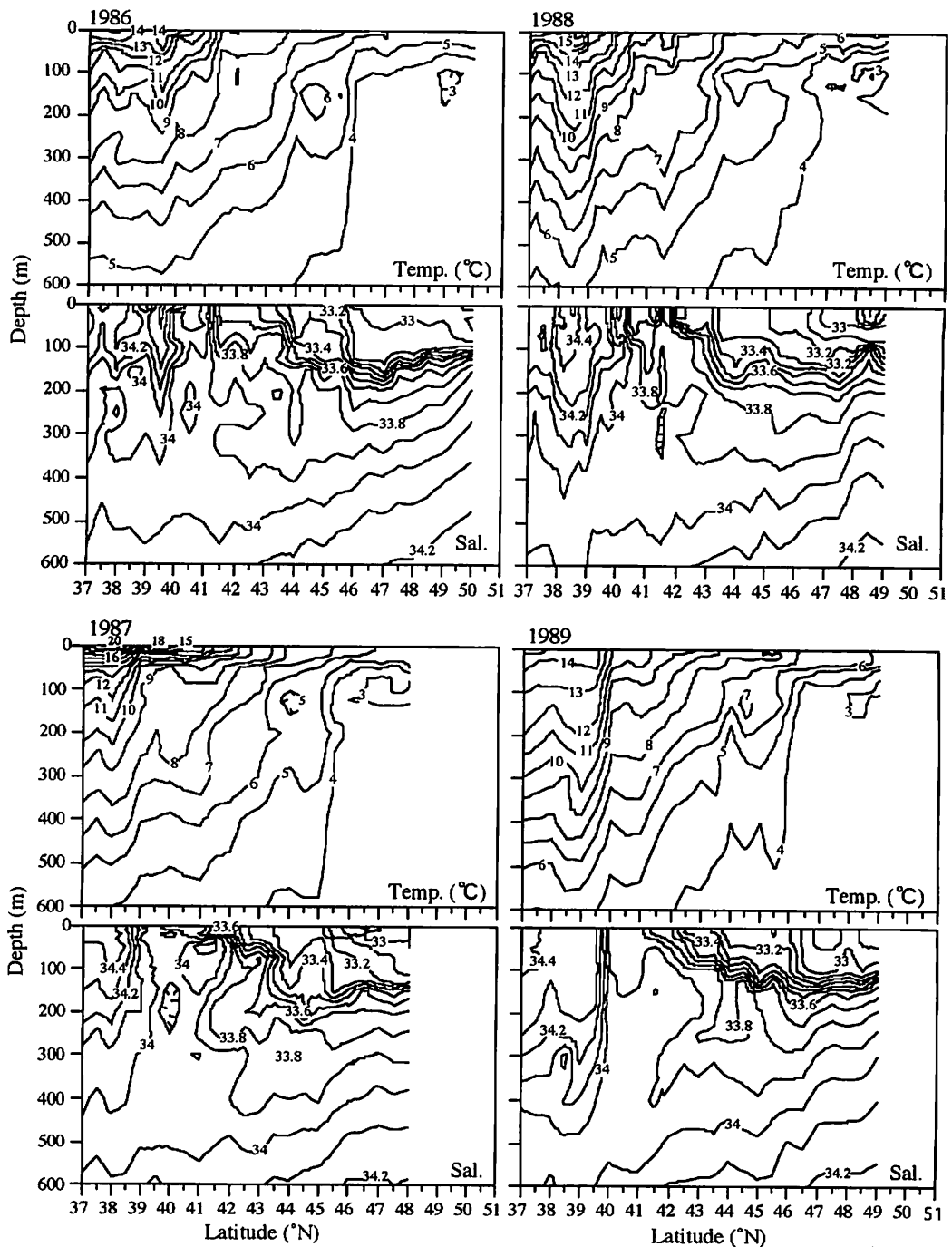


Fig. 3. Vertical sections of temperature and salinity along 180° longitude during the summers of 1986 through 1989.

maturity stages, with stages 1 and 2 most abundant (grand mean; 52.2% and 36.6%, respectively). The percentage of stage 4 specimens was the greatest (6.2%) for the SA population, followed by the TN (2.5%) and TS (1.1%) populations. Like *S. elegans*, all maturity stages

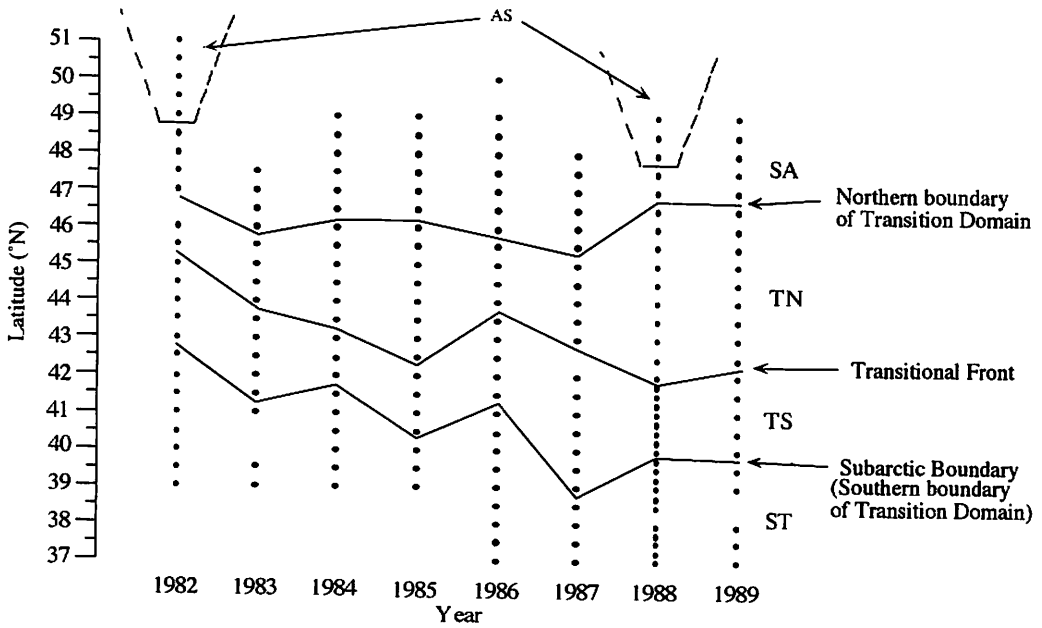


Fig. 4. Interannual changes in the locations of the Alaska Current System (AS), Subarctic Current System (SA), Northern Transition Domain (TN), Southern Transition Domain (TS) and Subtropical Current System (ST) of the northern North Pacific Ocean during the summers of 1982 through 1989. Closed circles show the position of sampling stations.

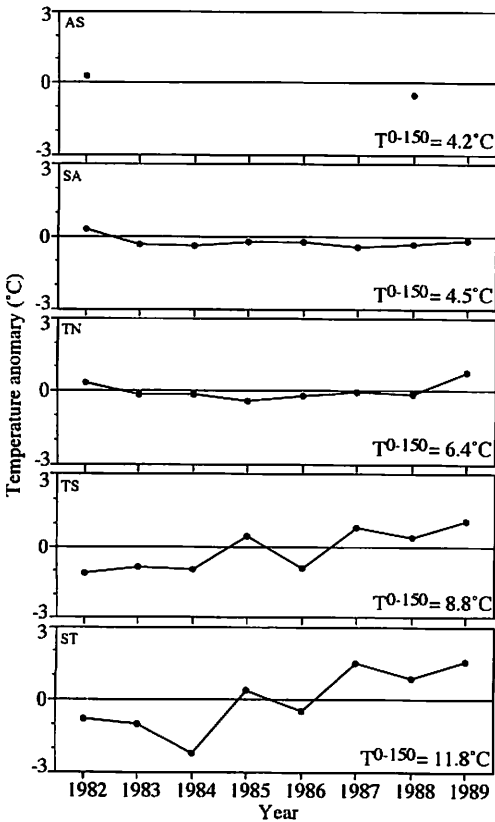


Fig. 5. Interannual variations in temperature anomalies in the top 150 m of the Alaska Current System (AS), Subarctic Current System (SA), Northern Transition Domain (TN), Southern Transition Domain (TS) and Subtropical Current System (ST) during the summers of 1982 through 1989.

Table 2. Abundance (individuals/1000 m³) of chaetognaths in five oceanic subareas in the central region of the northern North Pacific Ocean. All data obtained between 1982 to 1989 are combined (Total), then divided by the total number of stations (Mean). Number in parenthesis shows total number of stations. –; no occurrence.

Oceanic subareas	Species name										
	<i>E. hamata</i>	<i>K. subtilis</i>	<i>P. draco</i>	<i>S. hexaptera</i>	<i>S. lyra</i>	<i>S. scrippsae</i>	<i>S. elegans</i>	<i>S. pseudoserrato-</i> <i>dentata</i>	<i>S. minima</i>	<i>S. neodecipiens</i>	<i>S. zetesios</i>
Alaska Current System (8)											
Positive stations	5	–	–	–	–	–	8	–	–	–	–
Total	2154	–	–	–	–	–	19276	–	–	–	–
Mean	269	–	–	–	–	–	2409	–	–	–	–
Subarctic Current System (41)											
Positive stations	41	–	–	–	–	–	40	–	–	–	–
Total	473850	–	–	–	–	–	120735	–	–	–	–
Mean	11020	–	–	–	–	–	2808	–	–	–	–
Northern Transition Domain (48)											
Positive stations	48	–	–	–	1	20	48	–	–	1	1
Total	254891	–	–	–	66	7870	48747	–	–	77	102
Mean	5541	–	–	–	1	171	1060	–	–	2	2
Southern Transition Domain (42)											
Positive stations	42	3	–	2	7	42	41	–	4	10	5
Total	119189	296	–	206	1005	81011	38708	–	275	2534	528
Mean	2838	7	–	5	24	1929	922	–	7	63	13
Subtropic Current System (49)											
Positive stations	35	8	5	3	23	47	22	7	20	8	2
Total	26988	596	394	236	3699	79226	9807	797	3754	1310	164
Mean	551	12	8	5	75	1617	200	16	78	27	3

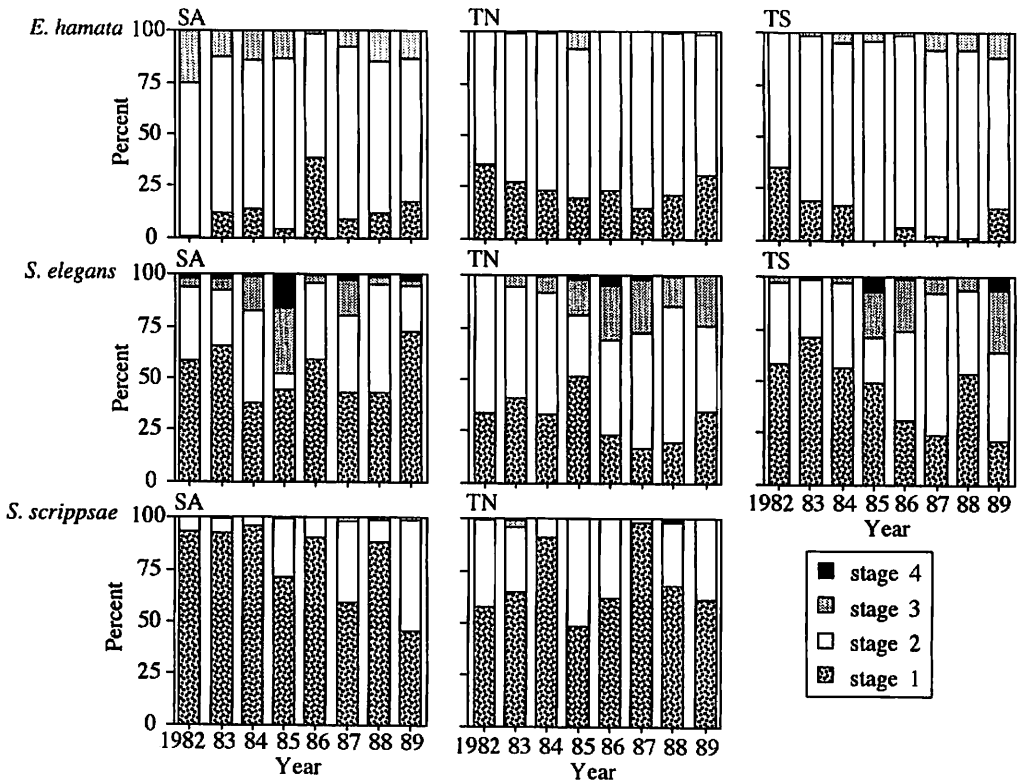


Fig. 6. Interannual variations in maturation stage compositions of *Eukrohnia hamata*, *Sagitta elegans* and *S. scrippsae* in the Subarctic Current System (SA), Northern Transition Domain (TN), Southern Transition Domain (TS) and Subtropical Current System (ST) during the summers of 1982 through 1989.

were observed for *S. scrippsae*. Maturity stages 1 and 2 were dominant (grand mean: 72.4% and 26.8%, respectively) and stage 4 was rare (<0.1%).

Interannual variations in the abundance of *Eukrohnia hamata* and *Sagitta elegans* in subareas SA, TN, TS and ST, and that of *S. scrippsae* in subareas TN, TS and ST are shown in Fig. 7. Variance analysis (two-way ANOVA) was performed to quantify the relative contribution of year-to-year and station-to-station variations to the observed (total) variations in the numerical abundance data for each species (Table 3). Year-to-year variation was the only significant source of variation for *E. hamata* in the SA and ST, *S. elegans* in the SA, TS and ST, and *S. scrippsae* in the ST. Although both year-to-year and station-to-station variations were significant sources of variation, the former was more important for *E. hamata* in the TN and the reverse was the case for *S. scrippsae* in the TN. These two sources of variation were not significant for *E. hamata* in the TS, *S. elegans* in the TN, or *S. scrippsae* in the TS.

The correlation between the abundance of *Eukrohnia hamata*, *Sagitta elegans* and *S. scrippsae* and the mean temperature in the top 150 m was investigated. For this purpose, data sets with *F*-values greater for year-to-year variation than station-to-station variation in Table 3 were selected. A significant negative correlation with mean temperature was found for *E. hamata* in the TS and ST, and for *S. elegans* in the ST (Table 4).

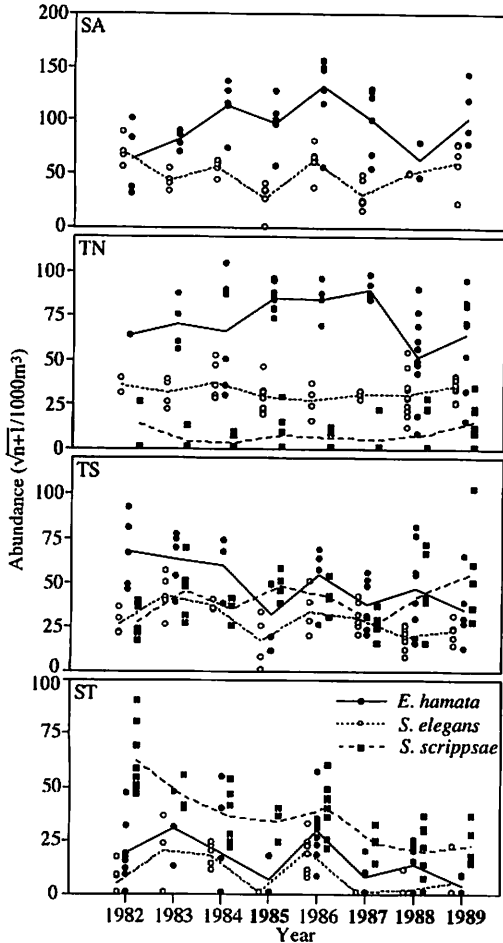


Fig 7. Interannual variabilities in the numerical abundances of *Eukrohnia hamata*, *Sagitta elegans* and *S. scrippsae* in the Subarctic Current System (SA), Northern Transition Domain (TN), Southern Transition Domain (TS) and Subtropical Current System (ST) during the summers of 1982 through 1989. Warm years in the ST and TS are denoted by bold face type.

Discussion

Many chaetognath species undertake diel vertical migrations (i.e., ascending at night and descending in daytime) (Kotori 1972; Pearre 1973; Terazaki & Marumo 1979; Terazaki 1992). Since the sampling time was not standardized in this study, it may be argued that the present numerical abundance data used for the analysis of regional and interannual variabilities include errors caused by vertical migration. Kotori (1976) noted that the entire population of *Sagitta elegans* in the northern North Pacific (50°N, 155°W) was most abundant at 25-m depth during daylight hours and at the surface during the night. At another station in the northern North Pacific (44°N, 150°E), Terazaki & Marumo (1979) observed that the diel vertical migration of *S. elegans* was most extensive for older stages and the change in depth was more than 100 m. Juvenile specimens, the largest component of the population, vertically migrated only a short distance (10–30 m) from <50-m depth during the day to the surface at night. In contrast to the largely epipelagic distribution of *S. elegans*, *Eukrohnia hamata* lives in deeper waters. In the northern North Pacific, the population maxima have been found at about 200-m depth during both day and night (Kotori 1976), suggesting that no appreciable diel migration occurs. Terazaki (1992) investigated the diel vertical migration of *S. scrippsae* in a Kuroshio warm core ring and found that the population was distributed broadly from the

Table 3. Variance analysis (two way ANOVA) for the abundance $[(n+1)^{1/2}/1000 \text{ m}^3]$ of *E. hamata*, *S. elegans* and *S. scrippsae*. SS: sum of squares. df: degree of freedom. MS: mean square. *: $p < 0.05$ **: $p < 0.01$.

Species	Subarea	Source of variation	SS	df	MS	F-value
<i>E. hamata</i>	SA	Year	13182.7	7	1883.2	2.67*
		Station	7691.0	7	1098.7	1.56
		Error	18325.5	26	704.8	
	TN	Year	8053.4	7	1150.5	3.45**
		Station	7316.9	9	813.0	2.44*
		Error	10339.9	31	333.5	
	TS	Year	5224.6	7	746.4	1.83
		Station	1588.5	7	226.9	0.56
		Error	11036.3	27	408.8	
	ST	Year	3980.5	7	568.6	2.98*
		Station	2111.7	10	211.2	1.11
		Error	5914.5	31	190.8	
<i>S. elegans</i>	SA	Year	8895.6	7	1270.8	6.23**
		Station	493.5	7	70.5	0.35
		Error	5301.1	26	203.9	
	TN	Year	486.7	7	69.5	0.92
		Station	944.9	9	105.0	1.39
		Error	2333.8	31	75.3	
	TS	Year	2611.4	7	373.1	4.47**
		Station	609.7	7	87.1	1.04
		Error	2255.6	27	83.5	
	ST	Year	3034.4	7	433.5	7.99**
		Station	594.5	10	59.5	1.10
		Error	1682.9	31	54.3	
<i>S. scrippsae</i>	TN	Year	954.7	7	136.4	2.68*
		Station	2358.7	9	262.1	5.14**
		Error	1580.1	31	51.0	
	TS	Year	3632.4	7	518.9	2.23
		Station	1634.5	7	233.5	1.00
		Error	6294.9	27	233.1	
	ST	Year	9336.7	7	1333.8	10.25**
		Station	2086.1	10	208.6	1.60
		Error	4032.4	31	130.1	

surface to 300-m depth (maxima at 200 m) during both day and night, and that only a portion of the population migrated upward after sunset. These reports suggest that the present method of vertical sampling at various times of the day does not contribute a serious source of errors in estimating the population size of these three dominant chaetognaths in the top 150 m. Repeated samplings at different times of the day during the *Oshoro Maru* cruise in the summer of 1996 confirmed this conclusion (Nishiuchi, unpublished data).

The present results show clearly that chaetognath assemblages change greatly from north to south depending on prevailing water masses. Among the 5 water masses sampled on the present sampling transect, the AS, which was recognized clearly only in 1982 and 1988, was characterized by low salinity water from the Gulf of Alaska (Favorite et al. 1976). According to Sund (1959), both *Eukrohnia hamata* and *Sagitta elegans* are dominant chaetognaths in the Gulf of Alaska but *E. hamata* was scarce in low salinity waters. Lea (1955) reported that salinity (below 28) limits the distribution of *E. hamata*. These observations, combined with

Table 4. Regression statistics of mean abundance [$Y: (n+1)^{1/2}/1000 \text{ m}^3$] of *E. hamata*, *S. elegans* and *S. scrippsae* on mean temperature integrated over the top 150 m ($X: ^\circ\text{C}$). *: $p < 0.05$. **: $p < 0.01$.

Species	Subarea	N	Regression model: $Y = aX + b$		
			a	b	r
<i>E. hamata</i>	SA	8	-39.62	264.58	-0.37
	TN	8	-13.74	160.95	-0.38
	TS	8	-13.69	168.35	-0.93**
	ST	8	-6.63	95.39	-0.75*
<i>S. elegans</i>	SA	8	42.93	-134.57	0.63
	TS	8	5.78	-5.07	0.59
	ST	8	-5.00	68.25	-0.73*
<i>S. scrippsae</i>	TS	8	4.31	3.56	0.39
	ST	8	-6.98	118.12	-0.65

the current pattern seen in this region (cf. Fig. 1), suggest that the *E. hamata* and *S. elegans* found in the AS in this study were likely to have been transported from the Gulf of Alaska and were thus distinct from the respective populations in the SA, TN or TS.

Sagitta elegans has been reported as the most numerically dominant chaetognath, followed by *Eukrohnia hamata*, in the northwestern North Pacific during summer, but the order of dominance of these two species was found to be reversed in the center of the northern North Pacific (Kotori 1976). In spring, *E. hamata* and *S. elegans* comprised 69% and 26%, respectively, of the total number of chaetognaths in the 0–150-m depth layer of the Oyashio region off the eastern part of Hokkaido (Kitou 1974). The present results from the central North Pacific are in general agreement with these two previous reports. However, the present results are not consistent with previous reports regarding the third most common species in the upper 150 m (*S. lyra* in Kotori's [1976] study in contrast to *S. scrippsae* in the present study). Considering the geographical differences between Kotori's (1976) study (largely western region of the northern North Pacific) and the present study (central region along 180°), dissimilar results for the third most dominant chaetognath (*S. lyra* and *S. scrippsae*) may be attributable to regional variations in the abundance of both species.

The abundances of *Eukrohnia hamata* and *Sagitta elegans* decreased in the TS and ST from north to south. At the same time, the abundance of *S. scrippsae* increased together with the abundances of *Krohnitta subtilis*, *S. hexaptera*, *S. lyra*, *S. minima*, *S. zetesios* and *S. neodecipiens*. *S. scrippsae* has been reported to be distributed from the Transition Domain to the northeastern Pacific Ocean in the "West wind drift region" (Alvario 1965). The latter 6 species are known to be widespread over tropical and subtropical regions (Pierrot-Bults & Nair 1991). Of these 6 subtropical/tropical species, *K. subtilis*, *S. hexaptera* and *S. minima* are epipelagic, and their distribution to the north is clearly limited by the Transition Front (Table 2). The other 3 species (*S. lyra*, *S. zetesios* and *S. neodecipiens*) are mesopelagic. The bathymetric distribution pattern of these three species, combined with the fact that the Transition Front is shallower than 150 m, explains why their distributions extended beyond the Transition Front. Nevertheless, only 1 out of 43 samples collected in subarea TN during the 8-year period belonged to this mesopelagic group. *Pterosagitta draco* and *S. pseudoserratodentata* occurred only in the southernmost subarea ST, which agrees well with a previous report that *P. draco* is distributed mainly in tropical regions and *S. pseudoserratodentata* is endemic to the North Pacific

Central Water Mass (Bieri 1959).

No mature specimens (stage 4) of *Eukrohnia hamata* were collected, in contrast to *Sagitta elegans* for which all maturity stages were found. While *S. elegans* inhabits depth less than 250 m in the subarctic region (Kotori 1976; Terazaki & Miller 1986), *E. hamata* lives between 200 and 300-m depth in the mid-latitude regions of the North Pacific and descends much deeper when it matures (Alvariño 1964). This "ontogenetic vertical migration" behavior of *E. hamata* is the likely cause for the lack of mature specimens collected from the 0–150-m depth layer. In the eastern subarctic North Pacific, the generation times of *E. hamata* and *S. elegans* were estimated to be 8 to 10 months and 6 to 10 months, respectively (Terazaki & Miller 1986). While development and reproduction of *E. hamata* continue throughout the winter, immature stages of *S. elegans* overwinter and begin reproduction in spring. Thus, *E. hamata* reproduces earlier in the year than *S. elegans*. This difference in reproductive season may have led to the dominance of maturity stage 2 for *E. hamata* and stages 1 and 2 for *S. elegans* collected in summer. As with *E. hamata*, mature specimens of *S. scrippsae*, which was abundant in subareas TS and ST, were very scarce. Terazaki & Miller (1986) noted that *S. scrippsae* is distributed in the upper 100 m during winter (late November to mid-March) and in the 250 to 500-m depth layer in late October. According to Kotori (1972), the maximum abundance of *S. scrippsae* occurs at 50 to 390 m in depth. However, there is little information about the life cycle of *S. scrippsae*, so it is difficult to speculate as to why we observed this particular maturity composition pattern.

According to Andou (1995), water temperatures in the top 400 m in the North Pacific central region (30°–50°N, 160°E–140°W) changed from cold conditions, which began in the late 1970s, to warm conditions during 1989 and 1990. This study period (1982–1989) overlaps the end of the regime shift, and the variations in water temperature in the ST and TS (Fig. 5) are considered to be the effect of this regime shift. The results of variance analysis indicate that variation between years rather than between stations prevailed in general for determining the numerical abundance of the three dominant chaetognaths (*Eukrohnia hamata*, *Sagitta elegans* and *S. scrippsae*) within the same subareas in the central northern North Pacific (Table 3). Temperature was an important cause of interannual variation only for *E. hamata* in the TS and ST, and *S. elegans* in the ST (Table 4). These results may be due to less pronounced interannual variations in mean temperature in the SA and TN than in the TS and ST (Fig. 5). As mentioned earlier, both *E. hamata* and *S. elegans* are cold water species, so it is doubtful whether these species can successfully reproduce in the warm TS and ST. This is particularly true in the warm years of 1985 and 1987 to 1989 (cf. Fig. 5). This observation, combined with the negative correlation of abundance and temperature, suggests *E. hamata* and *S. elegans* found in the TS and ST are likely to be sterile expatriates, as have been reported for other chaetognaths (cf. Pierrot-Bults & Nair 1991). Such sterile expatriation has also been reported for a calanoid copepod *Neocalanus cristatus* occurring in Sagami Bay, central Japan (Oh et al. 1991).

It is not clear what the driving force was for the significant interannual variations in the abundance of chaetognaths in the SA and TN, where the interannual variations in temperature were less pronounced. Abundance of food zooplankton and/or predators may be possible causes, along with environmental parameters other than temperature. Aebischer et al. (1990) analyzed long term records (33 years) of weather patterns and biomass of phytoplankton, zooplankton, herring and Kittiwake gulls in the North Sea, and found remarkable similarities in the trends among these four biological groups and climate data. This led us to examine the correlation between interannual variations in chaetognath abundance and those of total net

zooplankton biomass (i.e. the food of chaetognaths). The analysis indicated no significant correlation ($p > 0.1$) in the *Sagitta elegans*, *Eukrohnia hamata* or *S. scrippsae* living in all subareas, perhaps due to the relatively short-term data sets (8 years) and the inaccuracy in defining the food zooplankton of chaetognaths (copepod abundance would be better than total zooplankton biomass) in the present study.

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