

Review

# Life history strategy of the chaetognath *Sagitta elegans* in the World Oceans

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**Abstract**—*Sagitta elegans* is the best-studied chaetognath in the world ocean. This species typically inhabits the upper 100 to 150 m in the arctic and subarctic area of both the Atlantic and Pacific. *S. elegans* was also reported from the North Pacific Intermediate Water and the meso- and bathypelagic layer in the Sea of Japan. Diurnal vertical migration is recognized in the various waters. The size and number of grasping spines and teeth of *S. elegans* in the Sea of Japan are greater than those from the Pacific. They also have developed intestinal tissue containing oil droplets similar to meso- and bathypelagic species. These features are adaptations to the deep-water environment. Number of generations per year, life span and growth rate depend on the waters inhabited. In general, *S. elegans* mature at large sizes in lower temperatures and life span is short in warm regions. Food is also an important factor controlling their growth. Feeding activity of *S. elegans* in the various waters of the Pacific is high during the night time. The major food organisms are copepods. *S. elegans* inhabiting the open sea consume larger copepods compared to those in coastal waters. The percentage of secondary production consumed daily by *S. elegans*, was 36% in Bedford Basin, Nova Scotia, 10% in the Bering Sea and 4% in the western North Pacific, respectively.

**Key words:** distribution, migration, breeding, life cycle, feeding

## Introduction

*Sagitta elegans* is a chaetognath typically of the upper 100 or 150 m in the Arctic and Subarctic regions, and extends into the northern part of both the Atlantic and Pacific (Alvariño 1965). There have been quite a few synonyms use for this species but it is now considered that there are three different forms (Fraser 1952) which vary in size depending on temperature of the water in which they develop. The numbers of hooks and teeth vary slightly in the three forms. Fraser (1952) described the three forms as: *S. elegans elgans*, a coastal form with oceanic influence; *S. elegans arctica*, a broad-arctic form and *S. elegans baltica* as the smallest form found only in or near the Baltic Sea. In this paper, I review the distribution, migration, life cycle and feeding of *S. elegans* in the Atlantic and Pacific Ocean.

## Distribution and Migration

The southernmost record of *S. elegans* in the eastern Atlantic is off La Rochelle (northern Bay of Biscay) at about 46°43'N (Bainbridge 1963, Alvariño 1965), and the southern limit in the west Atlantic is near Cape Hatteras (about 36°N:

Bigelow and Sears 1939). It is the most abundant chaetognath in the Gulf of Maine, which is the most important center of reproduction at the southern boundary of its distribution region (Bigelow 1924). From the Gulf of Maine, it extends southward to the Chesapeake Bay in cold summers and reaches farther south in winter (Alvariño 1964, Grant 1977). The high temperature, or the combination of temperature with high salinity, at the edge of the Gulf Stream constitutes an impassable barrier.

*S. elegans* extends into the western Pacific to 38°N being present in the Oyashio waters, but when those waters become confluent with the Kuroshio the southern distribution is abruptly interrupted, even at deep levels, in the region where the two bodies of water meet (Alvariño 1964). *S. elegans* is abundant in Dabob Bay, Washington and off Oregon (King 1979, Johnson et al. unpubl.). Bieri (1959) considered the southern boundary to be at about 40°N to 41°N in the east Pacific. The southern most record of *S. elegans* in the west Pacific is the southern Japan Sea near the Tsushima Strait (Tokioka 1957, Terazaki 1993b), and Sagami Bay (Marumo 1966) where warm Tsushima and Kuroshio Currents covered the surface layer. Park (1970) reported the occurrence of this species from the Yellow Sea.

The spatial distribution and seasonal variability of

epipelagic chaetognaths along the Kurile Islands and off south-east Hokkaido, in the western subarctic Pacific Ocean, were investigated during the period from May 1990 to October 1992. *S. elegans* was dominant among the epipelagic species. Adults appeared in spring (April–May) and small individuals (Juveniles and Stage 1) were abundant in summer (June–July) when the strong thermocline developed. Juveniles were present exclusively in October 1990 and January 1991. Juvenile *S. elegans* inhabited a wide range of water temperatures compared with Stage 1, 2 and 3 individuals (Fig. 1). Juvenile habitat was less than 10°C in January–April and then increased in summer and autumn to 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). In Otsuchi Bay, northern Japan, *S. elegans* carried by the Oyashio cold current, appeared in spring (March–April) and disappeared in summer (July) when water tempera-

ture reached 15°C (Terazaki and Marumo, 1982).

Much of the work on vertical migration among chaetognaths concerns *S. elegans*. The evidence for vertical migration is largely based on the variations in the numbers caught at different points of time in relation to depth and not on experimentally determined responses to selected environmental factors. Various hypotheses have been put forward to explain vertical migration, for example, the availability of food in the surface layers and the advantage of lower metabolism at the deeper layers; avoidance of visual predation; horizontal dispersion and transport, and breeding migration (McLaren 1963, Pearre 1973, 1979, Longhurst 1976; Terazaki 1998).

The studies of diurnal vertical migration in the Polar Seas, Barents, White and Kara Seas, made by Bogorov (1939, 1940) are of special interest since they show the behaviour of the animals under a wide variety of light conditions through the seasons. *S. elegans* maintained an almost unchanged vertical distribution throughout a 24-hour period during the summer in the Barent Sea. Bogorov considered that the animal tend to occupy a definite level related to an optimum light intensity. In the Barents Sea, tidal effects force the animals to adjust constantly in order to maintain their levels with respect to this optimal light intensity.

Russell (1931) has studied in some detail the vertical distribution of *S. elegans* in the Plymouth region. He noticed that adults are more sensitive to light than young. In the Celtic Sea, the smallest *S. elegans* (2 to 6 mm) were found in the near-surface waters and did not migrate, but as their lengths increased they occupied deeper depth ranges and a proportion of the population started to migrate diurnally. Individuals which did not migrate, matured faster than those living in the colder water below the thermocline. Migration to surface waters by mature individuals seemed to be stopped by high surface temperature (17°C) and a sharp thermocline (Conway and Williams 1986).

Kotori (1972) reported the maximum abundance of this species was from 70 to 200 m and the species reached 500–610 m in the southern Bering Sea. *S. elegans* was usually distributed in the upper 250 m, but many individuals (mostly Stage 1 and 2) appeared in the mesopelagic layer between 250 and 1000 m in October and November at Ocean Station P (Terazaki and Miller 1986; Fig. 2). No *S. elegans* were collected from the surface layer on several sampling dates (late March, August, September, mid-November). In the summer of 1997, juveniles always inhabited the surface layer in the western subarctic Pacific and Bering Sea, but they inhabited the underlying layer in the eastern subarctic Pacific. Stage 1–3 concentrated into the upper 150 m in the western subarctic Pacific but were distributed widely from 20–300 m in the Bering Sea. Among them, Stage 2 and 3 migrated rather synchro-

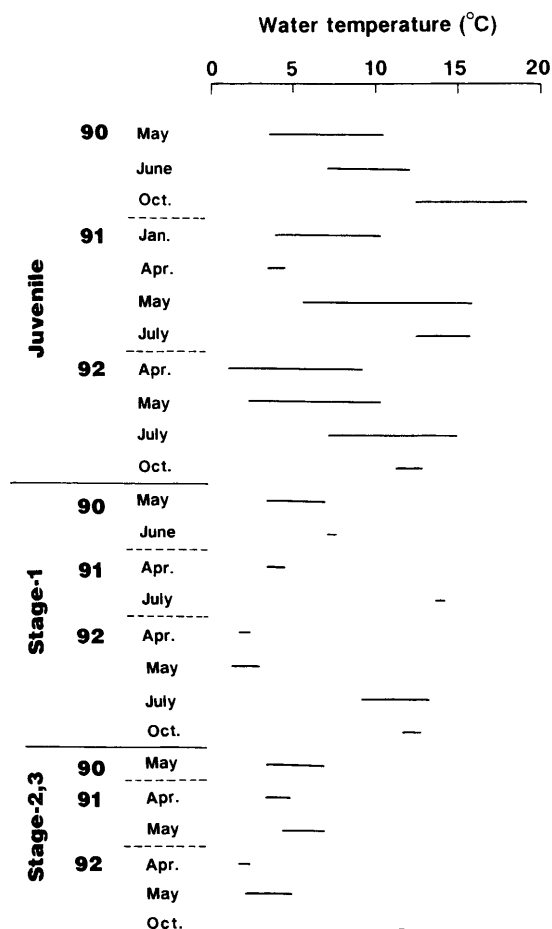
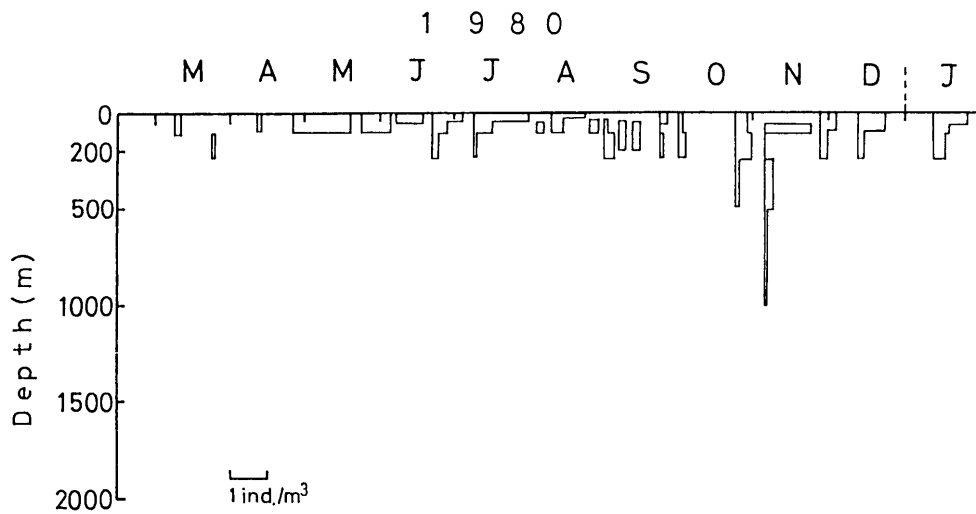


Fig. 1. Range of mean water temperatures from the habitats in which *Sagitta elegans* were collected during period from May 1990 to October 1992 off south-eastern Hokkaido, Japan. After Terazaki et al. (1995).



**Fig. 2.** Vertical distribution of *Sagitta elegans* at Station P (March 1980 to January 1981). Scale for individuals per  $\text{m}^3$  is shown. After Terazaki and Miller (1986).

nously over a wide vertical range in the eastern subarctic Pacific (Matsuda and Taniguchi 2001). In the shelf region of the northern Gulf of Alaska, two generations showed asynchronous diel vertical distribution patterns, with the smaller individuals found near the surface during the day whereas the large individuals were near the surface at night (Brodeur and Terazaki 1999). Seasonal changes in the vertical distribution of the proportion of the population that vertically migrated reflected the stage of maturity and the size of the individuals in Dabob Bay, Washington (King 1979). Small chaetognaths were non-migratory and distributed in the top 100 m. Stage 2 individuals were dispersed throughout the water column; some diel migration was evident. Ohman et al. (1983) reported that the copepod *Pseudocalanus* sp. exhibited an unusual reverse diel vertical migration in Dabob Bay, concurrently with a normal vertical migration by nocturnal invertebrate predator like *S. elegans*. Reduced spatial overlap with predators appeared to decrease mortality rate of adult female *Pseudocalanus*.

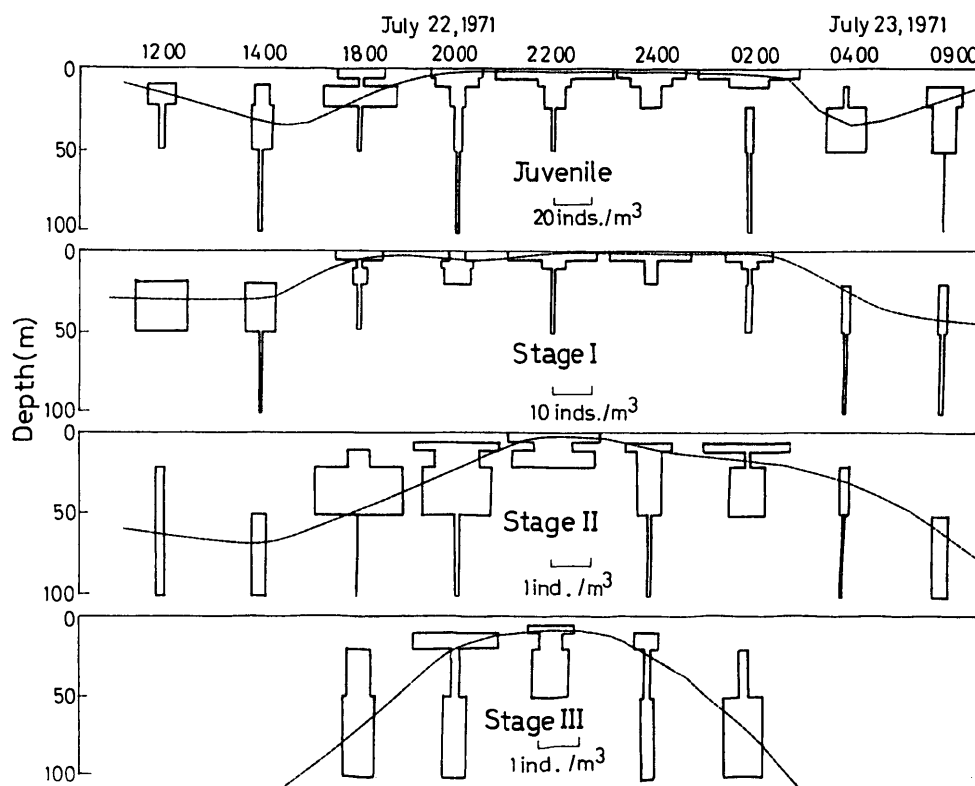
According to time series observations in the 0–300 m layer at  $45^{\circ}\text{N}$ ,  $160\text{--}10^{\circ}\text{E}$  on 13–14 May, 1991, the population density of *S. elegans* was heavily influenced by the sudden variation in light intensity at sunrise and sunset. None were collected in the layer above 40 m during the day although they moved up to the 0–40 m layer after sunset (Terazaki 1995). Well-defined data on diel vertical migration of *S. elegans* was obtained from every 2-hours observation at Stn. B ( $44^{\circ}\text{N}$ ,  $150^{\circ}\text{E}$ ) during July 22–23, 1971. Juvenile were distributed in the layer deeper than 10 m between 1200 and 1400 hrs. After sunset, they appeared in the surface at 1800 hrs and were most abundant in the 0–10 m layer in night-time between 2000 and 0200 hrs. Just before sunrise, they moved into the 10–50 m

layer at 0400 hrs. They were observed from 10 to 100 m at 0900 hrs. Adults of *S. elegans* showed the largest scale of vertical migration (Fig. 3). The average speed per hour of upward and downward migration was 8 m in ascent and 10 m in descent in juvenile, 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 and Marumo 1979). Kotori et al. (1987) investigated the vertical distribution of *S. elegans* under sea ice in Saroma Lake, a small Lagoon in Hokkaido, northern Japan in the daytime in February 1986. The maximum distribution layer was observed at a depth of 2 m beneath the undersurface of the ice.

The body size ranged from 15.4 mm to 27.1 mm and the abundance was estimated to be  $10\text{--}30\text{ inds. m}^{-3}$ .

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 recognized at about 300 m depth. *S. elegans* inhabited mainly the intermediate water existing under the core water. They reached the epipelagic layer of the KWCR by vertical migration from intermediate water but could not 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 spring, 1981 and 1982. Remarkable diel migration of Stage 1 and 2 individuals was recognized and the distance was 30–40 m (Terazaki et al. 1985).

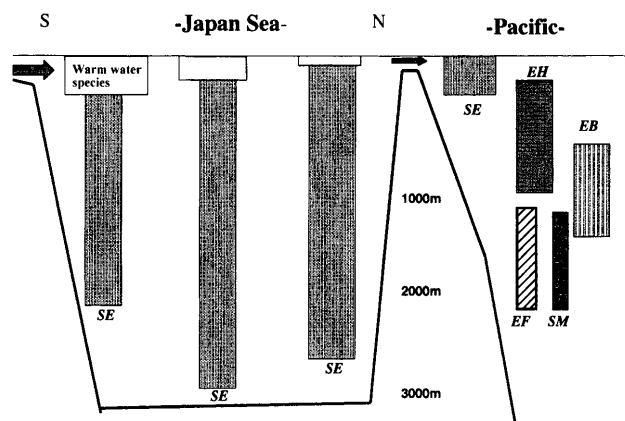
The Sea of Japan is a semi-isolated marginal sea connected with the Sea of Okhotsk, the North Pacific, and East China Sea through 4 shallow straits. The only important cur-



**Fig. 3.** Diurnal vertical migration of *Sagitta elegans* at St. B (44°N, 150°E) in western North Pacific on July 22–23, 1971. After Terazaki and Marumo (1979).

rent flowing into this sea today is the warm Tsushima Current flowing into the Sea of Japan through the southern strait. Between 10000 and 20000 yrs ago, the cold Oyashio Current flowed into the Sea of Japan through its northern straits. The epipelagic chaetognath *S. elegans* was introduced into this 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 current within the last 10000 yrs and inhabit the epipelagic layers. *S. elegans* is distributed as deep as 1000 m or more (Terazaki 1993b). Seventeen species belonging to 3 genera were collected from the Sea of Japan. The most abundant species was *S. elegans*, comprising 93.9 to 100.0% of the individuals collected from the 0 to 1000 m.

The vertical dispersal of *S. elegans* is facilitated by the absence of competitors such as *Eukrohnia hamata*, *E. bathypelagica*, *E. fowleri* and *S. macrocephala* in this marginal sea (Fig. 4). The size and number of grasping spines and teeth of the Sea of Japan specimens 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 (Terazaki 1993b). There is no specific level difference between the Sea of Japan and Pacific populations by the results of genetic



**Fig. 4.** Vertical distribution of chaetognaths in the Sea of Japan and Pacific. SE: *Sagitta elegans*, EH: *Eukrohnia hamata*, EB: *E. bathypelagica*, EF: *E. fowleri*, SM: *S. macrocephala*.

works (Thuesen et al. 1993).

**Life cycle**

Generally, the animals die after spawning (McLaren 1966). But Jakobsen (1971), King (1979) and Conway and Williams (1986) stated that *S. elegans* must spawn several times over a period of months.

The number of eggs contained in the ovary of individual

mature *S. elegans* is 50–100 (McLaren 1966) and the body length of newly hatched *S. elegans* ranges from 1.23 to 1.42 mm long (Kotori 1975). Seven-day-old larvae (1.94 mm long) have eight hooks at 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).

It has always been difficult to determine actual ages of chaetognaths because they are soft-bodied animals without definable landmarks in their development. Possible candidates might be the age pigment (lipofuscins) which have been experimentally investigated in crustaceans and fish, or pteridine, which has been used less broadly but with similar results (Nicol 1987). Generally, we estimate the life span of chaetognaths from the cohort analyses by using the size frequency distribution of body length and their maturity stages.

Many reports mention the breeding and life cycles of *Sagitta elegans*. Recently, Pearre (1991) reviewed the life cycle of *S. elegans* mainly inhabiting in the Atlantic. The number of generations produced each year increase with the distance from the poles (Owre 1960). *Sagitta elegans* produces one brood per year in the Arctic–Subarctic water (Kramp 1939). *S. elegans* has two to five (or more) broods towards the southernmost boundary of its distribution in temperate region (Table 1).

In the Arctic, Kramp (1939) found a single generation *S.*

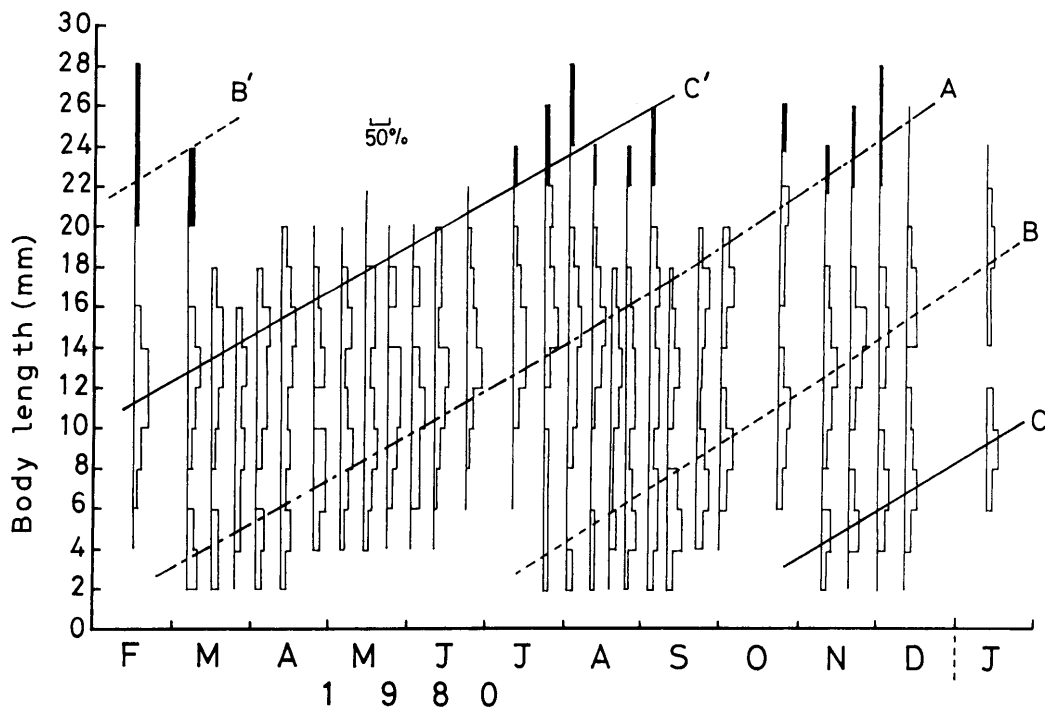
*elegans arctica* around Greenland, and Sameoto (1987) has reported an annual cycle in Baffin Bay. However, Bogorov (1940), Dunbar (1962) and McLaren (1966) reported that *S. elegans* was biennial in arctic waters, although a population of much smaller animals in the semi-landlocked arctic Ogac Lake appeared to be annual (Dunbar 1962, McLaren 1969).

In the eastern Atlantic, Pierce (1941) and Khan and Williamson (1970) reported one generation per year in the Irish Sea, whereas Conway and Williams (1986) reported three in the Celtic Sea. Wimpenny (1937) reported three generations per year in the North Sea. Jakobsen (1971) found one generation in Oslofjorden, western Norway, and Tande (1983) reported a single generation in Balsfjorden, northern Norway, although with possible multiple population modes. Øresland (1985) reported a single generation in Gullmarsfjorden, as did Båmstedt (1988) for Kosterfjorden, both in southern Sweden.

In the western Atlantic, Hunstman and Reid (1921) reported one generation in the Gulf of St. Lawrence, eastern Canada, although Weinstein (1972) found a biennial life cycle there. Sameoto (1971) reported two generation per year in each of four subpopulations in Saint Margaret's Bay, Nova Scotia- the first serious attempt to distinguish perceived maturity peaks from actual generation. Both Sameoto (1973) and Zo (1973) found two generations per year in the nearby Bedford Basin. Redfield and Beale (1940) and Sherman and

**Table 1.** Breeding season, number of yearly generations, estimate life span and size of fully matured individuals of *Sagitta elegans* in the world oceans.

Location (Lat.)	Breeding season	No. of generations	Life span (month)	Maturity size (mm)	Reference
Arctic Waters					
Hudson Bay (65N)		0.5	24	20–40	Dunbar (1962)
Eastern Atlantic					
Oslofjorden (60N)	April–late summer	1	12	18–30	Jakobsen (1971)
Gullmarsfjorden (58N)	March–August	1	12	15–31	Øresland (1985)
Irish Sea (54N)	April–Summer	1		12–24	Alvaren-Cadena (1993)
Celtic Sea (51–30N)	May–July	3		10–20	Conway & Williams (1986)
Western Atlantic					
Saint Margaret's Bay (44–30N)	Feb., June–July	2	3–7	13–30	Sameoto (1971)
Bedford Basin (44–30N)	March–June, Sept.–Dec.	2	<8	18–30	Zo (1973), Sameoto (1973)
Long Island Sound	April–May, late June	2		13–22	Tiselius & Peterson (1986)
Eastern Pacific					
Station P (50N)	Spring, Summer, Autumn	3	6–10	24–48	Terazaki & Miller (1986)
Dabob Bay (47–45N)	March–Aug.	2	4–5	17–30	King (1979)
Western Pacific					
Southern Hokkaido (42–43N)	May–June	1	12–24	27–35	Kotori (1999)
Site H (42N)	late spring–Summer	0.5	24	24–37	Nishiuchi (1999)
Sea of Japan					
off Tsugaru Pen. (41N)	Autumn (not clear)	0.5	24	26–42	Terazaki (unpubl.)
Yamato Bank (39N)	Spring	0.5	24	26–41	Nishihama & Hirakawa (1997)
Toyama Bay (37N)	March–May, Aug.	2	10–12	26–36	Terazaki (1993)



**Fig. 5.** Monthly size-frequency distribution for *Sagitta elegans* at Station P (February 1980 to January 1981). Shaded area represents proportion of individuals at full maturity. Lines A, B and C show growth curves for 1980 cohorts and B' and C' for 1979 cohorts. After Terazaki and Miller (1986).

Shaner (1968) reported one generation per year in the Gulf of Maine, but Clark et al. (1943) suggested that there were two on Georges Bank, adjacent to the south, and thought to be the source for most of the Gulf of Maine population. Clark and Zinn (1937) felt that there were four breeding periods per year immediately south of Cape Cod. Sweatt (1980) reported three generation in the adjacent Rhode Island Sound, as did Deevey (1952) for Block Island Sound, the next Sound to the south. Deevey (1956) thought it 'probable' that there were four in Long Island Sound, adjacent to Block Island Sound, but found the population very sparse. However, Tiselius and Peterson (1986) reported a seasonally very abundant population there, with two discernible cohorts during its time of residence.

In the eastern Pacific, *S. elegans* is the dominant chaetognath in Dabob Bay, Washington. Seasonal variability was pronounced; spring and summer levels of population abundance were approximately 5 times those of fall and winter. From November to April, population density of *S. elegans* was relatively constant suggesting low mortality. The abundance of the population increased sharply in May and June (King 1979). He reported one or (possibly) two generations per year from a population in Dabob Bay, and generation lengths were 4–5 months. *Sagitta elegans* was collected the whole year from Ocean Station P (50°N, 145°W) and abundance was low from February to April. Numbers rose in late spring and early

summer, mainly due to the increase of juvenile (Terazaki and Miller 1986). *S. elegans* had three spawning periods during the year and generation lengths were 6–10 months at Ocean Station P (Terazaki and Miller 1986: Fig. 5). Maximum body length of fully matured adults reached to 48 mm which was the largest in the world oceans.

The spawning period of *S. elegans* were in April–May in the western subarctic Pacific near the Kurile Islands (Terazaki 1995), in May–June in the coastal waters off southern Hokkaido (Kotori 1975), and in April in Otsuchi Bay (Terazaki and Marumo 1982), respectively. In the northwestern North Pacific off eastern Hokkaido, *S. elegans* were most abundant in early June to October, while they were always low in abundance during December to April. The main breeding period was observed in late May to early June and life span was 1 y or possibly 2. Nishiuchi (1999) found a biennial life cycle at Site H (41°30'N–42°30'N; 145°E–146°E) off southern Hokkaido. Body size of matured adults at Site H and Kotori's sampling area were close: 24–37 mm and 27–35 mm, respectively.

In the Sea of Japan, *S. elegans* inhabits the Japan Sea Proper Water characterized by low temperature (0.1–0.3°C), low salinity (34.0–34.1 PSU) and high dissolved oxygen content (5 to 6 ml<sup>-1</sup>) below the Tsushima warm Current. There is no remarkable variation in abundance of *S. elegans* through-

out the year. Many individuals were collected in August in Toyama Bay, southern Japan Sea, and two principal spawning periods were recognized in Toyama Bay, southern Japan Sea (Terazaki 1993a). One is in March–May and the other is in August. Life spans of both cohorts were 10–12 months. Another biennial life cycle was found in the Yamato Basin (Nishihama and Hirakawa 1997) and Station T (41°N, 140°E) off the Tsugaru Peninsula (Terazaki unpubl.) and the breeding seasons were spring and autumn (not clear), respectively.

Sameoto (1971) and Tiselius and Peterson (1986) reported that egg numbers were inversely related to developmental temperature. Growth rates of *S. elegans* increase with temperature (Sameoto 1971, 1973, Conway and Williams 1986). In general, chaetognaths mature at large sizes in lower temperatures (McLaren 1966, Sameoto 1971, 1973, Zo 1973, Pearre 1976). Therefore, growth rate of *S. elegans* inhabiting in the Arctic waters and the Sea of Japan is small compared with other waters and their life span is more than 2 y. Maximum body length can reach 40 mm in both waters. Generally, offshore population are larger at maturity and also more fecund at mature length.

The effect of food is much less well-documented than temperature effects. As chaetognaths swallow prey whole, the maximum size of their prey is limited by their mouth size. Russell (1932) speculated that food supply might affect the size of maturity of *S. elegans* off Plymouth. McLaren (1963)

also suggested that food supply may have affected generation length of *S. elegans* off Plymouth.

The life span of *S. elegans* in the eastern Pacific, is shorter than in the western Pacific (Terazaki and Miller 1986, King 1979, Kotori 1999, Nishiuchi 1999). The range of water temperature of habitats at Station P and Site H was 4.0–13.8°C and 2.0–17.0°C, respectively. Nishiuchi (1999) mentioned that *S. elegans* (Stage-2) inhabited deep and cold water layers during the 5 months from September to January. He speculated that *S. elegans* stopped the growth during this period.

Recently, Imai et al. (2002) compared annual productivity ( $\text{gCm}^{-2} \text{yr}^{-1}$ ) at Station KNOT (44°N, 155°E) with that reported for Station P. Annual productivity at Station P was 140 (Wong et al. 1995) and 217 (Boyd and Harrison 1999) as opposed to 89 (Imai et al. 2002) at Station KNOT.

Therefore, fast growth and short life span in the eastern Pacific might be caused by high temperature and high food availability, compared with the western Pacific. Terazaki and Miller (1986) also suggested that there were probably genetic differences among stocks.

### Feeding

The food of Chaetognaths is considered heterogeneous, including cannibalism, and representatives of every group among plankton: diatoms, ciliates, Tintinnids, Medusae,

**Table 2.** Food organisms of *Sagitta elegans* collected from the world ocean.

Location	Food organisms	Reference
Gullmarsfjorden	<i>Calanus</i> spp., <i>Temora</i> spp. (Copepoda)	Øresland (1987)
Irish Sea	<i>Pseudocalanus elongatus</i> , <i>Oithona</i> spp., <i>Acartia clausi</i> , <i>Centropages</i> spp., <i>Temora longicornis</i> (Copepoda), Polychaeta, Cladocerans	Alvarez-Cadena (1993)
Bedford Basin	<i>Tortanus discaudatus</i> , <i>Acartia longiremus</i> , <i>A. clausi</i> , <i>Pseudocalanus</i> <i>minutus</i> , <i>Temora longicornis</i> , <i>Eurytemora herdmani</i> , <i>E. hirundoides</i> , <i>Oithona similis</i> , <i>O. atlanticus</i> (Copepoda), Chaetognatha, Tintinnids Polychaeta, Rotifers	Pearre (1973)
Gulf of Alaska	<i>Neocalanus</i> spp., <i>Oithona</i> sp., <i>Pseudocalanus</i> sp. (Copepoda), <i>Sagitta elegans</i> (Chaetognatha), Euphausiacea, Ostracoda, Cirripedia	Brodeur & Terazaki (1999)
Station P	<i>Neocalanus cristatus</i> , <i>N. plumchrus</i> , <i>Oithona similis</i> , <i>Metoridia pacifica</i> (Copepoda), Chaetognatha	Sullivan (1980)
British Columbia Eastern Pacific	<i>Neocalanus plumchrus</i> (Copepoda), Fish larvae Copepoda, Euphausiacea, Medusae, Chaetognatha, Fish larvae, Crustacea larvae	Lee (1966) Alvarino (1985)
Western Pacific Otsuchi Bay	<i>Neocalanus</i> spp., <i>Metridia pacifica</i> , <i>Pseudocalanus</i> sp. (Copepoda) <i>Acartia clausi</i> , <i>Oithona</i> spp., <i>Pseudocalanus minutus</i> (Copepoda), <i>Themisto japonica</i> (Amphipoda), Euphausiacea	Terazaki (1995) Terazaki (1995)
Sea of Japan	<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>Discoconchoecia pseudodiscophora</i> (Ostracoda)	Terazaki (1993)

Crustacea, Copepoda, Amphipoda, Cladocera, larval stages of Crustacea, Mollusca, Pteropoda, Heteropoda, Chaetognatha, Tunicata, fish egg and larvae (Alvarino 1985, Feigenbaum 1982, Terazaki 1998). A list of food organisms of *Sagitta elegans* collected from various waters in the Atlantic and Pacific, is given in Table 2. 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 of high prey densities. *Eukrohnia hamata* apparently needs less food and is found mainly below the mixed layer with a vertical distribution restricted by temperature. The same prey species, those with the highest densities at Station P, make up the diet of both chaetognaths, although *E. hamata* eats significantly more small prey. The major prey of juvenile chaetognaths are small cyclopoid copepods, a group frequently overlooked in plankton survey. These species also comprise 41% of the diet of older chaetognaths, which prey in addition on Stage 5 copepodites of the largest copepods. The development of larval chaetognaths depends on the abundance of small prey but the older chaetognaths can handle prey of a wider spectrum of sizes (Sullivan 1980).

The largest components 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, were copepods such as *Pseudocalanus*, *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 size copepods such as *Acartia*, *Oithona* and *Pseudocalanus*. Therefore, *S. elegans* inhabiting the open sea, consume larger copepods compared to those in coastal water (Terazaki 1995).

In the Sea of Japan, a total of 1510 out of 6053 individuals were found to have one or more prey organisms in their gut. The predominant prey were copepods, and the proportion of Copepoda, Chaetognatha, Ostracoda and unidentified items in the gut of *S. elegans* were 74.6, 1.7, 3.4 and 20.3%, respec-

tively (Table 3). Most frequent were calanoid copepods such as species of *Neocalanus*, *Paracalanus*, *Scaphocalanus* sp. and *Aetideus* sp. (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 DT=digestion time in hours;  $FR_n$ =daily feeding rate expressed as number of prey per day;  $FR_w$ =daily feeding rate in terms of total prey weight; MPW=mean prey weight; NPC=number of prey per chaetognath, from gut content analysis.

The Daily feeding rate ( $FR_n$ ) of *S. elegans* inhabiting

**Table 3.** Food organisms in the gut of *Sagitta elegans* in the Sea of Japan. 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

**Table 4.** Daily feeding rate of *Sagitta elegans* in the world oceans.

Location	Mean temperature	Daily feeding rate	Reference
Bering Sea	4.0	0.27	Matsuda & Taniguchi (2001)
Gulf of Alaska	4.9	0.074	Brodeur & Terazaki (1999)
Eastern Pacific	5.1	0.07	Matsuda & Taniguchi (2001)
Western Pacific	3.5	0.180	Matsuda & Taniguchi (2001)
	4.5	0.344	Terazaki (1995)
Otsuchi Bay, Japan	5.5	0.609	Terazaki (unpub.)
Sea of Japan	1.0	0.071	Terazaki (unpub.)
Vineyard Sand Massachusetts	0	0.53–1.33	Feigenbaum (1982)
Gullmarsfjorden Sweden	6.0	0.18–1.00	Øresland (1987)



coastal water (Otsuchi Bay, Vineyard Sand and Gullmarsfjorden) was higher than that in the open ocean (Table 4). Low daily feeding rate less than 0.1 were reported from the northern Gulf of Alaska, eastern Pacific and Sea of Japan. Recently, Baier and Purcell (1997) studied the effects of sampling on apparent feeding by chaetognaths in the South Atlantic Bight, off the coast of North Carolina, USA, in February 1993. Prey loss from gut contents was substantial, with as much as 50% of prey lost in tows of greater than 2 min duration. Usually we spend much time sampling *S. elegans* in the open sea because they are distributed in deeper layers compared with the neritic waters. Therefore, it is not doubtful that the daily feeding rate in the open sea is under-estimated.

The FCR of *S. elegans* collected from 0–300 m layer at 45°N, 160–10°E ranged from 0 to 13.5% (mean=9.6%) and feeding activity was high during the night-time hours (Fig. 6). High feeding activity at night was recognized off Otsuchi Bay and 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 northern Japan Sea (Terazaki 1993b)). Pearre (1981) developed the following equation for the relationship between digestion time and temperature for *S. elegans*:

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

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 hr as the mean water temperature in the 0–300 m layer was

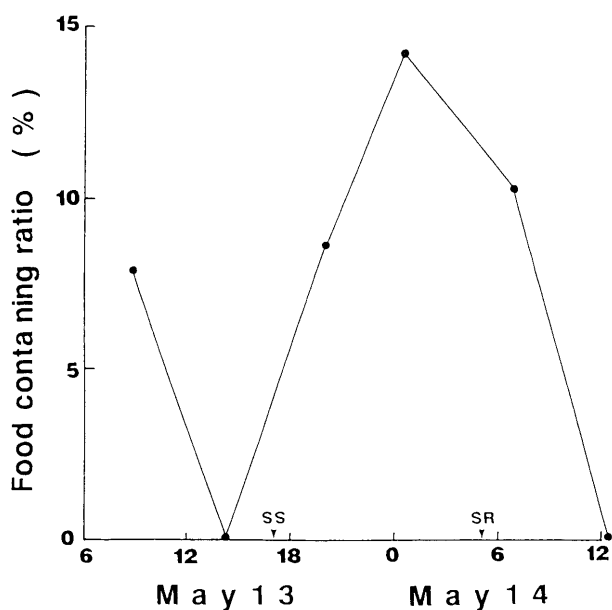


Fig. 6. Daily variations in the Food Containing Ratio (%) of *Sagitta elegans* in the 0–300 m layer at 45°N, 160–10°E in the western North Pacific. SS: sunset, SR: sunrise. After Terazaki (1995).

4.5°C. Therefore, the  $FR_n$  was 0.344 and the  $FR_w$  was 0.069 mg ind.<sup>-1</sup> day<sup>-1</sup> (i.e. 0.042 mgC ind.<sup>-1</sup> day<sup>-1</sup>). The population density of *S. elegans* in the 0–300 m layer, was ca. 150 inds.m<sup>-2</sup>. Therefore, they must have consumed 6.3 mgCm<sup>-2</sup> day<sup>-1</sup> from the 0–300 m layer of the water column. *S. elegans* could consume 4% of the total secondary production daily (Terazaki 1995).

Several workers have estimated the percentage of herbivores standing stock and/or secondary production consumed by a chaetognath population as an extension of their analysis 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), 10% in the Bering Sea during the summer (Kotori 1976) and 4% in western North Pacific during the spring (Terazaki 1995).

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