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Seasonal vertical distribution and population dynamics of the chaetognath *Parasagitta elegans* in the water column and hyperbenthic zone of Conception Bay, Newfoundland

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Abstract The vertical distribution and population dynamics of the chaetognath *Parasagitta elegans* Verrill were determined in the water column and hyperbenthic zone of Conception Bay, Newfoundland from April 1997 to June 1998. The water column depth at the study site (47°32.2′N; 53°07.9′W) was 235 m. The temperature below the thermocline was < 0 °C the year round. Chaetognath samples from the water column were collected with a Tucker Trawl. Those from the hyperbenthic zone, were collected with an epibenthic sledge. Depending upon whether the hyperbenthic zone was assumed to extend either 1 m or 10 m above bottom, the grand mean, areal abundance of chaetognaths in the hyperbenthic zone ranged from 6% to 40% of the total abundance in the water column (including the hyperbenthic zone), and the grand mean, areal biomass ranged from 25% to 77%. Large, mature individuals were collected only in the hyperbenthic zone, whereas small, immature individuals were collected primarily in the water column. According to body length and ovary maturity data, three cohorts were identified in the hyperbenthic zone during the study period. Within each cohort, the length frequency of reproductively mature individuals was bimodal, with groups of mean length 33 mm and 41 mm reproducing from May to October. The recruitment period of juvenile chaetognaths extended from July to February, coinciding with the recruitment period of copepods. The estimated individual growth rate of *P. elegans* was 1.0 mg C year^{-1}. The approximate generation time of the two groups of individuals with mean length at maturity of 33 mm and 41 mm was 450 and 780 days, respectively. This study demonstrates that a failure to sample the large, mature *P. elegans* living in the hyperbenthic zone leads to serious underestimates of the total abundance and biomass of chaetognaths and an inaccurate picture of seasonal population dynamics.

Introduction

Chaetognaths are gelatinous carnivores found throughout coastal and open ocean waters around the world, constituting 5–15% of mesozooplankton biomass (Longhurst 1985). Chaetognaths have an important functional role in marine food webs as predators of copepods and other zooplankton such as tintinnid ciliates, ostracods, euphausiids, appendicularian tunicates, and larval fish (Feigenbaum and Maris 1984; Øresland 1987). Although most studies of marine food webs have focused on the control of structure and function by nutrient supply, there is increasing realization of the importance of population regulation by predators (Brett and Goldman 1997; Pitta et al. 1998). Although a few species of north-temperate chaetognaths have been well studied, there have been suggestions recently that most published studies may be highly inaccurate due to limitations of conventional sampling methodology and equipment.

The present study is focused on the well-known chaetognath *Parasagitta elegans*, which is eurythermal, being reported from north-temperate and boreal sections of the Atlantic and Pacific Oceans, at water temperatures ranging from −1.5 °C to 21 °C (Alvariño 1965). Based on submersible dives (Deibel, unpublished) and benthic lander? video records (Rowe et al., unpublished), there appear to be extremely high concentrations of *P. elegans* within a few meters of the bottom in Conception Bay. Conventional zooplankton samples taken with nets towed in the water column do not include these hyperbenthic chaetognaths (Øresland 1987). According to a 3-year study of *P. elegans* in Oslofjord, high concentrations of *P. elegans* occurred regularly in the hyperbenthic zone but not in the water

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column (Jakobsen 1971). More recently, a study of *P. elegans* in the Gulf of Alaska, conducted with an epibenthic sledge, documented high concentrations within 1 m of the bottom during spring (Brodeur and Terazaki 1999).

As expected for a eurythermal organism, the life history of *P. elegans* seems to be differentially adapted to local conditions throughout its range. Growth rate of *P. elegans* varied seasonally in Bedford Basin, Nova Scotia, increasing with increasing temperature (Sameoto 1971). Conversely, growth was continuous the year round in Resolute Bay, Canadian Arctic (Welch et al. 1996). Presence or absence of seasonal variability in the growth, reproduction, and recruitment rates of *P. elegans* is important for the ecology and evolution of the entire food web, because of their strong preference for copepod prey. There is evidence that reproduction of *P. elegans* occurs synchronously with temporal pulses in copepod recruitment (Sameoto 1973; Welch et al. 1996). Thus, we predict that *P. elegans* will mature and reproduce when the abundance of copepods increases in Conception Bay. This test of the life history adaptation of *P. elegans* to a seasonally variable food supply is not confounded by a seasonal temperature cycle, as the water below the thermocline in Conception Bay is <0 °C the year round (Choe 1999). In the present study we examine the seasonal vertical distribution and the population dynamics of *P. elegans* in the water column and hyperbenthic zone of Conception Bay over a 16-month period.

Materials and methods

Sample collection

Parasagitta elegans Verrill were collected from April 1997 to June 1998 at a site in Conception Bay, Newfoundland with a bottom depth of 235 m (47°32.2′N; 53°07.9′W). Chaetognaths in the water column were collected in 0–50, 50–175, and 175–225 m depth strata using a 500-μm mesh, opening-and-closing Tucker Trawl, with a mouth area of 0.2 m^2 and total area of 1.5 m^2 (open-area to mouth-area ratio = 4.6). Duration of the oblique tows ranged from 3 min to 16 min, and the volume of water filtered was determined with a TSK flowmeter. Chaetognaths in the hyperbenthic zone were collected within 1 m of the bottom using an opening-and-closing epibenthic sledge, equipped with a 500-μm mesh net and TSK flowmeter. The mouth area of the sledge was 0.3 m^2, and the total area was 4.5 m^2, with an open-area to mouth-area ratio of 7.2. The sledge was equipped with a butterfly-valve door that was held closed by a length of surgical tubing when the sledge was suspended in the water column. Upon contact with the bottom, a lever caused the door to open. A magnetic switch on the door sent an acoustic signal to a hydrophone towed behind the boat, to indicate whether the door was open or closed. The acoustic transmitter (Vemco, Nova Scotia) also relayed depth and temperature information to the ship in real time. The sledge was towed on the bottom at 1.0–1.5 knots for 17–25 min. Upon retrieval of the sledge, the samples were immediately fixed in 4% buffered formaldehyde. Samples were collected every 1–2 weeks from April to June and monthly during other seasons. Only a few samples were collected during winter, due to harsh weather conditions. Most of the collections were made during the day, except for 17 June and 23 July 1997. In addition, two sets of day–night samples were collected from the hyperbenthic zone on 23 May 1997 and 23 June 1998, to examine diel variability in the vertical distribution of chaetognaths.

Sample analysis

Chaetognath samples from the water column were counted in their entirety. The number of chaetognaths counted in samples from the 50–175 m stratum ranged from 5 to 708 sample^{-1} ($n = 16$), while the number counted in samples from the 175–225 m stratum ranged from 19 to 778 sample^{-1} ($n = 16$). Chaetognaths in the upper mixed layer (0–50 m) were very small and were not collected quantitatively by the 500-μm Tucker Trawl. Therefore, no data from the upper mixed layer will be reported.

Sledge samples from the hyperbenthic zone generally contained too many chaetognaths for full enumeration. Therefore, most sledge samples were subsampled using a Motoda Box plankton splitter. The number of chaetognaths counted and measured ranged from 163 to 1057 subsample^{-1} ($n = 18$). The number of chaetognaths counted in each subsample resulted in 95% confidence intervals (i.e. analytical error) ranging from ±6 to 15% of the count (Alden et al. 1982).

Three-point moving averages were calculated for all samples by,

$$MA = A_{t(i-1)} + A_{t(i)} + A_{t(i+1)}/3 \ ,$$

where A is the areal abundance (m^{-2}) and $t_{(i)}$ represents time in days at the ith time point. The intrinsic rate of natural increase was calculated from the time series of moving averages using the following equation (Odum 1971):

$$r = [\ln MA_{t(i+1)} - \ln MA_{t(i)}]/t_{(i+1)} - t_{(i)} \ ,$$

where MA represents the three-point moving average abundance and t represents time in days at the ith time point.

In order to determine if unequal sampling intervals resulted in an underestimation of the mean abundance, the time-integrated, mean abundance was calculated using the equation,

$$A_t = \sum_{i=1}^{n} \left[A_{t(i)}(t_{i+1} - t_i)\right] \Bigg/ \sum_{i=1}^{n} (t_{i+1} - t_i)$$

where A is the abundance and t is the time in days at the ith time point.

The dry weight and carbon content of different length classes of *P. elegans* were obtained from non-fixed, lyophilized individuals. To obtain dry weight, one to five live chaetognaths were pooled in 1 mm length classes, rinsed briefly in distilled water to remove salt, and frozen at −80 °C. Frozen tissue was dehydrated in a lyophilizer for 48 h, then weighed to the nearest 0.1 mg. Next, lyophilized chaetognaths were ground in a glass pestle by hand, followed by carbon content determination using a Perkin-Elmer, model 2400 CHN analyzer standardized against acetanilide. The coefficient of variation of repeated carbon measurements of acetanilide was within 0.5% of the predicted value. Linear and nonlinear regression were applied to the data using Origin (Data Analysis and Technical Graphics, Microcal Software).

The life history stage of fixed *P. elegans* was determined by examining the state of gonad development using a dissecting microscope at 25× magnification. Stages I, II, or III were assigned to each chaetognath using the following criteria modified after Sameoto (1987): stage I – ovaries invisible or very small, testes undeveloped; stage II – ovaries visible, oocytes small and uniform in size, testes visible, seminal receptacles developing; stage III – ovaries well developed with great variation in oocyte diameter, testes and seminal receptacles well developed.

Chaetognath length was measured from head to tail, excluding fins, to the nearest millimeter. Body length and life history stage frequency distributions were plotted, and cohort analysis was applied by fitting a nonlinear, Gaussian function to the modes (Sameoto 1971, 1973). Finally, to estimate life span and secondary production of *P. elegans*, a time series was constructed of the mean body lengths of the three cohorts in each sample, and a logistic growth curve was fit to the data.

Results

Abundance and biomass

Highest volumetric concentrations of *Parasagitta elegans* occurred in the hyperbenthic zone (Table 1). The grand mean concentration in the hyperbenthic zone (27 m^{-3}) was 6–16 times higher than those in the water column. The grand mean, areal abundance of *P. elegans* below 50 m (including the hyperbenthic zone) was 463 ± 347 m^{-2}. The time-integrated mean abundance below 50 m was 674 m^{-2}. The grand mean abundance in the hyperbenthic zone constituted 6% of the total water column abundance below 50 m.

The areal abundance of *P. elegans* had a pronounced seasonal trend (Fig. 1A) driven largely by abundance changes in the water column (Fig. 1B, C). Areal abundance in the 50–175 m stratum increased from a minimum in July 1997 to a maximum in November 1997, followed by a precipitous decrease by February 1998 (Fig. 1B). The increase in abundance was linear ($r^2 = 0.96$, $n = 5$). Areal abundance in the 175–225 m stratum was relatively low and variable, with a single peak in February 1998 (Fig. 1C). There was no obvious temporal trend of areal abundance in the hyperbenthic zone (Fig. 1D). The monotonic increase in areal abundance for the total water column from July 1997 to February 1998 was highly linear ($r^2 = 0.93$, $n = 6$). The intrinsic rate of natural increase [(birth rate)–(death rate)] was positive throughout most of this period (i.e. from August 1997 to February 1998), with a maximum value in October of 0.02 day^{-1} (Fig. 2). Mortality rates generally exceeded birth rates from April to August.

The dry weight of *P. elegans* ranged from 0.70 to 17.4 mg, increasing exponentially with increasing body length. The dry weight is expressed as $\log_{10}Y = 3.24 \log_{10}X - 4.19$ ($n = 56$, $r^2 = 0.96$, $P < 0.001$), where Y is dry weight in milligrams and X is length in millimeters. The exponent of the power curve was close to the allometrically expected value of 3.0 (i.e. 3.24). Carbon content is expressed as $Y = 0.43X - 0.02$ ($n = 72$, $r^2 = 0.98$, $P < 0.001$), where Y is carbon in milligrams and X is dry weight in milligrams. Carbon content ranged from 0.12 to 0.80 mg, increasing as a constant proportion of dry weight (i.e. 43%). These equations were used to convert the length-frequency distributions of the samples to dry weight and carbon frequency distributions, which were then summed to give the total areal biomass values (Table 1; Fig. 3).

The grand mean, areal biomass of *P. elegans* was 365 ± 269 mg C m^{-2} (Table 1). The grand mean, areal biomass in the hyperbenthic zone constituted 25% of the total water column biomass below 50 m. Thus, 25% of the biomass was located in 0.4% of the water column. The seasonal cycle of biomass was more variable than was the cycle of abundance. However, the three highest values of total areal biomass occurred between August 1997 and February 1998 (>1500 mg C m^{-2}, Fig. 3A), with the peak value occurring in August 1997, at essentially the same time as the maximum population growth rate (Fig. 2). The maximum, areal biomass in the 50–175 m stratum, the 175–225 m stratum, and the hyperbenthic zone occurred in November, February, and May, respectively (Fig. 3B–D).

Life history stage and cohort analyses

Unlike in the upper water column, mature *P. elegans* dominated the life history stage frequency distributions in the hyperbenthic zone in spring and summer (Fig. 4). Populations in the 50–175 m stratum were mostly stage I (78 ± 14% overall), as were those in the 175–225 m stratum (68 ± 18%). The chaetognaths in the deeper of these strata were slightly larger, however, with 95% of the body lengths <33 mm in the 175–225 m stratum versus <30 mm in the 50–175 m stratum (data extracted from Fig. 6). All three life history stages were well represented in the hyperbenthic zone, with stage III dominating over the entire study period (46 ± 26%, Fig. 4C). The chaetognaths in the hyperbenthic zone were by far the largest in the water column, with 95% of body lengths <45 mm (data extracted from Fig. 5). The proportion of stage I individuals was significantly higher in the water column than in the hyperbenthic zone (t-test, $P < 0.004$), whereas the proportion of stage III individuals was significantly higher in the hyperbenthic zone than in the water column (t-test, $P < 0.001$).

In the 50–175 m stratum, mature chaetognaths were present only in the summer, whereas immature stage I animals made up almost the entire population through the fall and winter (Fig. 4A). The pattern was generally

Table 1 *Parasagitta elegans*. Mean abundance and biomass in the three depth strata of Conception Bay, Newfoundland, from April 1997 to June 1998. The hyperbenthic zone was taken to be the zone within 1 m of the bottom. We sampled the water column with a Tucker Trawl and the hyperbenthic zone with an epibenthic sledge, both with 500-μm mesh nets (see "Methods")

Depth	Concentration (m^{-3})	Areal abundance (m^{-2})	% of Total abundance	Biomass		% of Total biomass	n
				(mg dry wt m^{-2})	(mg C m^{-2})		
50–175 m	1.7 ± 2.1	210 ± 266	46	252 ± 432	109 ± 186	30	16
175–225 m	4.5 ± 5.9	223 ± 293	48	367 ± 363	158 ± 156	45	16
Hyperbenthic zone	27 ± 20	27 ± 20	6	211 ± 190	91 ± 82	25	18
Total		463 ± 347	100	848 ± 625	365 ± 269	100	16

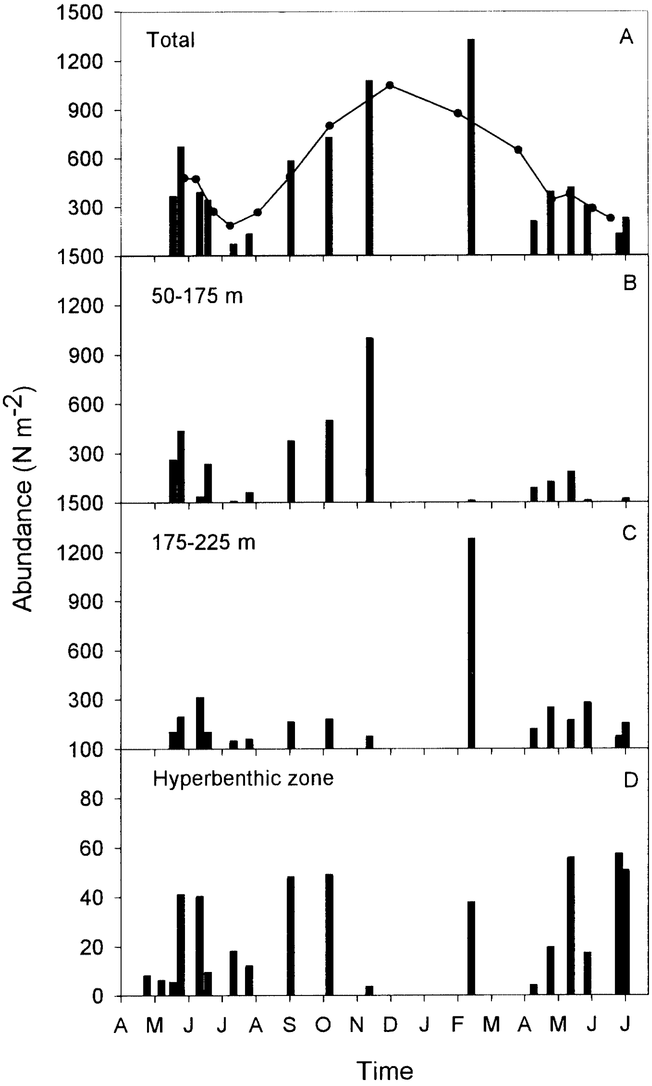


Fig. 1A–D *Parasagitta elegans*. **A** Total areal abundance (m^{-2}) as the sum of the abundance in the two water column strata (i.e. 50–175 m and 175–225 m) and the hyperbenthic zone from April 1997 to July 1998 in Conception Bay, Newfoundland. **B** Areal abundance in the 50–175 m stratum, **C** in the 175–225 m stratum, and **D** in the hyperbenthic zone (i.e. 1 m above bottom)

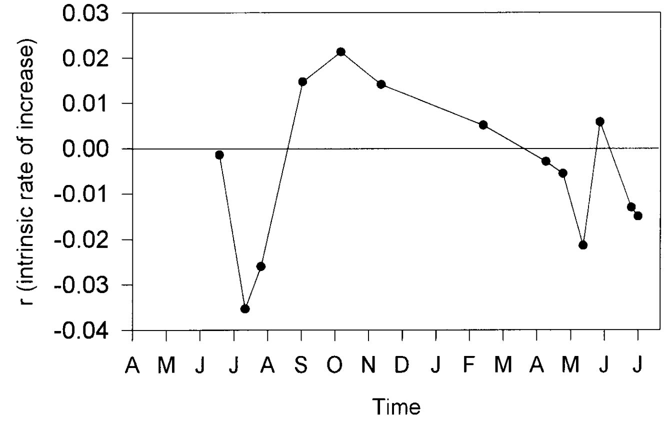


Fig. 2 *Parasagitta elegans*. The intrinsic rate of natural increase calculated from a three-point moving average of the total areal abundance data in Fig. 1A (see "Methods"). The *horizontal line* represents zero population growth, i.e. births = deaths. The *X*-axis extends from April 1997 to July 1998

the same in the 175–225 m stratum (Fig. 4B). In the hyperbenthic zone, mature stage III chaetognaths peaked in May/June, and then decreased steadily in relative abundance from June until November. At the same time, immature stage I individuals increased in relative abundance, peaking in October 1997 (Fig. 4C) when the rate of population increase was maximal (Fig. 2). There were essentially no mature stage III chaetognaths anywhere in the water column from November to February. There was a gradual transition from stage I to stage II throughout the winter, with the relative abundance of stage II chaetognaths peaking in late winter and early spring, from February to April (Fig. 4C).

Three, distinct cohorts were identified in the hyperbenthic zone during the study period (Fig. 5). Cohort analysis was applied only to data from the hyperbenthic zone, since the length and life history stage modes were most clear in this zone and since all three life history stages were present year round. Cohort 1 developed from stage II to mature stage III in April and May 1997, at a mean length of ca. 43 mm. These stage III chaetognaths appeared to spawn in May and June 1997, after which they disappeared from the samples. At about the same time (i.e. May and June 1997), a portion of cohort 2 matured from stage II to stage III at a mean length of ca. 33 mm. These mature chaetognaths likely spawned in July and August 1997, disappearing from the samples by October 1997. The remaining portion of cohort 2, which continued migrating into the hyperbenthic zone from the water column through August 1997 (Fig. 6), continued growing over the winter of 1997/98, reaching stage III at a mean length of 41 mm from April to June of 1998 (Fig. 5).

Cohort 3, which were the offspring of the spring and summer spawning of mature individuals in both cohorts 1 and 2, began appearing in the water column samples in late July and August 1997 (Fig. 6). Recruitment of cohort 3 into the 500-μm mesh samples from the water column appeared to peak in October 1997 (Fig. 6), coincident with the maximum population growth rate of the entire study period (Fig. 2). These chaetognaths from cohort 3 began appearing in the hyperbenthic zone in November 1997, and continued to grow and mature over the winter and spring, a portion reaching mature, stage III status at a mean length of 29 mm in May and June 1998 (Fig. 5). Just as in June 1997, the smaller cohort in June 1998 (i.e. cohort 3) consisted of some individuals that developed to maturity and a portion that remained immature (Fig. 5). Thus, over the study period we observed two groups of mature, stage III individuals in cohort 2, one group maturing at the mean length of 33 mm from May to June 1997, and the other maturing at the mean length of 41 mm from May to June 1998 (Fig. 7). The presence of large stage III individuals in cohort 1 in 1997 with a mean length 43 mm and that of small stage III individ-

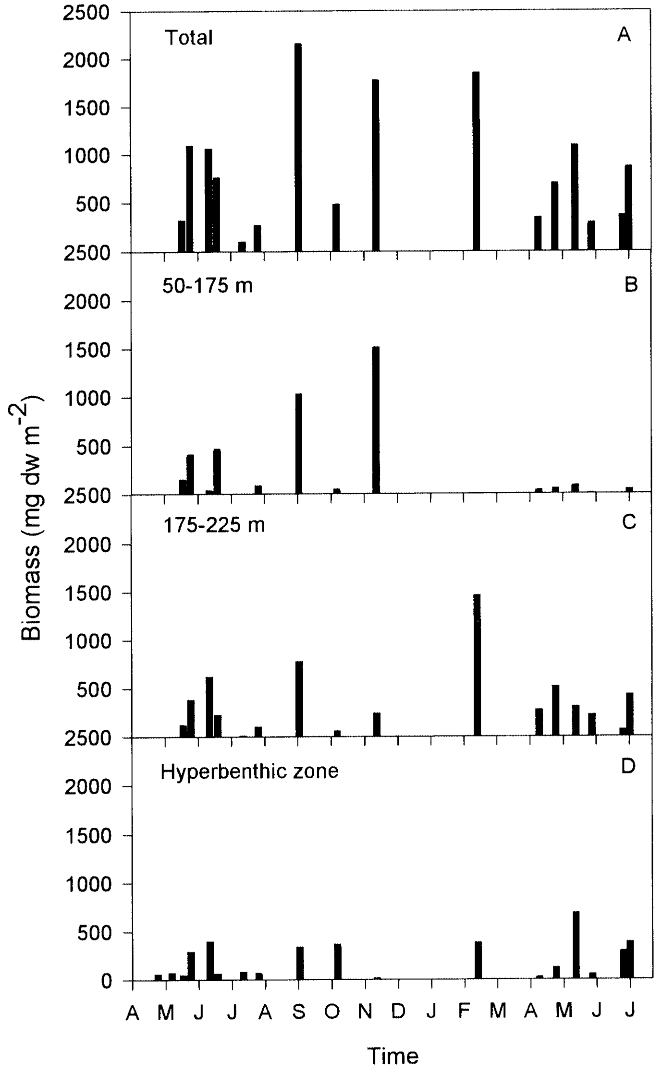


Fig. 3A–D *Parasagitta elegans*. **A** Total areal biomass (mg dry wt m^{-2}) as the sum of biomass in the two water column strata (50–175 m and 175–225 m) and the hyperbenthic zone from April 1997 to July 1998. **B** Areal biomass in the 50–175 m stratum, **C** in the 175–225 m stratum, and **D** in the hyperbenthic zone

uals in cohort 3 in 1998 with a mean length of 29 mm further indicates that there were two groups of *P. elegans* in Conception Bay maturing at different body lengths (Fig. 7). We confirmed that the individuals that spawned in their first year and those that spawned in their second year were of the same species, i.e. *P. elegans* (Øresland, personal communication). Thus, in a given May/June period in Conception Bay, there were two size classes of mature, spawning chaetognaths, originating from different cohorts, one maturing at a mean body length of ca. 30 mm, and the other at a mean body length of ca. 40 mm (Fig. 7).

Regardless of maturity status, the mean body length of all three cohorts increased linearly with time (Fig. 8). The logistic equation describing the mean length of *P. elegans* as a function of time is,

$$Y = -46.9/1 + (X/509.1)^{1.388} + 65.5(n = 21) \ ,$$

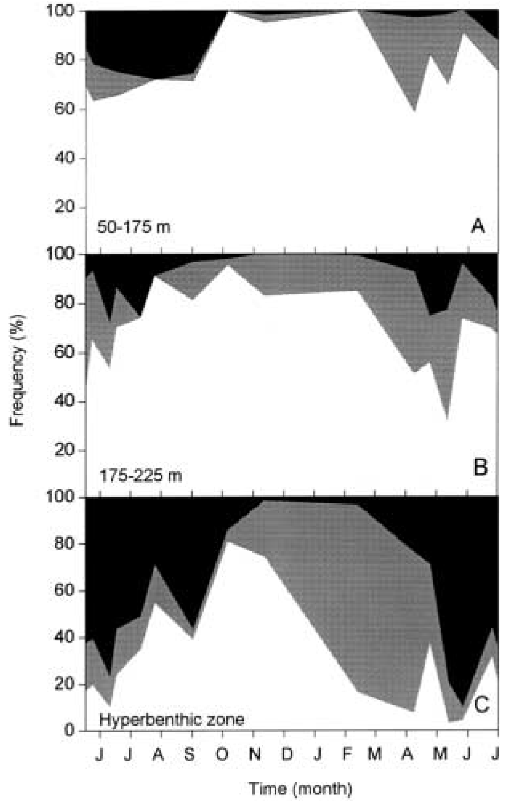
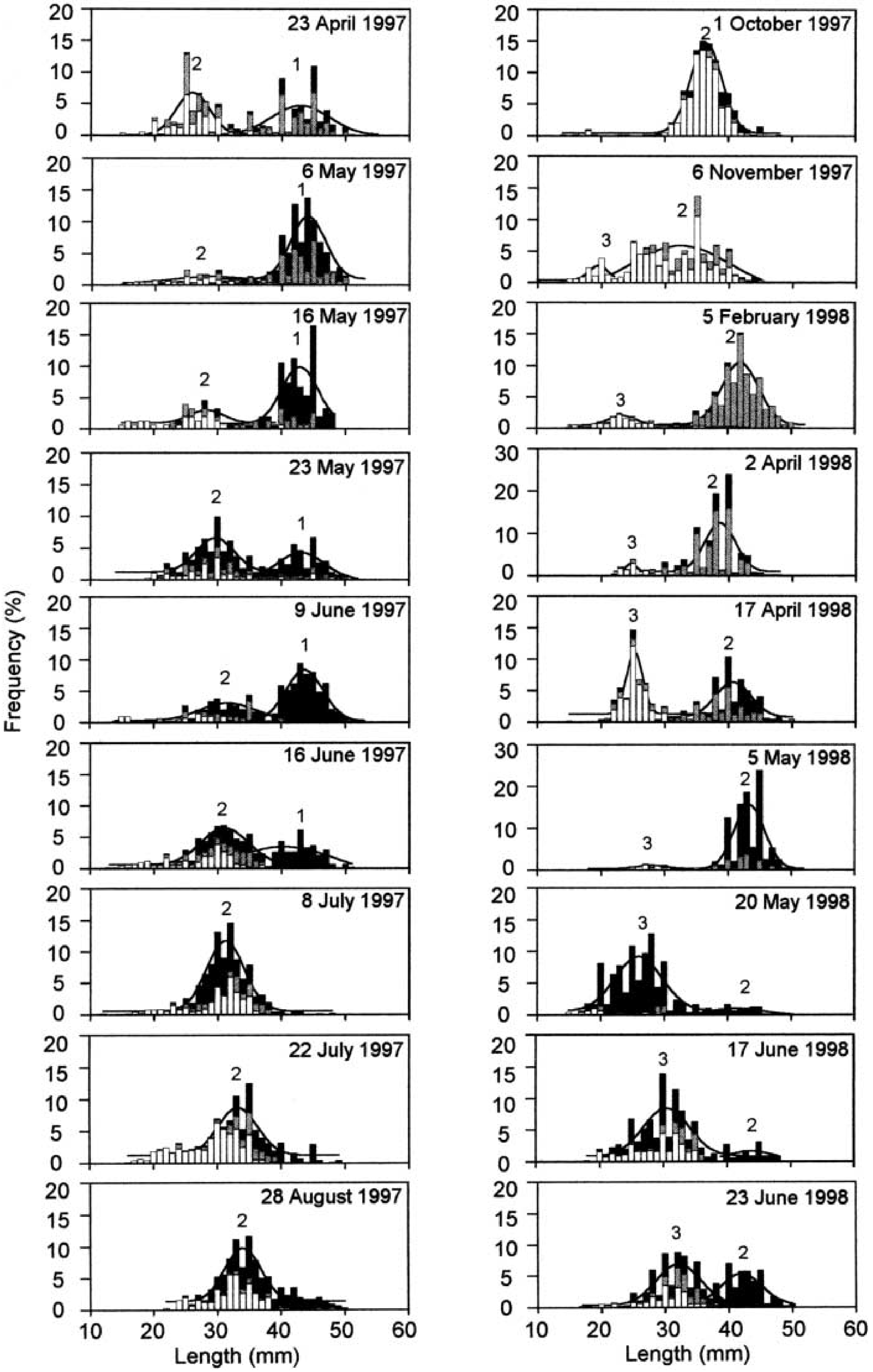


Fig. 4A–C *Parasagitta elegans*. **A** Life history stage frequency distribution in the 50–175 m stratum, **B** in the 175–225 m stratum, and **C** in the hyperbenthic zone (*white* stage I; *gray* stage II; *black* stage III). The *X*-axis extends from June 1997 to July 1998

where Y is the mean length in millimeters and X is the time in days. Day 0 was defined as that time when the smallest individuals appeared in our 500-μm mesh samples (i.e. November 1997). Solving this equation for the individual growth rate gives a value of 25.3 mm year^{-1}, or 2.28 mg dry wt year^{-1} and 1.0 mg C year^{-1}, using the allometric equations previously shown. The growth curve starts at a mean length of 18.6 mm and ends at 43.2 mm on day 560. Since individuals with a mean length < 18.6 mm were not sampled quantitatively by our 500-μm mesh nets, the time required for growth to 18.6 mm is not known. However, since we have concluded that cohort 3 originated from the spawning of cohort 1 in May 1997 (Fig. 5), the time required for growth from spawning to 18.6 mm was approximately 210 days. Therefore, the generation time of those chaetognaths that spawned in their first year at a mean length of 33 mm was ca. 450 days, and the generation time of those chaetognaths that spawned in their second year was ca. 780 days. As presented above, we conclude from the evidence that *P. elegans* is semelparous in Conception Bay, meaning that the mean generation time equals the mean life span.

Diel distribution in the hyperbenthic zone

Based on a limited sample set, it appeared that large, mature *P. elegans* displayed typical diel vertical mi-

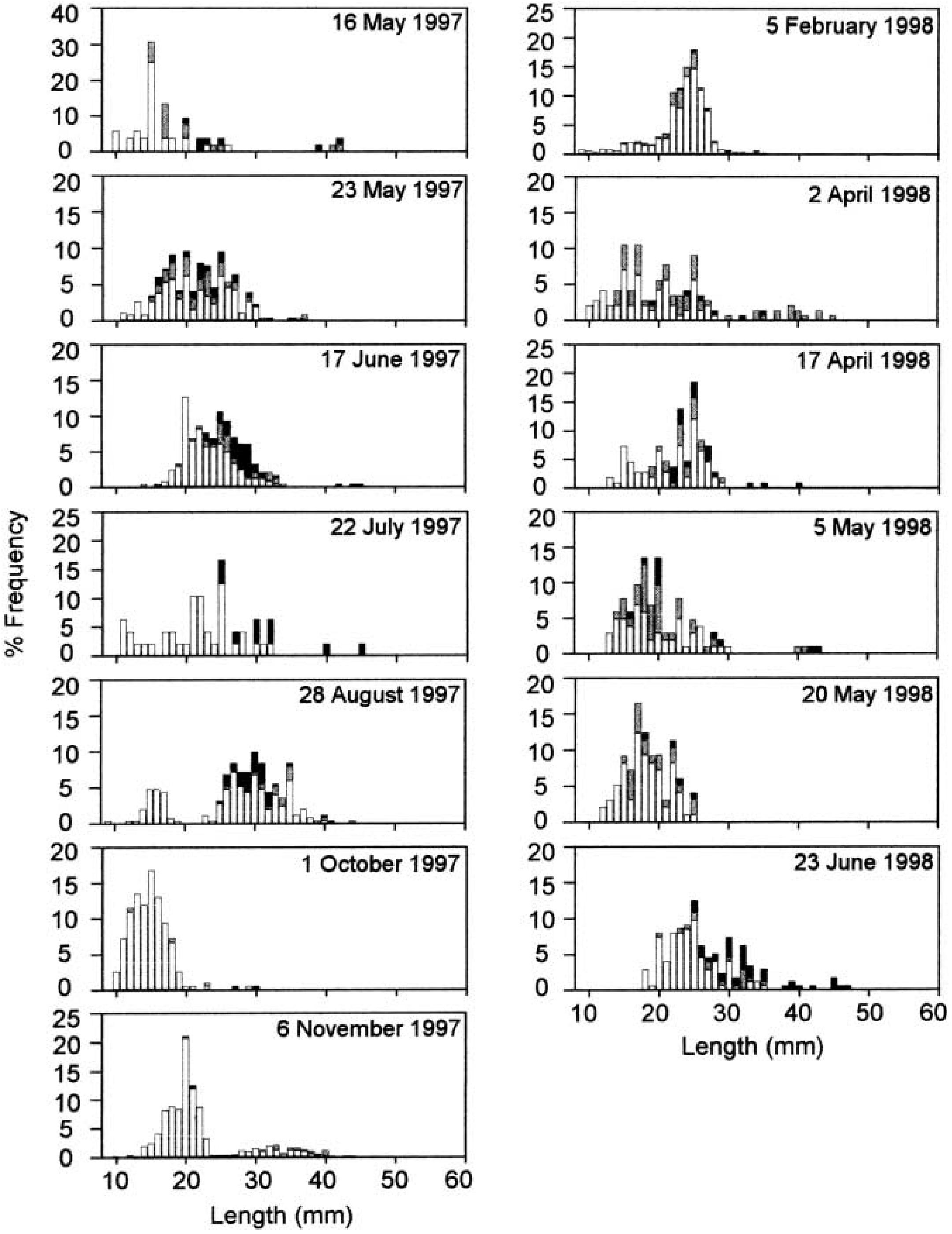

Frequency (%)
Length (mm)
23 April 1997
6 May 1997
16 May 1997
23 May 1997
9 June 1997
16 June 1997
8 July 1997
22 July 1997
28 August 1997
1 October 1997
6 November 1997
5 February 1998
2 April 1998
17 April 1998
5 May 1998
20 May 1998
17 June 1998
23 June 1998
1
2
3
0
5
10
15
20
30
10
20
30
40
50
60

◄

Fig. 5 *Parasagitta elegans*. Body length and life history stage frequency distribution in the hyperbenthic zone from 23 April 1997 to 23 June 1998 (*white* stage I; *gray* stage II; *black* stage III). *Smoothed lines* are Gaussian curves fit to the modes of the data (see "Methods"). *Numbers 1, 2 and 3* refer to cohorts 1, 2, and 3

Fig. 6 *Parasagitta elegans*. Body length and life history stage frequency distribution in the water column (50–225 m) from 16 May 1997 to 23 June 1998 (*white* stage I; *gray* stage II; *black* stage III)

gration in Conception Bay in the spring (i.e. downward during the day and upward during the night), while small, immature chaetognaths displayed reverse diel vertical migration (i.e. upward during the day and downward at night) (Fig. 9). The proportion of individuals in the smaller length mode was significantly higher in the hyperbenthic zone during the night than the day (*t*-test, $P < 0.05$), and the proportion of individuals in the larger length mode was significantly higher in the hyperbenthic zone during the day than the night ($P < 0.04$, Fig. 9). Similarly, the proportion of stage I individuals was significantly higher in the



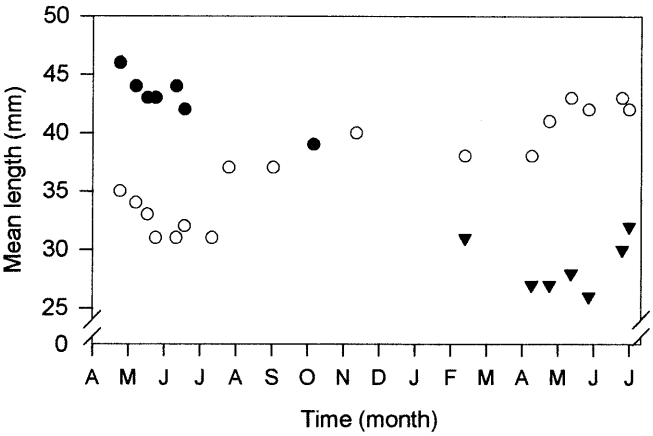


Fig. 7 *Parasagitta elegans*. Mean length-at-maturity for cohort 1 (*closed circle*), cohort 2 (*open circle*), and cohort 3 (*triangle*), shown in Fig. 5, from April 1997 to July 1998

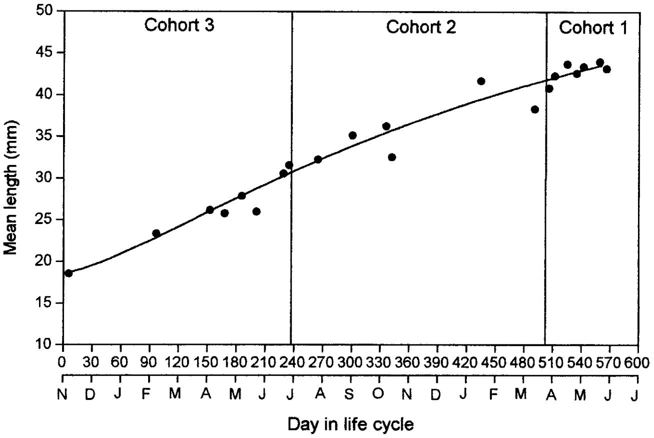


Fig. 8 *Parasagitta elegans*. Mean body length of cohorts 1–3 in the hyperbenthic zone. The cohorts were plotted as a continuous growth curve following the approach of Welch et al. (1996). Day 0 was defined as that time when the smallest individuals appeared in the samples, i.e. at $L = 18.6$ mm. Mean body lengths of cohorts 1–3 were obtained from 23 April to 16 June 1997, 8 July 1997 to February 1998, and from November 1997 to 23 June 1998, respectively

hyperbenthic zone during the night than the day ($P < 0.001$), and the proportion of stage III individuals was significantly higher in the hyperbenthic zone during the day than the night ($P < 0.001$). Since the length and maturity stage distributions were expressed in proportions in Fig. 9, it was not clear exactly which length and maturity stage groups made diel migrations. However, the nearly equal concentrations of chaetognaths in the day and night samples on 23 June 1998 indicated that larger, mature individuals migrated down to the hyperbenthic zone during the day and migrated away from the hyperbenthic zone during the night. Conversely, smaller, immature individuals displayed a reverse migration pattern.

Discussion

Throughout the study, high concentrations of *Parasagitta elegans* occurred in the hyperbenthic zone in contrast to the upper water column of Conception Bay. Our hyperbenthic sledge collects samples only from the zone within 1 m of the bottom. However, the near-bottom zone of elevated zooplankton concentration may extend up to 10 m above the bottom in Conception Bay (Deibel, observation from a submersible dive). In fact, the limited sampling we have done with a larger hyperbenthic sledge containing two nets, one above the other, generally indicated higher concentrations of *P. elegans* in the 1–2 m zone above the bottom than in the 0–1 m zone (Mumm et al., unpublished data). If we assume for the moment that the abundances in Table 1 are representative of the bottom 10 m of the water column rather than the bottom 1 m (as is done in Table 1), then the mean, areal abundance in the hyperbenthic zone may be as much as 40% of the total abundance of chaetognaths in the entire water column below 50 m. Under the same assumption, the biomass of chaetognaths in the hyperbenthic zone may be ca. 77% of the total biomass below 50 m. This confirms the hypothesis of Øresland (1987) that failing to sample chaetognaths in the

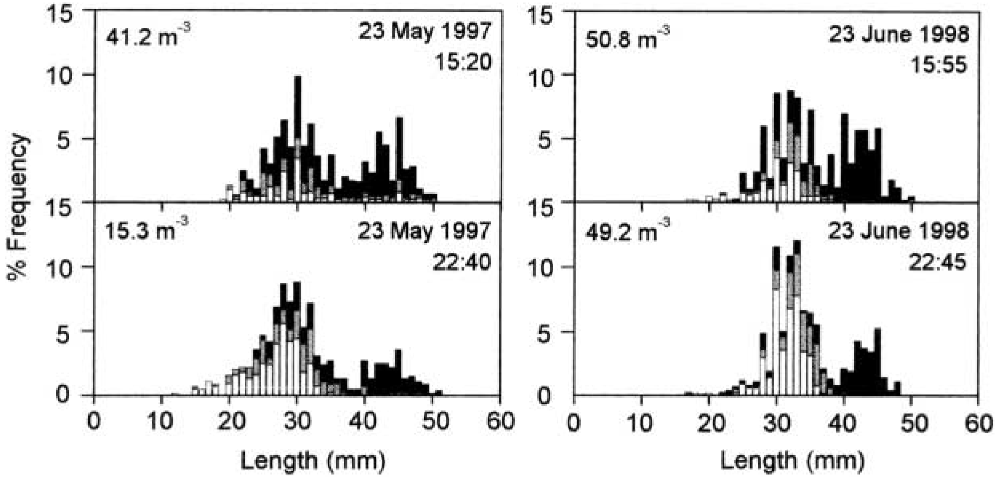


Fig. 9 *Parasagitta elegans*. Body length and life history stage frequency distributions in the hyperbenthic zone during paired, day and night samples taken on 23 May 1997 and 23 June 1998 (*white* stage I; *gray* stage II; *black* stage III). Time of day shown beneath each date in hh: mm. Concentrations shown in upper left hand corner of each panel are totals for each sample

hyperbenthic zone results in a severe underestimate of population abundance and biomass. This is particularly important when samples are collected in the daytime, when large, mature chaetognaths migrate close to the bottom.

In addition, the maximum length of *P. elegans* in Conception Bay was 52 mm, at a mean annual temperature below the thermocline of ca. −1.0 °C. In the Canadian Arctic, the maximum reported length of *P. elegans* was 45 mm, at a mean annual temperature of −1.5 °C (Welch et al. 1996). However, Welch et al. (1996) likely did not capture the largest chaetognaths living in the hyperbenthic zone with their vertical net tows in the water column, which reached only within 7 m of the bottom. Thus, we conclude that estimates of the maximum body size and generation time of *P. elegans* could be in error if the hyperbenthic zone is not adequately sampled.

There is also evidence of ontogenetic vertical migration by *P. elegans* in Conception Bay. The increase in the total abundance of *P. elegans* from July 1997 to February 1998 was the consequence of spawning by mature individuals in the hyperbenthic zone from May to at least August 1997 (Fig. 5). This spawning activity resulted in an accumulation of small, immature individuals in the upper water column beginning in July and August 1997 (Fig. 6). The movement of maximum abundance from the 50–175 m to the 175–225 m depth stratum from November 1997 to February 1998 is consistent with the ontogenetic migration of chaetognaths deeper in the water column as they grow and mature.

The reproduction and recruitment of *P. elegans* in Conception Bay occurred synchronously with the development of copepod prey populations. In this study, the abundance of *P. elegans* increased linearly from July 1997 to February 1998 (Fig. 1). Thirty years of continuous plankton recorder data from the northeastern Newfoundland shelf (1960–1992) indicate that the mean abundance of copepods increases linearly from July to September each year, and remains high until December before decreasing (Myers et al. 1994). This corresponds with observations of spawning of *P. elegans* in Bedford Basin, Nova Scotia, in the spring, with subsequent spawning events occurring every year immediately after an increase in copepod biomass (Sameoto 1973). Furthermore, King (1979) observed the maturation of *P. elegans* in Dabob Bay, Washington, during spring, coincident with the development of the first spring cohort of small copepods. Finally, recruitment of young-of-the-year *P. elegans* in the Canadian Arctic also coincides with the occurrence of large numbers of copepod nauplii (Welch et al. 1996).

Length-at-maturity of *P. elegans* was bimodal in Conception Bay. For example, the mean length-at-maturity of cohort 2 was 33 mm in 1997, and 41 mm in 1998 (Fig. 7). A possible explanation for these observations is the effect of food limitation on growth and maturation of *P. elegans*. However, a large portion of cohort 2 reached sexual maturity in the spring and summer of 1997, while at the same time a large portion remained immature. This pattern is inconsistent with food-limited development of *P. elegans*. Another possibility is that *P. elegans* was iteroparous in Conception Bay, spawning in the spring and summer of 1997 and then again in the spring of 1998. However, the increasing proportion of immature individuals in the hyperbenthic zone from May to August is due to the disappearance of post-spawning adults and addition of immature individuals from the water column. In addition, careful, microscopic examination of the large (>30 mm), immature individuals in cohort 2 during the fall of 1997 revealed no evidence of the degeneration of spent gonads, such as residual mesentery cords adhering to the oocytes or well-developed seminal vesicles. Sameoto (1971) concluded that the length-at-maturity of *P. elegans* depended on the mean temperature over their life time, but *P. elegans* in Conception Bay grew continuously throughout the year and matured at different body sizes even though the temperature below 50 m was <0 °C the year round (Fig. 8). There could be two genetically distinct populations of *P. elegans* in Conception Bay, but at present there is no explanation for the bimodal length-at-maturity.

In St. Margaret's Bay and Bedford Basin, Nova Scotia, the growth rate of *P. elegans* increased as the temperature increased, and almost ceased when the temperature reached its annual minimum of 1–2 °C (Sameoto 1971, 1973). However, in the Canadian high Arctic, *P. elegans* grows continuously throughout the year, despite temperatures near the freezing point of seawater (Welch et al. 1996). Interestingly, the growth rate of *P. elegans* in Resolute Bay, Canadian Arctic, of 2.83 mg dry wt individual^{-1} year^{-1} (calculated from the growth curve equation and the equation describing the length:dry weight ratios in Welch et al. 1996) was very close to that of *P. elegans* in Conception Bay, of 2.28 mg dry wt individual^{-1} year^{-1}. Thus, although Conception Bay is located at 47°N latitude and Resolute Bay at 75°N, *P. elegans* appears to grow at essentially the same rate. This suggests similar habitat characteristics of these two bays, likely due in large part to the chilling effect of the Labrador Current on the sub-thermocline climate of Conception Bay.

There is no consensus on the diel vertical migration behavior of *P. elegans*. Some investigators have observed typical diel vertical migration by mature *P. elegans*, but not by immature individuals (King 1979; Sullivan 1980). Others have observed typical diel migration by mature *P. elegans* (i.e. downward during the day) and reverse migration by immature individuals (i.e. downward during the night) (Brodeur and Terazaki 1999). Such ontogenetic shifts in vertical migration behavior may be an adaptation to minimize predatory mortality, from both conspecifics and other predators (Brodeur and Terazaki 1999). In Conception Bay, *P. elegans* also showed ontogenetic differences in vertical migration behavior during May and June, with large, mature individuals moving downward during the day, and small, immature individuals moving downward at night. Reverse migration by the small individuals appeared to result in a reduction in predatory loss to larger chaetognaths. Large chaetognaths in the hyperbenthic zone were highly cannibalistic (i.e. 15.3% of the total prey, $n = 733$, Choe 1999), while the smaller individuals in the water column showed almost no cannibalism (i.e. 0.4% of the total prey, $n = 496$).

Our study took place in the deep depositional zone of Conception Bay, where the mean currents are weak (deYoung and Sanderson 1995). The estimated residence time of water in the upper mixed layer is 30 days, and deep water exchange below the sill (150 m depth) takes place primarily in the winter and spring (deYoung and Sanderson 1995). However, the advective effects on temporal changes in the abundance and distribution of *P. elegans* in Conception Bay appear to be minimal. For example, a sharp decline in the intrinsic rate of increase occurred in July 1997 (Fig. 2), although there was little change in the temperature, salinity, and density (δ_t) in the hyperbenthic zone from June to July (temperature, salinity, and δ_t ranged from −0.9 to −1.2 °C, 32.89 to 32.94‰, and 26.44 to 26.49 kg m^{-3}, respectively). Furthermore, a sudden appearance of small, mature chaetognaths on 20 May 1998 in the hyperbenthic zone (Fig. 5) was not caused by water mass exchange, since there was no change in density of the near-bottom water mass (data not shown). Finally, the smooth, continuous growth curve (Fig. 8) and biologically reasonable, temporal transition of maturity stages (Fig. 4) indicate insignificant effect of advection on chaetognath populations of Conception Bay.

We conclude that the failure to adequately sample the large, mature chaetognaths living in the hyperbenthic zone of coastal fjords results in serious underestimation of total abundance and biomass and inaccurate conclusions regarding maximum size, length-at-maturity, generation time, and annual production. The cause of high concentrations of large *P. elegans* in the hyperbenthic zone remains to be determined. *P. elegans* in the hyperbenthic zone reached maturity at different body lengths in the absence of temperature variation, challenging the accepted theory of the temperature dependence of length-at-maturity of chaetognaths. Ontogenetic shifts in diel vertical migration in the hyperbenthic zone likely result in a reduction of cannibalistic mortality of small chaetognaths. The continuous growth and annual production rates of *P. elegans* in Conception Bay at sub-zero water temperatures are typical of reports from the Canadian Arctic, despite the location of the study site near 47°N latitude. This confirms the strong effect of the cold Labrador Current on the fjords of eastern Newfoundland.

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