Life cycle and growth rate of the chaetognath *Parasagitta elegans* in the northern North Pacific Ocean

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Abstract: Breeding periods and growth rate of the typical boreal epipelagic chaetognath *Parasagitta elegans* (Verrill) were investigated in the northwestern North Pacific off eastern Hokkaido. Seasonally, *P. elegans* were most abundant in the epipelagic layers in early June to October, while they were always poor in abundance during December to April. It is suggested that the decrease in abundance in early December was partly due to vertical migration into water deeper than 150 m in winter. The main breeding period of the chaetognath was observed in late May to early June. Some cohorts produced by the spawning populations were able to be traced at least until early December. Thus, the mean growth rate of the cohorts was estimated to be 0.03 to 0.29 mm d^{-1}, averaging approximately 0.1 mm d^{-1}, which corresponds to 3 mm month^{-1}. This value is lower than that (5 to 6 mm month^{-1}) reported from the Gulf of Alaska, eastern North Pacific. Although the generation length of *P. elegans* is still uncertain in the present area, it is probably longer than that in the northeastern Pacific Ocean, being 1 year or possibly 2 years. This suggests that reproductive and high growth periods in *P. elegans* are seasonally more strictly defined in the western parts of the North Pacific Ocean than in the eastern, due to the larger magnitude of seasonal fluctuations in oceanographic conditions in the former than in the latter.

Key words: chaetognath, *Parasagitta elegans*, breeding period, growth rate, northern North Pacific

Introduction

Parasagitta elegans (Verrill) (Tokioka 1965; Bieri 1991) or *Sagitta* (*Parasagitta*) *elegans* Verrill (Terazaki 1997) is a boreal chaetognath widely distributed throughout the epipelagic layers of the subarctic seas (e.g. Nishiuchi et al. 1997). Its reproduction and life history has been studied in depth (Kotori 1979), and it is undoubtedly the most researched chaetognath on the planet (Pearre 1991). However, in the North Pacific Ocean, information on the breeding period, growth rate, generation length and life history of this chaetognath remains limited (see also recent review by Terazaki 1998). King (1979) reported one or (possibly) two generations per year from a population in Dabob Bay, a fjord attached to Hood Canal in Puget Sound, Washington, northwestern USA. Terazaki & Miller (1986) reported that this species had three spawning periods during the year (April to May, August to September, and October to December), and that the generation length was 6 to 10 months at Ocean Station P in the Gulf of Alaska, eastern subarctic Pacific. In the northwestern North Pacific Ocean, Terazaki et al. (1995) confirmed that *P. elegans* was spawning in April–May (Kotori 1975).

The purpose of this study is to describe the seasonal cycles of abundance, population structure, breeding period and growth rates of *P. elegans* in the northwestern North Pacific Ocean. The results will be compared with previous studies mainly carried out to the eastern side of the North Pacific Ocean.

Materials and Methods

Zooplankton samples were collected from 150-m depth to the surface by vertical tows of a North Pacific standard net (Norpac net, 45-cm mouth diameter, 0.33-mm mesh opening; Motoda 1957, 1994) bimonthly from 18 February 1992 to 6 December 1995, at 4 to 5 stations (Fig. 1). At Stn P11, the tows were made from the bottom (about 100-m depth) to the surface. In addition, one sample collected in an oblique tow from 465-m depth to the surface using Bongo nets (70-cm mouth diameter, 0.33-mm mesh opening) at Stn P13 at night on 5 December 1996 was also analyzed. A flowmeter (Rigosha) was mounted at the center of the mouth ring of the nets to estimate the volume of water
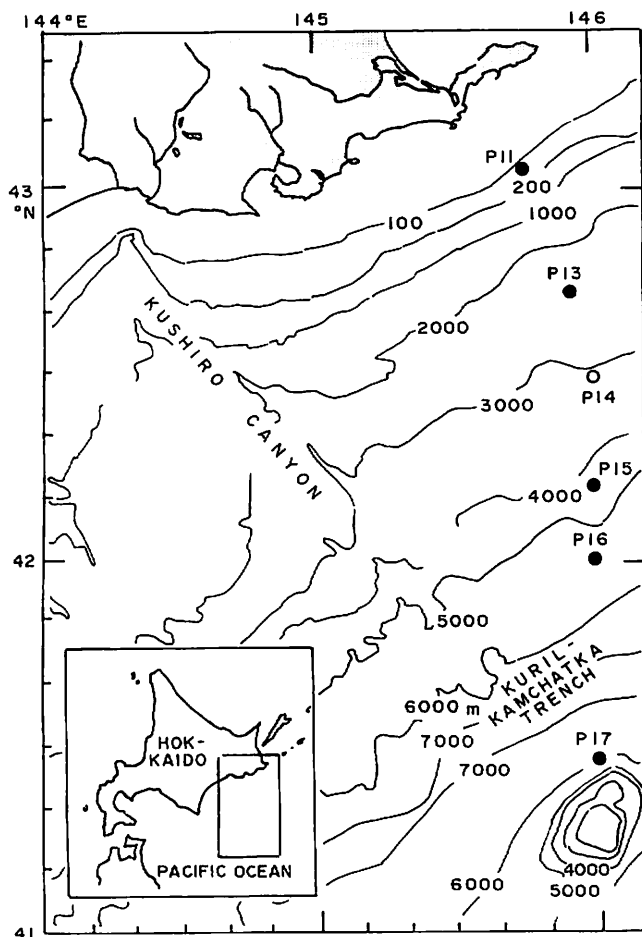
Fig. 1. Sampling stations in the northwestern North Pacific Ocean. Samples were collected mainly at the 5 stations shown with *solid circles*. An *open circle* indicates the location of an additional station at which occasional samplings were made. Depth contours are shown.

filtered. A depth meter (MDS-D, Alec Electronics) was used to register the depth of the Bongo net haul. All samples were collected during cruises of the R.V. *Hokushin Maru* of the Hokkaido Kushiro Fisheries Experimental Station, Kushiro, Hokkaido. They were fixed in a 10% formalin–sea water solution. A total of 114 samples were collected and examined for this study. Seventy-two of these were collected at night, 32 during the day, and 10 were obtained during twilight hours. However, all samples were treated disregarding differences in the time of collection, because the *Parasagitta elegans* population in the northern North Pacific is most abundant in the upper 100 m during both the day and night (Kotori 1976), although Terazaki & Miller (1986) found that some younger-stage animals (mostly immature specimens and not larvae or juveniles; see Kotori 1976 for the definition of the developmental stages of this species) appeared in the mesopelagic layer between 250 and 1000 m in October and November at Ocean Station P (50°N, 145°W) in the northeastern North Pacific Ocean.

CTD casts were carried out with a Seabird CTD meter at each station, and the hydrographic data collected on the cruises of the *Hokushin Maru* will be published in the "Data Record of Oceanographic Observations" by the Hokkaido Fisheries Experimental Station.

In the laboratory, chaetognaths were separated from the composite samples. Species were identified and counted under a stereo microscope. The body length of *P. elegans*, from the tip of the head to the end of the tail excluding the tail fin, was measured for 715 individuals in total collected from 1992 through 1994 and in 1996. The maturity stages of the ovaries were determined for the individual specimens after staining with a solution of neutral red. The ovaries of Stage I are minute with no visible ova when viewed under a stereo microscope of low magnification ($\times$40); Stage II has broad ovaries but with no ova of full size (300 μm in diameter, see Huntsman & Reid 1921; McLaren 1969; Zo 1973; Kotori 1975); Stage III has ovaries with at least one ovum of full size.

Hypothetical cohorts were extracted from the length–frequency distribution by probability paper methods (Harding 1949). The growth rate of *P. elegans* was estimated from the temporal change in mean length of individuals in the hypothetical cohorts.

Results

Seasonal variation in abundance

In 1992, 1994 and 1995 (Fig. 2), the maximum mean abundance of *Parasagitta elegans* was observed from late July to early August (mean, 1.7–5.3 indiv. m^{-3}), while in 1993 (Fig. 2) peaks occurred both in early June (4.2$\pm$6.0 indiv. m^{-3}, mean$\pm$SD) and in early October (4.8$\pm$7.3). A clear peak in abundance was observed only once in 1992 during late July (Fig. 2).

Additionally, the mean values of abundance were always lower than 1 m^{-3} from early December to April throughout the 4 years except on 18 and 19 February 1992 (Fig. 2). On 5 December 1996, the abundance of this species was estimated to be 0.6 m^{-3} (768 indiv. haul^{-1}; water volume filtered was 1286.8 m^3) from 465-m depth to the surface at Stn P13 at night.

Breeding periods

Mature individuals of *Parasagitta elegans* were observed from February to early October (Fig. 3). Two cohorts were also found in the upper 465 m at Stn P13 on 5 December 1996, as in December 1992 to 1994 (Fig. 3). The larger cohort averaged 31.05$\pm$2.17 mm (mean$\pm$SD) in length and the smaller 18.19$\pm$4.93 mm. No fully matured animals were found in either case.

Although fully matured animals occurred from February to October, the majority of individuals less than 4 mm in length were found in late May to early June (Fig. 3). Thus, it is likely that the main breeding period of this chaetognath
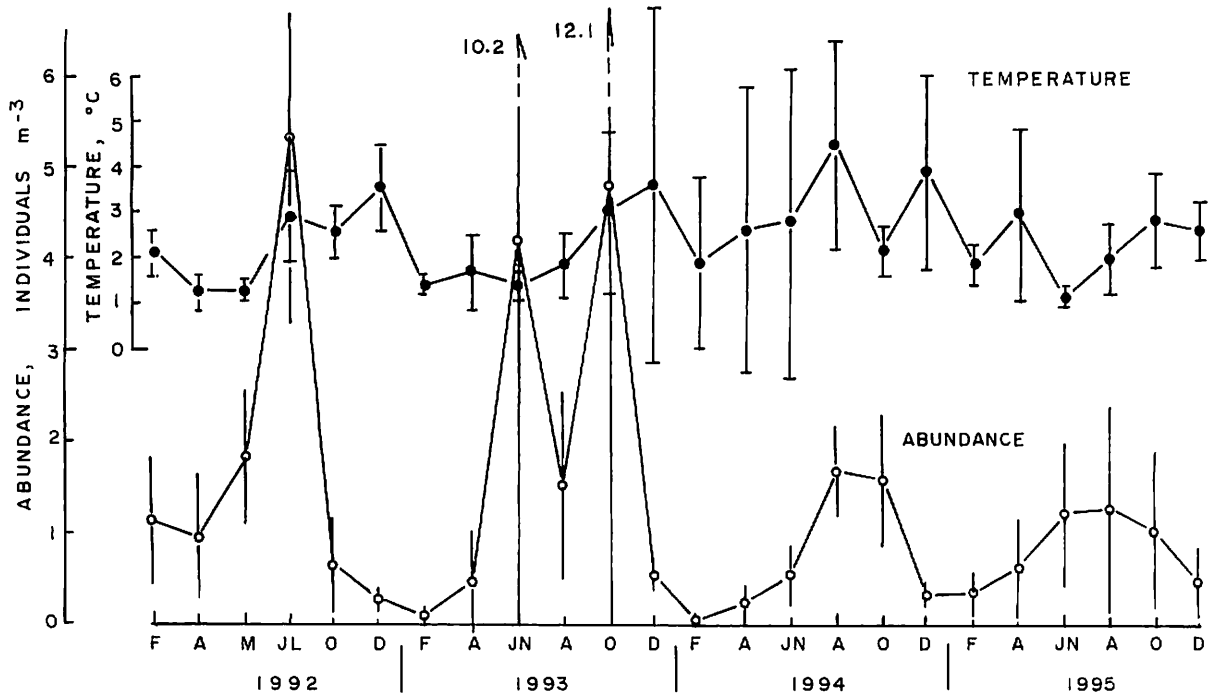
Fig. 2. Bimonthly average catch (abundance, mean±SD) standardized to number per m³ for *Parasagitta elegans* in the upper 150 m and sea water temperature (mean±SD) at a depth of 100 m from 18 February 1992 to 6 December 1995 in the northwestern North Pacific Ocean. *Bars* indicate standard deviation (SD).

was in late May to early June in this area.

Growth rate

The distribution and abundances of *Parasagitta elegans* are partly attributed to advective supply, which makes analysis of population dynamics difficult in the study area. However, it is probable that the main breeding period of this chaetognath was in late May to early June as outlined above, and a cohort produced in this period by the breeding population of *P. elegans* was able to be traced at least until ealy December (Fig. 3A–C). The body length of fully mature animals was 27.3–34.7 mm.

There were three cohorts present on 21 May 1992 (Fig. 3A). The average length of *P. elegans* in the largest cohort was 30.08±2.20 mm (mean±SD), in the middle cohort was 16.62±2.59 mm, and in the smallest cohort (Cohort P) was 2.69±0.69 mm. The growth of Cohort P was able to be traced from May to November, 1992 (Fig. 3A), and probably through to June, 1993 (Fig. 3B).

Cohort P reproduced after about one year in late May, giving rise to Cohort Q (Fig. 3B). The growth of Cohort Q was able to be clearly traced until 15 April 1994 (Fig. 3C). Although we were unable to find any fully mature adult forms in late May to early June in 1994, Cohort R would be the offspring of Cohort Q if Cohort Q were fully mature after about one year, as was the case for Cohort P (Fig. 3C).

Cohorts P and Q included two groups (Groups P' and Q'), respectively, growing more rapidly than their sister

group (Fig. 3B). A cohort of intermediary size appeared on 5 October in 1992 (denoted by the letter X in Fig. 3A) and it was not clear if this cohort corresponded to be Group P' or not. It appears that Group P' bred in spring in 1993 (Fig. 3B).

Our results (Fig. 3C) suggest that Cohort R did not split into two groups of differing growth rates, as was the case for Cohorts P and Q, but instead consisted of one group. There were 4 independent cohorts co-occurring during the period from 1 to 4 August 1994. The smallest cohort (mean length±SD, 3.68±0.48 mm) was probably the offspring of the largest one (28.44±2.20 mm). Growth of this cohort (Cohort T) was able to be traced until 6–7 December 1994 (Fig. 3C).

Consequentially, we were able to calculate the growth rate of each hypothetically extracted cohort or group as shown in Fig. 4.

Discussion

In the eastern subarctic Pacific Ocean, Terazaki & Miller (1986) recorded two peaks in abundance for *Parasagitta elegans* at Ocean Station P from May to July and in October 1980. Our results (Fig. 2) indicate that *P. elegans* were most abundant from early June to October with no clear peaks in abundance in the three years 1993, 1994 and 1995, and that abundances varied from year to year. A clear peak in abundance was observed only once, in late July in 1992. Abundances were always lower during the December to April pe-
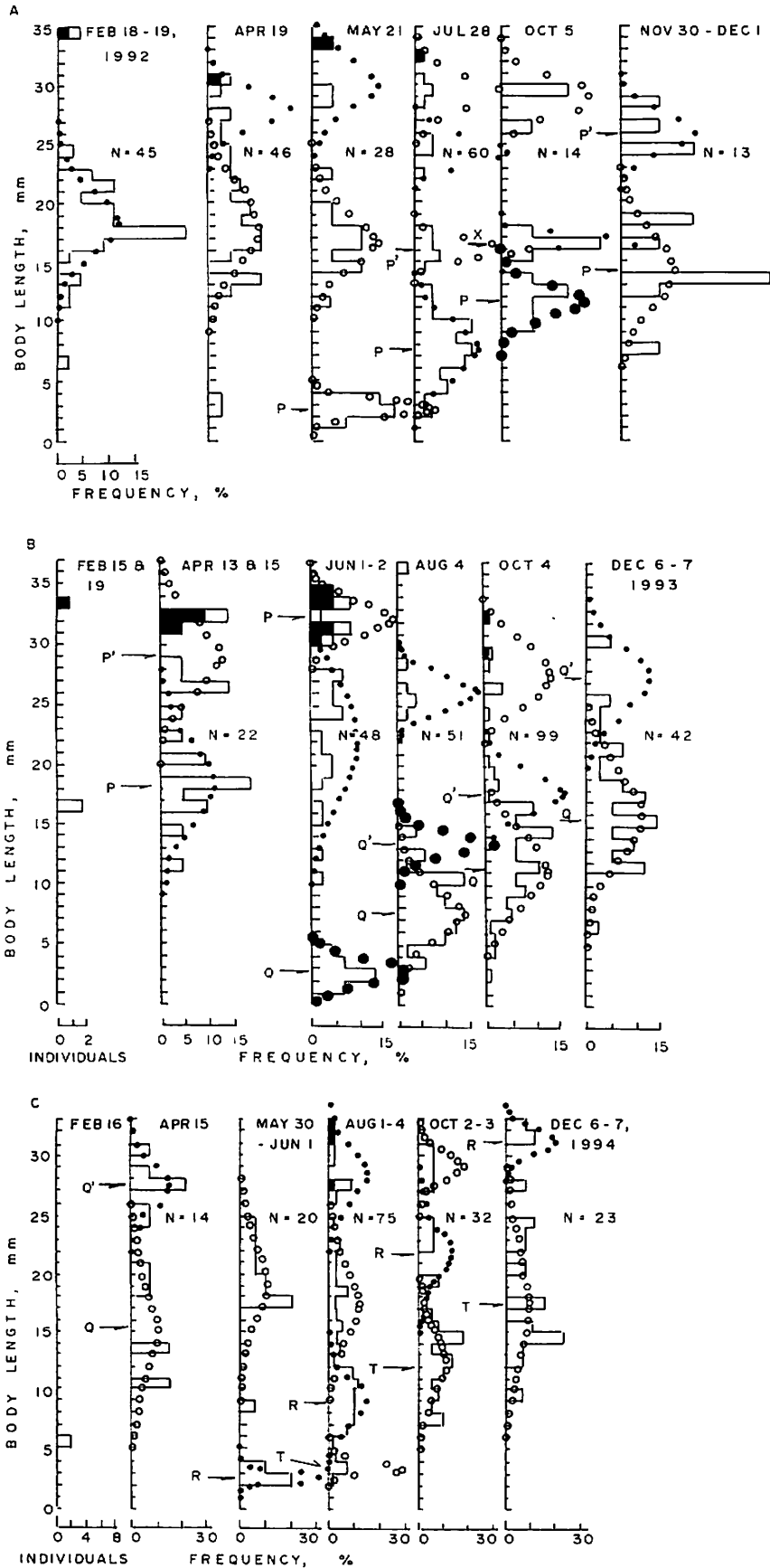
Fig. 3. Bimonthly size-frequency distribution of *Parasagitta elegans* in the upper 150 m through three years: 1992 (**A**), 1993 (**B**) and 1994 (**C**) in the northwestern North Pacific Ocean. *Dotted lines* superimposed on the histogram were determined by probability paper methods. *Shaded area* represents proportion of individuals at full maturity (Stage III, see text). *Arrows* with letters P, Q, R, T, P' and Q' indicate mean length of hypothetically extracted cohorts (Cohorts P, Q, R and T) and Groups P' of Cohort P and Q' of Cohort Q, respectively. An *arrow* with a letter X (5 October 1992) indicates the mean length of an uncertain cohort, the origin of which cannot be determined.
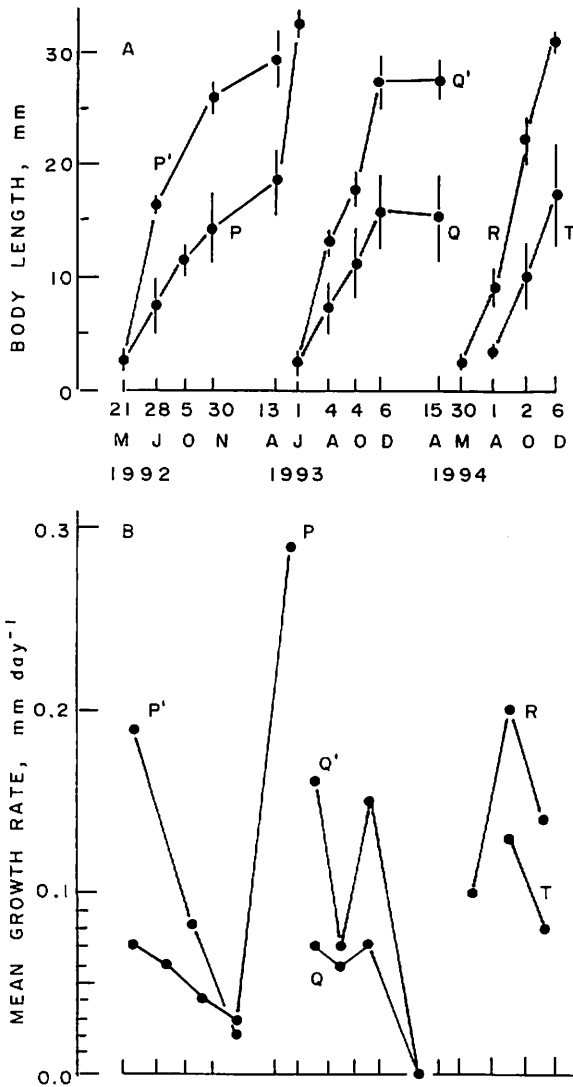
Fig. 4. Increment of mean body length (mean±SD, A) and estimated growth rates (B) of four hypothetically extracted cohorts (Cohorts P, Q, R and T) and two groups (Groups P' of Cohort P and Q' of Cohort Q) of *Parasagitta elegans* from 21 May 1992 to 6 December 1994 in the northwestern North Pacific Ocean. Bars indicate standard deviation. See also Fig. 3.

riod than at any other time for all 4 years from 1992 to 1995.

Terazaki & Miller (1986) suggested that *P. elegans* migrate into waters deeper than 150 m during winter, because many individuals (mostly Stage I and II) appeared in the mesopelagic layer between 250 and 1000 m in October and November at Ocean Station P (50°N, 145°W). Our results indicate that the abundance of *P. elegans* in the upper 465 m at Stn P13 was $0.6 \, m^{-3}$ on 5 December 1996, and this is comparable to the values obtained for the upper 150 m through December to April from 1992 to 1995 (Fig. 2). This implies that the 0–150 m water column contained only one third the number of individuals ($0.6 \, m^{-3} \times 150 \, m = 90 \, m^{-2}$) of *P. elegans* present in the 0–465 m column (0.6

$m^{-3} \times 465 \, m = 279 \, m^{-2}$) in early December, suggesting that the apparent decrease in abundance in early December (Fig. 2) was partly due to vertical migration into layers deeper than 150 m.

By our estimation, the mean growth rate of *P. elegans* varied from 0.03 to $0.29 \, mm \, d^{-1}$, averaging around 0.1 mm d^{-1} (Fig. 4). This value corresponds to 3 mm month^{-1}. Thus, in the present area, on the basis of this value it would take 10 months for *P. elegans* to be able to breed if the animals were fully mature at 30 mm in body length. However, our results (Fig. 3A, B) suggest that Cohort Q, which occurred in early June 1993 for the first time, was the offspring of Cohort P, born in late May 1992. Our data (Fig. 4) also suggest that the growth rate during December to April is lower than the rate from late May to early December, and it is therefore probably safe to assume that the generation length of *P. elegans* is indeed approximately one year in the present area. Sameoto (1971) revealed that the generation length for *P. elegans* was related to the in situ temperature. Approximately constant values (738 to 1077 degree-days) were produced by multiplying the generation length (days) and the cumulative temperature (°C) in waters where a population of this species lived (Sameoto 1971). If the generation length of *P. elegans* were one year in the present area, the mean in situ temperature at which the population grew would be 2 to 3°C on the basis of the above-mentioned observation. If we assume that the temperature at a depth of 100 m (1.25 to 3.44°C, mean±SD=2.03±0.70°C, Fig. 2) was the ambient one for Cohort P from 21 May 1992 to 1–2 June 1993, it would be comparable to the in situ temperature of 2–3°C deduced by Sameoto's degree-day method.

On the other hand, it is also suggested that the estimated growth rate of Cohort P during April to June in 1993 was unusually high (Fig. 4). If the cohort of largest size that occurred in June 1993 (hypothetically labeled Cohort P) was in fact not the adult stages of Cohort P but rather Cohort P' (Fig. 3B), the intermediate-sized cohort (21.71±4.78 mm in length, mean±SD) that occurred in early June 1993, would be the true Cohort P. The largest cohort present from 4 August 1993 (Fig. 3B) to 15 April 1994 (hypothetically labeled Group Q' of Cohort Q after 6–7 December 1993, Fig. 3C) would also then correspond to Cohort P. On the basis of this assumption, Cohort P matured in late May to early June of 1994, about 2 years from its first appearance on 21 May 1992 (Fig. 3A), and the generation length would therefore be about 2 years.

The generation length of *Parasagitta elegans* is known to vary regionally. For example, in eastern Arctic waters off Canada, generation length has been estimated at 2 years (Dunbar 1962), but was 1 year in Ogac Lake, Buffin Island (McLaren 1969). King (1979) documented that the *P. elegans* population bred continuously from March through August, with a peak in June and July in Dabob Bay, northwestern USA, and suggested one (possibly two) generations per year. In the northeastern North Pacific Ocean, Terazaki & Miller (1986) recorded that *P. elegans* had three spawn-

ing periods from February 1980 to January 1981 (April to May, August to September, and October to December) at Ocean Station P. Thus, they believed that the mean growth rates were 5 to 6 mm per month for this species in the area. These values are at least twice as high as ours (3 mm month^{-1}). Kotori (1976) reported that the body length of newly hatched larvae of *P. elegans* was 1.23 mm, and that they reached 2.20 mm in the laboratory after 11 d under a starvation regime at a temperature of about 4°C. Thus, the growth rate can be calculated as 0.09 mm d^{-1} in this case, and this value appears to be comparable to the present values (Fig. 4).

Although the generation length of *Parasagitta elegans* is still uncertain in the present area, it is probably longer than that in the northeastern Pacific Ocean, being 1 year or possibly 2 years.

According to Terazaki & Miller (1986), surface water temperatures ranged from 6 to 13.8°C during their observations. It ranged from 4 to 16°C from June to December 1993 in the present area. It seems that the range of seasonal change in surface water temperature was greater in our area than at Station P. Recently, Saito et al. (1998) suggested that the magnitudes of seasonal fluctuations in oceanographic characteristics such as sea surface temperature, nutrient concentrations and plankton biomass are larger in the northwestern Pacific than at Station P, and hence it may be possible that periods of successful reproduction and high growth of *Parasagitta elegans* are seasonally more strictly defined in the western Pacific Ocean than in the northeastern.

Acknowledgments

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