

# Life history, distribution, seasonal variability and feeding of the pelagic chaetognath *Sagitta elegans* in the Subarctic Pacific: A review

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**Abstract:** *Sagitta elegans* Verrill is the dominant epipelagic chaetognath species in Pacific Subarctic Waters. In this paper, the seasonal variability, horizontal distribution, vertical distribution, diel migration, breeding, life cycles, gut contents and feeding activity of *S. elegans* are reviewed. The southern-most records of this species in the Pacific Ocean is in the southern Japan Sea near the Tsushima Strait and in Sagami Bay where warm Tsushima and Kuroshio Currents, respectively, cover the surface layer. Diel vertical migration of *S. elegans* has been observed in various water masses and adults show migration of a larger scale compared to that seen in smaller animals. *S. elegans* is distributed as deep as 1000 m or more in the Japan Sea and the vertical dispersal of this species is facilitated by the absence of competitors such as *Eukrohnia hamata*, *E. bathypelagica*, *E. fowleri* and *S. macrocephala*. The number of generations produced each year increases with the distance from the north pole. Generation times are 4–5 months in Dabob Bay, 6–10 months at Ocean Station P and 10–12 months in Toyama Bay, respectively. Copepods are the predominant prey of *S. elegans* regardless of water mass. The percentage of secondary production consumed daily by *S. elegans* was 10% in the Bering Sea and 4% in the Western Gyre during the summer.

**Key words:** ecology, chaetognath, *Sagitta elegans*, subarctic Pacific

## Introduction

Chaetognaths are found in every marine habitat, from the sea floor to all pelagic zones of coastal waters and the open oceans. Although small (2–120 mm), they are often abundant, and play an important role in the marine food web as the primary predators of copepods. The biomass of chaetognaths has been estimated as 10–30% of that of copepods in the world oceans, so they are of great significance in transferring energy from copepods to higher trophic levels. Therefore, the role of chaetognaths in marine ecosystems is a very important consideration in international programs such as the Joint Global Ocean Flux Study (JGOFS) and the Global Ocean Ecosystem Dynamics (GLOBEC) Programs. To JGOFS, they are important because they package and redistribute carbon in the vertical plane, in particular because they mediate transport of material from the surface to the deep sea. To GLOBEC, they are important as part of the biological conveyor belt that transfers carbon from the lower to the uppermost trophic

**Table 1.** Chaetognaths reported to occur in waters adjacent to Japan. After Terazaki (1984).

	Tropical Seas 1968	Kuroshio 1966–1972	Suruga Bay 1964–1965 Marumo & Nagasawa 1973	Sagami Bay 1964–1965 Marumo & Nagasawa 1973	Otsuchi Bay 1978–1979 Terazaki & Marumo 1982	Off Sanriku 1955–1960 Kitou 1974	Ishikari Bay 1975–1976 Kotori & Kobayashi 1979	Japan Sea 1966–1968 Kitou 1974	Northern North Pacific 1957–1969 Kotori 1976
<b>Pelagic species</b>									
<i>Sagitta bedoti</i>	+	+	+	+					
<i>S. bipunctata</i>	+	+				+			
<i>S. crassa</i>		+	+	+	+			+	
<i>S. delicata</i>						+			
<i>S. elegans</i>					+	+	+	+	+
<i>S. enflata</i>	+	+	+	+	+	+	+	+	+
<i>S. ferox</i>	+	+	+	+	+	+		+	
<i>S. hexaptera</i>	+	+	+	+		+		+	+
<i>S. maxima</i>									+
<i>S. minima</i>	+	+	+	+	+	+	+	+	+
<i>S. nagae</i>		+	+	+	+	+	+	+	+
<i>S. neglecta</i>	+	+	+	+	+	+		+	+
<i>S. pacifica</i>	+	+	+	+	+	+		+	+
<i>S. pseudoserratodentata</i>	+	+	+	+		+		+	
<i>S. pulchra</i>	+	+				+			
<i>S. regularis</i>	+	+	+	+	+	+	+	+	
<i>S. robusta</i>	+	+	+	+	+	+			
<i>Pterosagitta draco</i>	+	+	+	+	+	+		+	+
<i>Krohnia pacifica</i>	+	+	+	+		+		+	
<i>K. subtilis</i>	+	+		+		+		+	
<b>Meso- &amp; bathypelagic species</b>									
<i>Sagitta decipiens</i>		+	+	+				+	
<i>S. lyra</i>	+	+	+	+		+		+	+
<i>S. macrocephala</i>									+
<i>S. neodecipiens</i>		+	+	+					+
<i>S. scrippsae</i>									+
<i>S. zetesios</i>		+							+
<i>Eukrohnia hamata</i>		+	+	+		+			+
<i>E. bathypelagica</i>									+
<i>E. fowleri</i>									+
<b>Total number of species</b>	<b>16</b>	<b>22</b>	<b>18</b>	<b>19</b>	<b>9</b>	<b>20</b>	<b>5</b>	<b>16</b>	<b>17</b>

levels, such as those occupied by fish and marine mammals.

About 30 species belonging to 4 genera of pelagic chaetognaths occur in waters adjacent to Japan (Terazaki 1984; Table 1). *S. elegans* is a key species in subarctic waters and there are many reports describing the biology of this species. For example, Russell (1935, 1936, 1939) used *S. elegans* and *S. setosa* as biological indicators of hydrological conditions, and paid special attention to the life history and annual fluctuations in abundance of these two species in the Plymouth region. He proposed that in the Plymouth region *S. elegans* was an indicator of the influence of Atlantic Water and *S. setosa* that of English Channel Water; when the Atlantic Water inflow into the northern North Sea increased, the populations of *S. setosa* in the Channel were pushed towards the western side of the Channel and this species appeared off Plymouth; when the Atlantic Water inflow was weak, the Channel Water moved into the North Sea, allowing the Atlantic Water to enter the Channel from the west, so that *S. elegans* became preponderant off Plymouth. '*S. setosa*' waters are characteristically poor in plankton and have a low phosphate value during winter while '*S. elegans*' water, enriched through upwelling along the Atlantic slope, has a high phosphate maximum in winter, a large number of planktonic species and a much higher plankton biomass.

The reproduction and life history of *S. elegans* has previously been reviewed by Kotori (1979) but much knowledge has accrued about the biology and ecology of *S. elegans* in the Subarctic Pacific since his review.

This paper gives an up-to-date review of the ecology of *S. elegans* relating to seasonal variability, distribution, life history and feeding in the Subarctic Pacific.

### Seasonal Variability

*Sagitta elegans* has been collected throughout the year at Ocean Station P (50°N, 145°W), their abundance being low from February to April, and high in late spring and early summer, mainly due to an increase in the number of juveniles (Fig. 1; Terazaki & Miller 1986). *S. elegans* is the dominant chaetognath in Dabob Bay, Washington, and population densities of *S. elegans* found during 1972–1973 are presented in Fig. 2. Seasonal variability was pronounced; population abundance levels in spring and summer were approximately 5 times those in fall and winter. From November to April, the population density of *S. elegans* was relatively constant suggesting low mortality. The abundance of the population increased sharply in May and June (King 1979).

The spatial distribution and seasonal variability of epipelagic chaetognaths along the Kurile Islands and off south-east Hokkaido, in the western subarctic Pacific Ocean, was investigated from May 1990 to October 1992. *S. elegans* was the dominant chaetognath species in the epipelagic zone. Adults occurred in spring (April–May) and small individuals (juveniles and Stage 1) were abundant in summer (June–July) when a strong thermocline developed. Juveniles occurred exclusively in October 1990 and January 1991 (Fig. 3). The temperature regime in which juveniles occurred was less than 10°C in January–April and then increased in summer and autumn to values higher than 18°C at the southernmost station in October, 1990. In contrast, large individuals (Stages 2 and 3) inhabited water colder than 7°C throughout the year except during October 1992 (Terazaki et al. 1995).

Kotori (1985) examined chaetognath populations collected from 1968 to 1972 in the north-western North Pacific Ocean between 40°N and 43°N. The survey area was divided into warm and cold water regions. *S. elegans* appeared rather constantly throughout all seasons; the difference in abundances between winter and summer in the cold water region was insignificant

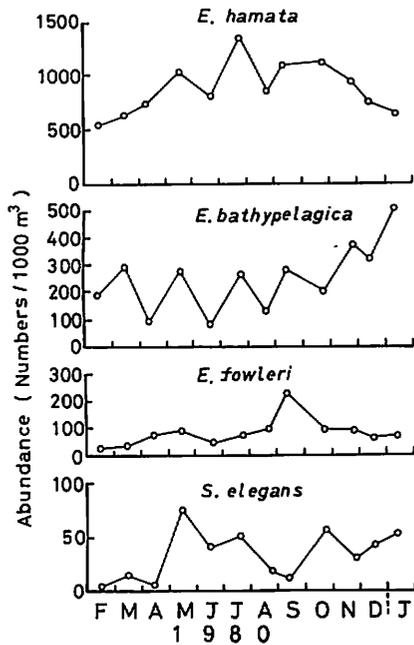


Fig. 1. Monthly average catch standardized as number of individuals per 1000 m<sup>3</sup> for the four most abundant species at Ocean Station P (February 1980 to 11 January 1981). After Terazaki & Miller (1986).

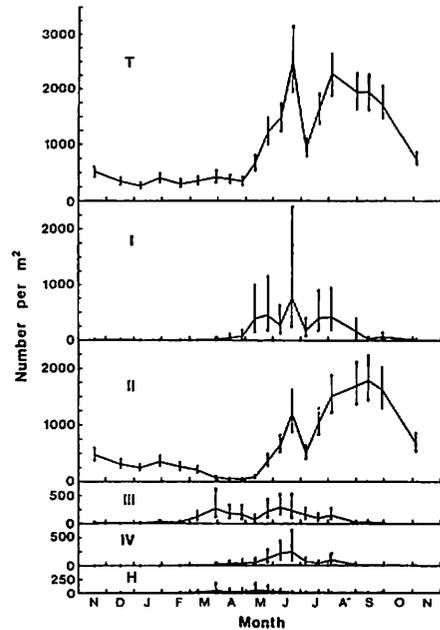


Fig. 2. Abundance of total population and by stage of *Sagitta elegans* in the 0–175 m layer of Dabob Bay from November 1972 through November 1973. Line connects geometric mean densities; vertical bars represent 95% confidence intervals. T: Total population; I: Stage 1; II: Stage 2; III: Stage 3; IV: Stage 5; H: Headless (spent). After King (1979).

(Fig. 4). Although juveniles (2.1–7.9 mm in length) were also found throughout all seasons, larvae (less than 2.2 mm in length) were only found in summer (July) and autumn (October).

In Otsuchi Bay, northern Japan, *S. elegans*, transported by the cold Oyashio Current, occurred in spring (March–April) and disappeared in summer (July) when the water temperature reached 15°C (Terazaki & Marumo 1982).

*S. elegans* was collected from Yamato Tai in the central area of the Japan Sea in spring, summer and autumn and maximum numbers (2.06 indiv. m<sup>-3</sup>) were recorded in May 1990 (Nishihama et al. 1995).

There is a remarkable variation in the abundance of *S. elegans* in Toyama Bay, southern Japan Sea, throughout the year with many individuals collected in August (Terazaki 1993a). Many juveniles of *S. elegans* occurred in spring and summer from late March to August. In particular, juveniles <5 mm were captured in March–May, June and August (Fig. 5). The number of juveniles in autumn and winter was very low (<0.1 indiv. m<sup>-3</sup>) and no individuals <8 mm long were collected during this period. Stages 1 and 2 were collected almost right throughout the year, and they were most abundant in March–April and September–December. Adults (Stage 3) occurred in all seasons except summer (mid-July–mid-September). The body length of *S. elegans* at Stage 3 ranged from 26 to 36 mm.

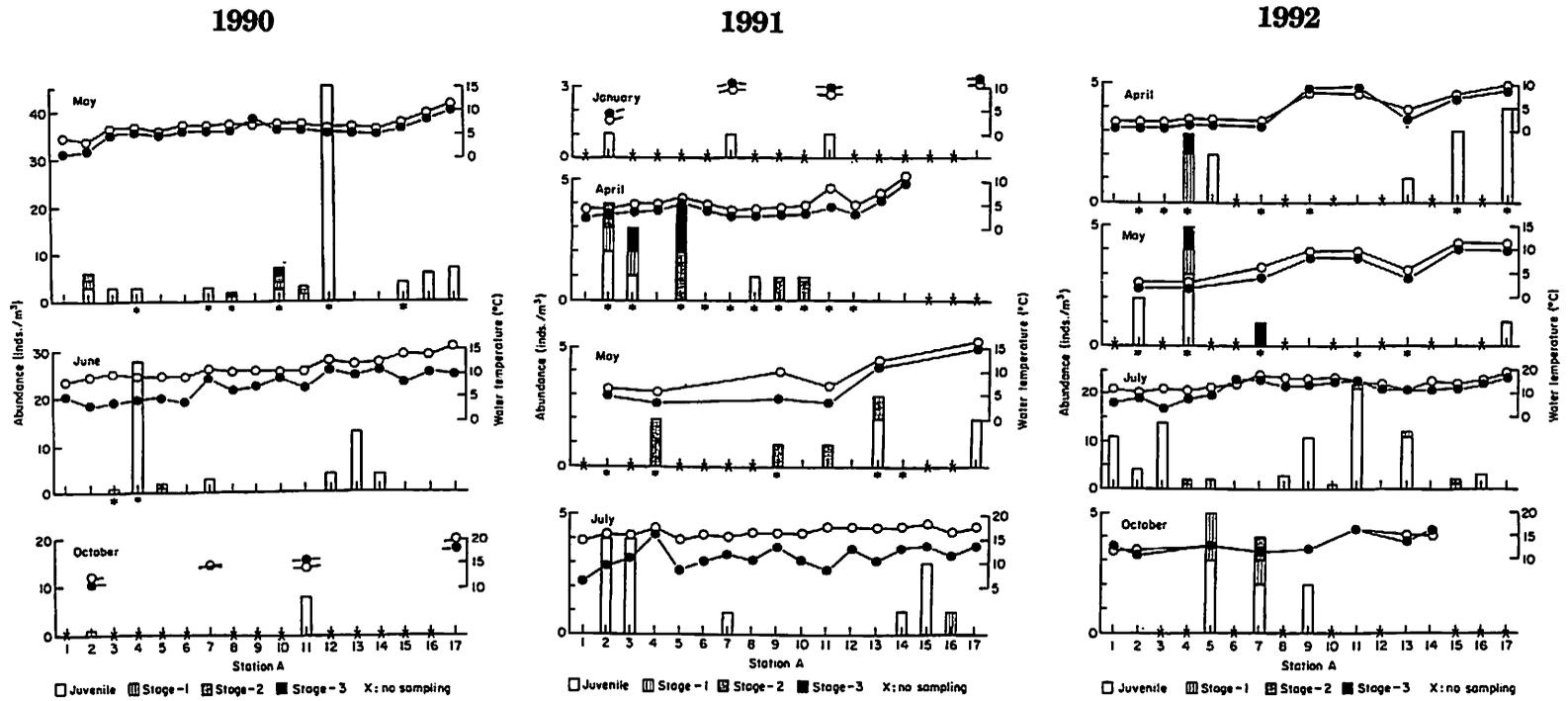


Fig. 3. Abundance of *Sagitta elegans* from 1990 to 1992 along A-line, off southeastern Hokkaido. Stars indicate the occurrence of *Neocalanus cristatus*. Open and solid circles indicate water temperature at the surface and 20-m depth, respectively. After Terazaki et al. (1995).

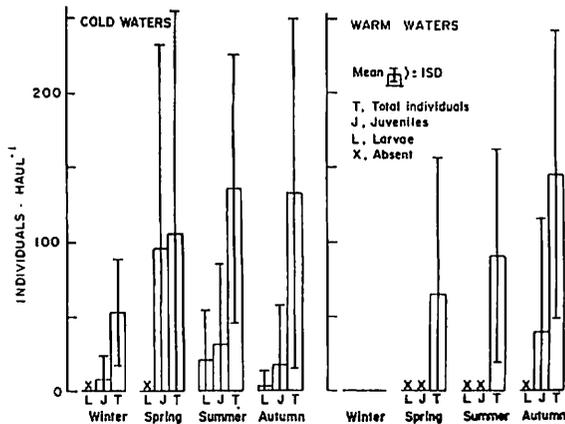


Fig. 4. Seasonal change in the abundance of *Parasagitta* (= *Sagitta*) *elegans* in the cold water masses and warm water masses in the northern North Pacific Ocean, 1968–1972. After Kotori (1985).

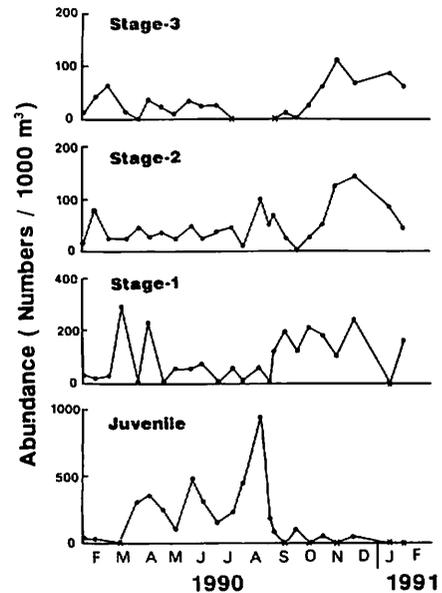


Fig. 5. Seasonal variations in the numerical abundance of Stages 3, 2, 1 and juvenile individuals of *Sagitta elegans* in Toyama Bay. Crosses indicate zero abundance. After Terazaki (1993a).

### Horizontal Distribution

*Sagitta elegans* is a chaetognath typical of the upper 100 or 150 m in the Arctic and Subarctic regions, and its distribution extends into the northern part of both the Atlantic and Pacific Oceans (Alvariño 1964; Pierrot-Bults & Nair; Fig. 6). The extent of the distribution of *S. elegans* (Alvariño 1964) appears to be controlled by the concentration of oxygen in the water, because *S. elegans* was only found in northern Pacific waters with oxygen values of more than  $6 \text{ ml l}^{-1}$ , and this could also be a limiting factor preventing the spread of this chaetognath to deeper layers. Specimens of *S. elegans* from the Arctic are larger than those from more southern, warmer regions, but there are no characters sufficient enough to warrant relegation of these arctic specimens to a different species or form; the extent of growth depends on the water mass inhabited (Fraser 1952; Alvariño 1965).

The distribution of *S. elegans* extends into the Pacific to  $38^\circ\text{N}$  and is present in waters of the Oyashio Current. However where the Oyashio Current collides with the Kuroshio Current, *S. elegans* is no longer present, even in deeper layers, in the region where the two bodies of water meet (Alvariño 1964). Bieri (1959) considered the southern boundary of its distribution to be at about  $40^\circ\text{N}$  to  $41^\circ\text{N}$ .

The southern most records of *S. elegans* in the Pacific is in the southern Japan Sea near the Tsushima Strait (Tokioka 1957; Park 1970; Terazaki 1993b) and in Sagami Bay (Marumo 1966) where the warm Tsushima and warm Kuroshio Currents covered the surface layer.

*S. elegans*, in the eastern part of the Bering Sea, appeared most abundantly ( $25 \text{ indiv. m}^{-3}$  on the average through 52 stations), where *Eukrohnia hamata* was absent (Kotori 1976). *S. elegans* was also abundant in the area off the eastern coast of Kamchatka, the Kurile Islands and

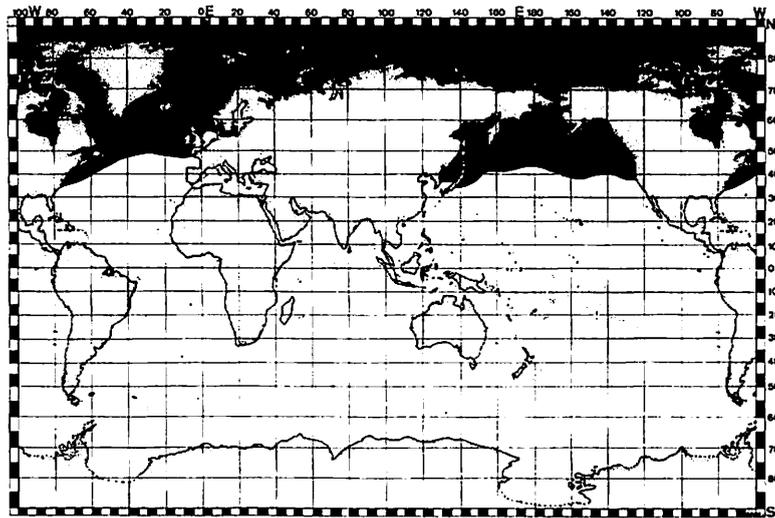


Fig. 6. Geographical distribution of *Sagitta elegans*. After Pierrot-Bults & Nair (1991).

Hokkaido. It also appears to be relatively abundant in the southern coastal waters along the Aleutian Islands. The abundance of this species, however, decreased rapidly into the southern region beyond 50°N in the central parts of the northern North Pacific Ocean (Kotori 1976).

The spatial distributions of *S. elegans* along the Kurile Islands and off southeastern Hokkaido, in the western subarctic Pacific Ocean, were investigated during the period from May 1990 to October 1992. Juveniles were distributed mainly in the frontal mixing zones which were determined through the existence of an acceleration potential anomaly (APA) at an isopycnal density surface of  $26.6 \delta_\theta$ . The position of the frontal mixing zone was variable, meandering in cyclonic and anticyclonic eddies. Catches of *S. elegans* were taken at temperatures ranging from 4.5 to 22.2°C (Fig. 7). Variability in the abundance of juvenile within the frontal mixing zone is thought to be caused by predation rather than food limitation because microzooplankton, which are known to be preyed on by juveniles, were abundant enough to meet the food requirements of juveniles in the study area (Terazaki et al. 1995).

Seventeen species belonging to 3 genera were collected from the Japan Sea (Terazaki 1984). The most abundant species was *S. elegans*, comprising 93.9 to 100% of the individuals collected from 0 to 1000 m (Fig. 8).

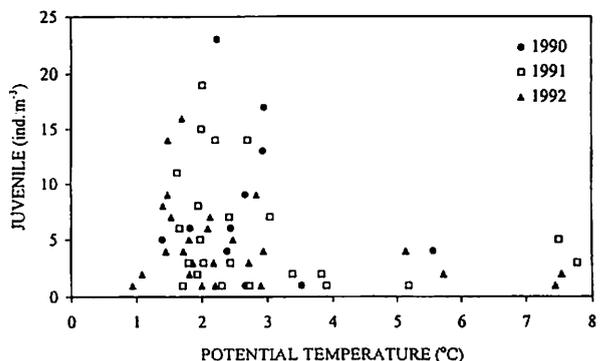


Fig. 7. Relationship between the abundance of juvenile *Sagitta elegans* and the potential temperature at the isopycnal surface of  $26.6\sigma_\theta$  in their habitats during the summers of 1990, 1991 and 1992. After Terazaki et al. (1995).

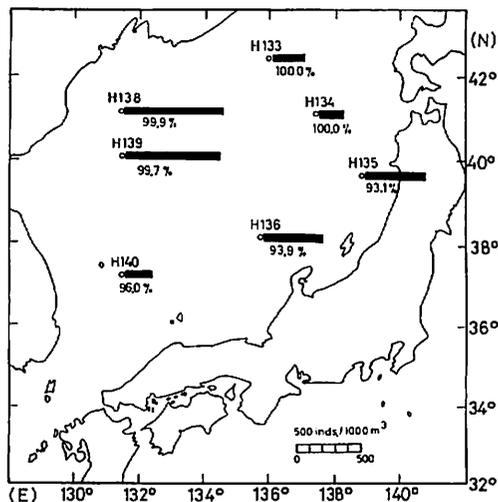


Fig. 8. Horizontal distribution and relative abundance of *Sagitta elegans* in samples collected with an ORI net (0 to 1000 m) in the Japan Sea, summer 1970. After Terazaki (1993b).

### Vertical Distribution

Kotori (1972) reported that the maximum abundance of this species was from 70 to 200 m and the species reached depths of 500–610 m in the southern Bering Sea. *Sagitta elegans* was usually distributed in the upper 250 m at Ocean Station P both day and night, but many individuals (mostly Stages 1 and 2) appeared in the mesopelagic layer between 250 and 1000 m in October and November (Terazaki & Miller 1986; Fig. 9). No *S. elegans* individual was present in the surface layer on several sampling dates (late March, August, September, mid-November).

Seasonal changes in the vertical distribution of the vertically migrating portion of the population were similar in regard to the maturity stage and size of the individuals to those in Dabob Bay (King 1979). Small chaetognaths were non-migratory and were distributed in the top 100 m.

According to time series observations in the 0–300 m layer at 45°N, 160°10'E on 13–14 May 1991, the population density of *S. elegans* in this layer was heavily influenced by the sudden change in light intensity at sunrise and sunset. None were collected in the layer above 40 m during the day although they moved into the 0–40 m layer after sunset (Terazaki 1995).

Chronologically precise information on the diel vertical migration of *S. elegans* at Stn. B (44°N, 150°E) on 22–23 July 1971 was obtained from observations at 2-h intervals. Juveniles were distributed in the upper layer, shallower than 10 m, between 1200 and 1400 h. After sunset at approximately 1800 h, they appeared at the surface and were most abundant in the 0–10 m layer between 2000 and 0200 h. Just before sunrise (0400 h), they moved to the 10–50 m layer. They were observed to occur from 10 to 100 m at 0900 h. Adults of *S. elegans* showed the largest vertical migration (Fig. 10). The average speed per hour of upward and downward migration was 8 m in ascent and 10 m in descent in the juvenile stage, 14 m and 18 m in Stage 1, 20 m and 27 m in Stage 2, and 30 m and 30 m in Stage 3, respectively (Terazaki & Marumo 1979).

Kotori (1972) however suggested that individuals of less than 9 mm in length did not migrate vertically and that a thermocline at 10–50 m impeded the upward nocturnal migration of *S. elegans* longer than 20 mm in the northern North Pacific.

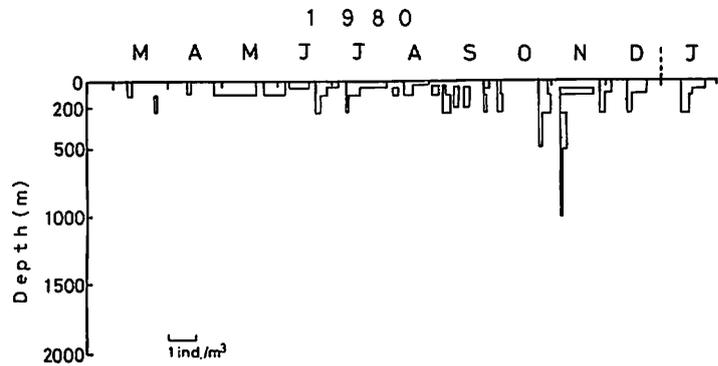


Fig. 9. Vertical distribution of *Sagitta elegans* by month at Ocean Station P (March 1980 to 11 January 1981). After Terazaki & Miller (1986).

Kotori et al. (1987) investigated the vertical distribution of *S. elegans* under sea ice during the day in Lake Saroma, a small lagoon in Hokkaido, northern Japan in February 1986. Body size ranged from 15.4 mm to 27.1 mm and abundance was estimated to be 10–30 indiv. m<sup>-3</sup>. Maximum abundance was observed at a depth of 2 m beneath the undersurface of the ice (Fig. 11).

The vertical distribution and diel migration of chaetognaths were investigated in a Kuroshio warm-core ring (KWCR) and adjacent waters during two cruises in August and September 1987. A strong seasonal thermocline had developed in the upper 50 m of the ring core in September and the bottom of the core was at about 300-m depth. *S. elegans* was abundant mainly in the intermediate water existing under the water of the core. They reach the epipelagic layer of the KWCR by vertical migration from the intermediate water but cannot survive in the KWCR because *S. elegans* cannot adapt to the changes in temperature and salinity (Terazaki 1992).

*S. elegans* was distributed in the upper 300 m in the vicinity of Otsuchi, northern Japan in the springs of 1981 and 1982. Diel migration of Stage-1 and -2 individuals was observed and the distance migrated was 30–40 m (Terazaki et al. 1985).

The Japan Sea is a semi-isolated marginal sea connected with the Sea of Okhotsk, North Pacific, and the East China Sea through four shallow straits. The only major current flowing into this sea today is the warm Tsushima Current flowing into the Japan Sea through the

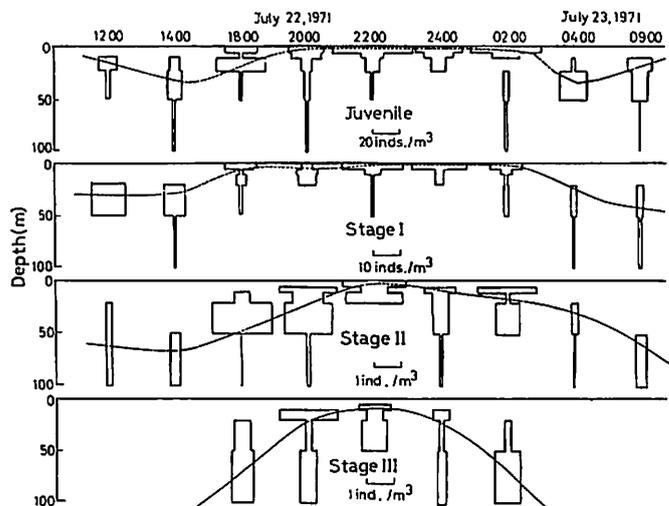


Fig. 10. Diel vertical migration of *Sagitta elegans* at Stn B (44°N, 150°E) on July 22–23, 1971. After Terazaki & Marumo (1979).

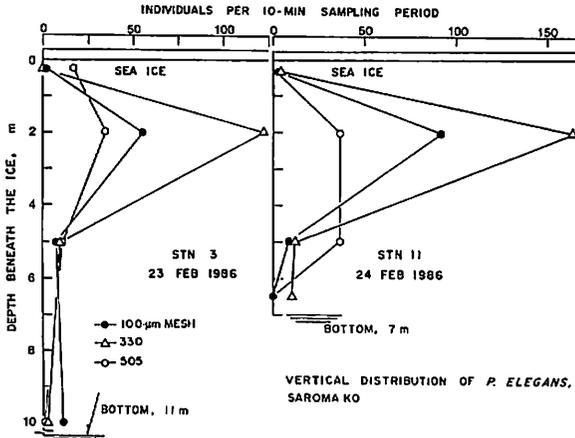


Fig. 11. Vertical distribution of *Parasagitta* (= *Sagitta*) *elegans* under sea ice during the day when sampled with nets of different mesh sizes at Stns. 3 and 11 in Lake Saroma, February 1986. After Kotori et al. (1987).

southern strait. Between 20,000 and 10,000 yr ago, the cold Oyashio Current flowed into the Japan Sea through its northern straits. The epipelagic chaetognath *S. elegans* was introduced into the Japan Sea during this period, but shallow straits prevented the invasion of deep-sea chaetognaths. All other chaetognath species were introduced into this sea by the warm Tsushima Current within the last 10,000 yr and inhabit the epipelagic layers. *S. elegans* is distributed as deep as 1000 m or more (Terazaki 1993b). The vertical distribution of *S. elegans* at 40°N, 139°E is shown in Fig. 12. The vertical dispersal of *S. elegans* is facilitated by the absence of competitive chaetognaths such as *Eukrohnia hamata*, *E. bathypelagica*, *E. fowleri* and *S. macrocephala* in this marginal sea. The size and number of grasping spines and teeth of specimens from the Japan Sea are larger than those from the Pacific. They have also developed intestinal tissue containing oil droplets, like meso- and bathypelagic species. These features are adaptations to the deep-water environment.

In Ishikari Bay, Hokkaido, the warm Tsushima current covered the shallow upper 40-m layer and *S. elegans* was distributed only below 40 m where the cold water mass of the Japan Sea was present (Kotori & Kobayashi 1979).

### Life History

There are many reports describing the breeding and life cycles of *Sagitta elegans*. The number of generations produced each year increases with the distance from the North Pole

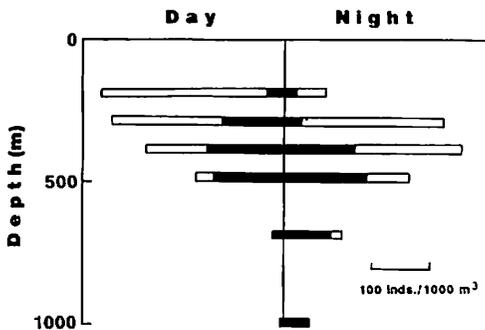


Fig. 12. Vertical distribution of *Sagitta elegans* as collected with MTD nets at 40°N, 139°E on September 7-8, 1985. Shaded area represents the proportion of adults (Stage 3). After Terazaki (1993b).

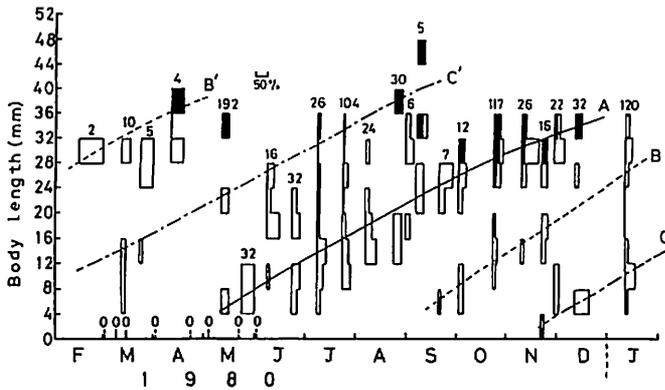


Fig. 13. Monthly size-frequency distributions of *Sagitta elegans* at Ocean Station P (February 1980 to 11 January 1981). Shaded area represents the proportion of fully matured individuals. Lines A, B and C show growth curves for 1980 cohorts and B' and C' for 1979 cohorts. The total number of individuals between 0 and 2000 m is shown for each sample. A zero above a tick mark on the abscissa indicates the absence of *S. elegans*. After Terazaki & Miller (1986).

(Owre 1960). *S. elegans* produces one brood per year in the Arctic-Subarctic waters (Kramp 1939). *S. elegans* produces two to five (or more) yearly broods towards the southernmost boundary of its distribution range in temperate regions.

In the Pacific, King (1979) reported one or possibly two generations per year regarding the population in Dabob Bay, with generation lengths of 4–5 months. *S. elegans* had three spawning periods during the year and generation lengths were 6–10 months at Ocean Station P (Terazaki & Miller; Fig. 13).

The spawning period of *S. elegans* is in April–May in the western Subarctic Pacific near the Kurile Islands (Terazaki et al. 1995), in May–June in the coastal waters off southern Hokkaido (Kotori 1975), and in April in Otsuchi Bay (Terazaki & Marumo 1982). Recently Kotori (1985) suggested that the breeding period of *S. elegans* in the northwestern North Pacific was not restricted to any particular season, unlike that of *S. elegans* in the high arctic regions, but continued throughout the warm seasons of the year.

There were two principal spawning periods in Toyama Bay, southern Japan Sea, one was in March–May and the other in August (Terazaki 1993a). The life spans of both cohorts were 10–12 months (Table 2).

Jakobsen (1971), King (1979) and Conway & Williams (1986) stated that *S. elegans* must spawn several times over a period of months. The animals die after spawning (McLaren 1966). The number of eggs contained in the ovary of a mature individual of *S. elegans* is 50–100 (McLaren 1966) and the body length of newly hatched *S. elegans* ranged from 1.23 to

Table 2. Breeding season, number of yearly generation and estimated life span of *Sagitta elegans* in the Subarctic Pacific.

Area	Breeding season	No. of generations	Life span
Dabob Bay <sup>1</sup>	March–August	2	4–5 months
Station P <sup>2</sup>	Spring, Summer, Autumn	3	6–10
Kurile Island <sup>3</sup>	April–May		
Southern Hokkaido <sup>4</sup>	May–June		
Otsuchi Bay <sup>5</sup>	April		
Toyama Bay <sup>6</sup>	March–May, August	2	10–12

<sup>1</sup> King (1979), <sup>2</sup> Terazaki & Miller (1986), <sup>3</sup> Terazaki et al. (1995), <sup>4</sup> Kotori (1975), <sup>5</sup> Terazaki & Marumo (1982), <sup>6</sup> Terazaki (1993b).

1.42 mm (Kotori 1975). Seven-day-old larvae (1.94 mm long) have eight hooks on each side of the head (Kotori 1975). The size at first feeding of *S. elegans* is 1.28–1.70 mm (Kuhlmann 1977; Pearre 1980).

### Feeding

The food of chaetognaths is considered very heterogeneous. Cannibalism has been observed and representatives of every planktonic group occur in gut contents: diatoms, ciliates, Tintinnia, Medusae, Crustacea, Copepoda, Amphipoda, Cladocera, the larval stages of Crustacea, Mollusca, Pteropoda, Heteropoda, Chaetognatha, Tunicata, fish eggs and fish larvae (Alvarino 1985). A list of food organisms ingested by *Sagitta elegans* collected from the Pacific, is given in Table 3. At Ocean Station P, *S. elegans* lives and feeds primarily in the upper water column (0–25 m) and the vertical distribution of this species may be explained primarily by its requirement for prey at high densities. *Eukrohnia hamata* apparently needs less food and is found mainly below the mixed layer with its vertical distribution restricted by temperature. The same prey species, those with the highest densities at Station P, make up the diet of the both chaetognaths, although *E. hamata* eats significantly smaller prey. The major prey of juvenile chaetognaths are small cyclopoid copepods, a group frequently overlooked in plankton surveys. These species also comprise 41% of the diet of older chaetognaths, which also prey on Stage 5 copepodites of the largest copepods. The development of larval chaetognaths depends on an abundance of small prey items but the older chaetognaths can handle prey of a wide spectrum of sizes (Sullivan 1980).

The largest component of the gut contents of *S. elegans* (9.0–23.0 mm, 17.0 mm in mean body length) collected from the western Subarctic Gyre, was copepods such as *Pseudocalanus* spp., *Metridia pacifica* and *Neocalanus* spp. The size of food organisms ranged from 1.0 mm to 3.5 mm (mean=2.0 mm). In coastal waters off Otsuchi Bay, *S. elegans* chiefly consumed small-sized copepods such as *Acartia*, *Oithona* and *Pseudocalanus*. Therefore, *S. elegans* inhabiting the open sea consumes larger copepods compared to those in coastal waters

**Table 3.** Food organisms of *Sagitta elegans* collected from the Subarctic Pacific. After Terazaki (1995).

Area	Food
Gulf of Alaska <sup>1</sup>	<i>Neocalanus</i> spp., <i>Oithona</i> sp., <i>Pseudocalanus</i> sp. (Copepoda); <i>Sagitta elegans</i> (Chaetognatha)
Station P <sup>2</sup>	<i>Neocalanus cristatus</i> , <i>N. plumchrus</i> , <i>Oithona similis</i> , <i>Metridia pacifica</i> (Copepoda); Chaetognatha
British Columbia <sup>3</sup>	Fish larvae; <i>Neocalanus plumchrus</i> (Copepoda)
Dabob Bay <sup>4</sup>	Copepoda
N.E. Pacific <sup>5</sup>	Fish larvae; Copepoda; Euphausiacea; Medusae; Crustacea larvae; Chaetognatha
N.W. Pacific <sup>6</sup>	<i>Neocalanus</i> spp., <i>Metridia pacifica</i> , <i>Pseudocalanus</i> sp. (Copepoda)
Japan Sea <sup>7</sup>	<i>Neocalanus</i> spp., <i>Paracalanus parvus</i> , <i>Acrocalanus gracilis</i> , <i>Scaphocalanus</i> sp., <i>Oithona</i> sp., <i>Aetideus</i> sp., <i>Unidinopsis</i> sp. (Copepoda); <i>Sagitta elegans</i> (Chaetognatha); <i>Conchoecia pseudodiscophora</i> (Ostracoda)
Otsuchi Bay <sup>6</sup>	<i>Acartia clausi</i> , <i>Oithona</i> spp., <i>Pseudocalanus minutus</i> (Copepoda); <i>Parathemisto japonica</i> (Amphipoda); Euphausiacea

<sup>1</sup> Brodeur & Terazaki (unpublished data), <sup>2</sup> Sullivan (1980), <sup>3</sup> Lee (1966), <sup>4</sup> King (1979), <sup>5</sup> Alvarino (1985),

<sup>6</sup> Terazaki (1995), <sup>7</sup> Terazaki (1993a).

**Table 4.** Food organisms in the gut of *Sagitta elegans*. After Terazaki (1993b).

Food organisms	%
Copepoda	
<i>Neocalanus</i> spp.	5.1
<i>Paracalanus parvus</i>	1.7
<i>Pracalanus</i> sp.	3.4
<i>Acrocalanus gracilis</i>	1.7
<i>Scaphocalanus</i> sp.	1.7
<i>Oithona</i> sp.	1.7
<i>Undinopsis</i> sp.	1.7
<i>Aetideus</i> sp.	1.7
Unidentified calanoids	50.8
Unidentified copepods	5.1
Chaetognatha	
<i>Sagitta elegans</i>	1.7
Ostracoda	
<i>Conchoecia pseudodiscophora</i>	3.4
Unidentified organisms	20.3

(Terazaki 1995).

In the Japan Sea, a total of 1510 out of 6053 indiv. of *S. elegans* were found to have one or more prey organisms in their guts. The predominant prey items were copepods, and the proportion of Copepoda, Chaetognatha, Ostracoda and unidentified items in the gut of *S. elegans* was 74.6, 1.7, 3.4 and 20.3%, respectively (Table 4). Most frequent were calanoid copepods such as species of *Neocalanus*, *Paracalanus* and *Scaphocalanus* (Terazaki 1993b).

The food containing ratio (FCR: number of the *S. elegans* containing food organisms in the gut/total number of *S. elegans* examined) is used as an index of feeding activity.

Natural feeding rates can be estimated from an analysis of gut contents if an estimate of the digestion time is also available (Bajkov 1935). The appropriate equations are:

$$FR_n = NPC(24)/DT, \quad FR_w = (FR_n)(MPW)$$

where  $FR_n$  = daily feeding rate expressed as number of prey per day; NPC = number of prey per chaetognath, from gut content analysis; DT = digestion time in hours;  $FR_w$  = daily feeding rate in terms of total prey weight; MPW = mean prey weight.

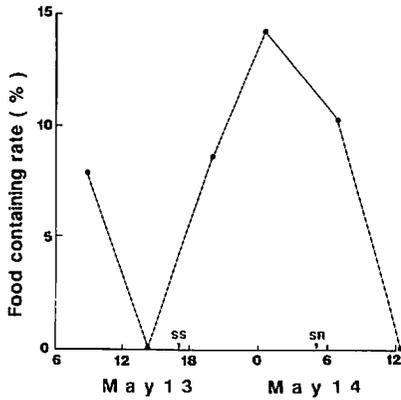
The FCR of *S. elegans* collected from the 0–300 m layer at 45°N, 160°10'E ranged from 0% to 13.5% (mean=9.6%) and the feeding activity was highest during the nighttime hours (Fig. 14). The NPC was 0.344. High feeding activity during the night was observed off Otsubuchi Bay and the NPC was very high (0.94). The NPC of *S. elegans* at Ocean Station P (Sullivan 1977) was 0.458–0.550.

There were no marked differences in FCR between day and night except at 200-m depth at 40°N, 139°E in the northern Japan Sea (Table 5).

Pearre (1981) developed the following equation for the relationship between digestion time and temperature for *S. elegans*:

$$DT = 10.24e^{-0.095T}$$

where DT = digestion time in hours, and  $T$  = temperature in °C. The DT of *S. elegans* collected from 45°N, 165°10'E was 6.7 h when the mean water temperature in the 0–300 m layer was



**Fig. 14.** Daily variation in the FCR (%) of *Sagitta elegans* in the 0–300 m layer at 45°N, 160°–10'E. SS: sunset, SR: sunrise. After Terazaki (1995).

4.5°C. Therefore, the  $FR_n$  was 0.344 and the  $FR_w$  was 0.069 mg indiv.<sup>-1</sup> d<sup>-1</sup> (i.e. 0.042 mgC indiv.<sup>-1</sup> d<sup>-1</sup>). The population density of *S. elegans* in the 0–300 m layer was approximately 150 indiv. m<sup>-2</sup>. Therefore, they must have consumed 6.3 mgC m<sup>-2</sup> d<sup>-1</sup> from the 0–300 m layer of the water column. The primary productivity level of this area during spring was 1700 mgC m<sup>-2</sup> d<sup>-1</sup> (Taniguchi 1972). Assuming that the conversion efficiency from primary production to secondary production at 45°N, 165°10'E is 10% (Ryther 1969), *S. elegans* would consume 4% of the total secondary production daily (Terazaki 1995).

Several workers have estimated the percentage of herbivore standing stock and/or secondary production consumed by the chaetognath population as an extension of their analyses of feeding rates and metabolic activity. The percentage of secondary production consumed daily by *S. elegans* was more than 100% in St. Margaret's Bay, Nova Scotia, during the winter and early spring (Sameoto 1972), 36% in Bedford Basin, Nova Scotia (Sameoto 1973), and 10% in the Bering Sea during summer (Kotori 1976).

### Future Prospects

Tokioka (1965) and Bieri (1991) divide the genus *Sagitta* into different genera. According to their taxonomic method, *Sagitta elegans* belongs to the Genus *Parasagitta*. However the relationship between these genera remains unclear. Interesting preliminary attempts have been made using numerical methods to examine the relationship between chaetognath genera and species groups within genera, and these may well prove themselves successful as more is discovered about the taxonomic structure of chaetognaths. A more promising approach is that of examining sequence similarities in the variable regions of the 18 and 28S rDNA loci of differ-

**Table 5.** Food containing ratio (%) of *Sagitta elegans* at 40°N, 139°E in the northern Japan Sea. After Terazaki (1993b).

Sampling depth (m)	Day	Night
200	10.8	0
300	2.8	2.0
400	1.0	3.2
500	5.8	1.0
700	0	2.0
1000	0	0

ent species.

Studies on the feeding behaviour, growth, reproduction and chemical analyses of *Sagitta elegans* in the western Pacific Subarctic Water have not been done to the same degree as in the Atlantic or eastern Pacific. It is necessary to gather data such as this and to relate it to horizontal and vertical distributions of *S. elegans* in western Pacific Subarctic Waters.

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