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Seasonal variation in the biochemical composition of the chaetognath *Parasagitta elegans* from the hyperbenthic zone of Conception Bay, Newfoundland

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ABSTRACT: The biochemical composition of the chaetognath *Parasagitta elegans* from the hyperbenthic zone of Conception Bay, Newfoundland, was determined from April 1997 to June 1998. Lipid and carbohydrate levels (% dry weight) were relatively high in the spring and summer and low in the fall and winter. Conversely, the relative protein level was low in the spring and summer and high in the fall and winter. Carbon level was generally high in the spring and summer of 1997 but low from fall to the following spring, whereas inorganic ash level showed the opposite seasonal trend. Lipid and carbohydrate levels and the C/N ratio were positively correlated with chaetognath maturity stage, while protein levels were negatively correlated with chaetognath maturity. These results indicate that *P. elegans* were lipid- and carbohydrate-rich while maturing during spring and summer, and that immature individuals were protein-rich while achieving somatic growth during fall and winter. This increase in the levels of lipid and carbohydrate occurred when mature copepods increased in the spring and summer rather than when total abundance of copepods increased in the fall. Thus, it appears that food quality rather than quantity affects the biochemical levels and reproductive cycle of *P. elegans*. In addition, the maximum abundance of adult copepods occurred 3 wk after the peak of the spring bloom, and the maximum relative abundance of mature *P. elegans* occurred 3 wk later. This suggests that there is tight coupling of energy transfer from primary producers to carnivorous hyperbenthic chaetognaths following the spring phytoplankton bloom in Newfoundland coastal waters. Therefore, seasonal variation in the biochemical composition of *P. elegans* in the hyperbenthic zone of Conception Bay is closely related to its reproductive cycle and to food quality. Furthermore, it is clear that the chaetognath reproductive cycle is synchronized with the massive energy input from the annual spring phytoplankton bloom.

KEY WORDS: *Parasagitta elegans* · Chaetognath · Biochemical composition · Seasonal variation · Reproductive cycle · Trophodynamics

INTRODUCTION

In temperate and polar waters, seasonal variation in the biochemical composition of zooplankton is related to food availability and the reproductive cycle. Copepods, euphausiids, amphipods, ctenophores and medusae may experience an increase in lipid levels in response to the spring phytoplankton bloom (Sargent et al. 1978, Percy 1979, Falk-Petersen 1981, Percy & Fife 1981, Alonzo et al. 2000, Pasternak et al. 2001). Many crustaceans such as copepods, euphausiids and benthic amphipods store lipid in the form of wax esters and triacylglycerols to be utilized for subsequent reproductive maturation prior to the next bloom (Littlepage 1964, Lehtonen 1996, Falk-Petersen 1981, Hopkins et al. 1984, Kosobokova 1999, Niehoff et al. 1999,

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Alonzo et al. 2000, Pasternak et al. 2001). This strategy can be beneficial when the release of juveniles is matched with abundant food. In contrast, gelatinous zooplankton generally reproduce as soon as the food supply becomes favorable. For example, scyphomedusae (Lucas 1994) and ctenophores (Kremer 1993) reproduce when copepod abundance increases in the spring. Antarctic salps form enormous numbers of chain-forming sexual blastozooids ('salp bloom') at the onset of primary production or under favorable feeding conditions (Foxton 1966).

Although there are 2 previous studies of seasonal variation in the biochemical composition of chaetognaths (Reeve et al. 1970, Båmstedt 1978), causes of the variability are uncertain (see 'Discussion'). The present study reports temporal variation in the biochemical composition and reproductive cycle of the boreal chaetognath *Parasagitta elegans* from the hyperbenthic zone of Conception Bay, Newfoundland, in relation to food availability over a 14 mo period. The hyperbenthic zone of Conception Bay has several advantages for examining the biochemical variability of *P. elegans*. We have shown that individuals of all reproductive stages are highly concentrated in the hyperbenthic zone, 1 to 2 m above the bottom, making a study of the entire life cycle possible (Choe & Deibel 2000). Secondly, temperature and salinity in the hyperbenthic zone are relatively constant year-round (i.e. –1°C, and 33‰, deYoung & Sanderson 1995), enabling examination of biological factors in the absence of confounding seasonality in physical conditions. Finally, there is much historical data on biological dynamics in Conception Bay. The spring phytoplankton bloom begins in late March, with peak phytoplankton biomass being reached in April (Redden 1994). Some species of benthic and hyperbenthic invertebrates respond quickly to this pulse of energy by laying down lipid stores (Parrish et al. unpubl. data). However, we do not know whether, or how, gelatinous carnivores such as *P. elegans* respond to seasonal pulses of energy from lower trophic levels. This is the question addressed in this paper.

MATERIALS AND METHODS

Sample collection. *Parasagitta elegans* were collected from April 1997 to June 1998 at a site in Conception Bay, Newfoundland, with a bottom depth of ca. 235 m (47° 32.2' N, 53° 07.9' W). Individuals in the hyperbenthic zone were collected within 1 m of the bottom with an opening and closing epibenthic sledge equipped with a 500 µm-mesh net and Tsurumi-Seiki-Kosakusho (TSK) mechanical flowmeter. The sledge was fitted with a butterfly-valve door which 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, and a magnetic switch on the door sent an acoustic signal to a hydrophone towed behind the boat to indicate door status. The acoustic transmitter (Vemco) also relayed depth and temperature data to the boat in real time. The sledge was towed on the bottom at 1.0 to 1.5 knots for 17 to 25 min. The samples were collected every 1 to 2 wk from April to June and monthly during other months, but only a few samples were obtained during winter due to bad weather.

Cod-end contents from an initial sledge tow were fixed in 4% buffered formaldehyde-seawater for later determination of the body size and maturity stage of chaetognaths. Live individuals from a second, replicate tow were examined under a dissecting microscope. Healthy individuals without food and parasites in their guts were removed, rinsed quickly in distilled water and blotted on pre-combusted glass-fiber (GF/C) filters. The individuals were stored at –80°C and later lyophilized for 2 d for biochemical analyses.

Chemical analyses. Total lipid was determined by a gravimetric procedure after chloroform/methanol extraction (Bligh & Dyer 1959). Carbon and nitrogen were determined with a Perkin-Elmer CHN analyzer (Model 2400) standardized with acetanilide. The coefficient of variation of carbon measurements from replicate samples of acetanilide was 0.5%. Total protein was estimated by multiplying nitrogen content values by 5.8. This nitrogen-protein conversion factor is based on the nitrogen fraction in protein of bacteria, algae and aquatic animals, and is accurate within 3% (Gnaiger & Bitterlich 1984). Carbohydrate was extracted from the lyophilized tissue by boiling in a solution of 5% trichloroacetic acid containing 50 mg silver sulphate (Barnes & Heath 1966). The concentration of carbohydrate was determined by the phenol-sulphuric acid colorimetric procedure (Dubois et al. 1956). Ash content was obtained by reweighing dried samples after combustion at 450°C in a muffle furnace overnight. The carbohydrate assay required 60 mg of lyophilized tissue, while 60 mg was used for the lipid assay, 3 to 15 mg for ash content and 3 to 6 mg for CHN analysis, requiring pooling 40 to 641 individuals, depending on the body sizes of the individuals available. All assays were carried out in triplicate except the CHN analyses, which were done in duplicate. The levels of the various constituents were expressed in terms of % dry weight to normalize for seasonal changes in body size and mass.

Body length and gonad maturity. The body length of preserved chaetognaths was measured from the tip of the head to the tip of the tail, excluding fins, to the

nearest millimeter, and the stage of maturity was determined under a M5 Wild stereo microscope at 25× magnification according to Sameoto (1987): Stage I: ovaries are visible or very small and testes are undeveloped; Stage II: ovaries are visible but eggs are small and uniform, testes are developed and visible, seminal receptacles are developing; Stage III: ovaries are well-developed with many eggs larger than others, seminal receptacles are well developed.

Abundance of copepods in water column and hyperbenthic zone. From May 1997 to June 1998, copepods were collected from 2 depth intervals in the water column (50 to 175 and 175 to 225 m) with a closing Tucker Trawl fitted with a 500 µm-mesh net and TSK flowmeter. The copepods in the hyperbenthic zone were collected at the same time as chaetognaths were collected using the benthic sledge. The abundance and stages of copepod species were determined from subsamples with a Motoda zooplankton splitter (Motoda 1959). The minimum number of major copepod species counted within each developmental stage was 30, resulting in maximum 95% confidence intervals (i.e. analytical error) ranging from 30 to 56% of the count (Alden et al. 1982).

Statistical analyses. The raw time-series data were arcsine-transformed prior to statistical analyses. In order to depict the general trend in our temporal data, we applied the cumulative sum (CUSUM) technique to the normal standard deviates. This procedure displays changes in the level of the variables as well as the point of onset of such changes (Page 1954, Barnard 1959, Woodward & Goldsmith 1964, Davis & Goldsmith 1972). First, each raw time-series was transformed to a series of the normal standard deviate by calculating the relative change of each data point from the grand mean. Next, these transformed time-series were smoothed by the cumulative sum of each normal standard deviate as follows:

$$S_1 = (y_1 - k)$$
$$S_2 = (y_1 - k) + (y_2 - k) = S_1 + (y_2 - k)$$
$$S_3 = S_2 + (y_3 - k), \text{ ... to}$$

$$S_t = S_t - 1 + (y_t - k) = \sum_{i=1}^{t} (y_i - k)$$

where S is the cumulative sum and t is the time in days at the ith time point, and k is the normal standard deviate, $(y_i - \mu)/\delta$. A positive slope in a time-series of CUSUM reflects an extended period of raw data values above the grand mean and a negative slope reflects extended periods below the grand mean. Finally, simple correlation analysis was applied to the data expressed in CUSUMS using SPSS statistical software (SPSS 9.0.0 1998).

RESULTS

Seasonal variation in biochemical composition

Parasagitta elegans was protein-rich, which is typical of gelatinous zooplankton. The grand mean (±SD) protein and lipid levels were 64.4 ± 3.7% and 13.1 ± 1.5% of dry weight, respectively, followed by carbohydrate at 0.6 ± 0.1%. The grand means for carbon and ash levels were 41.3 ± 0.8% and 11.8 ± 2.3%, respectively, and the mean C/N ratio was 4.4 ± 0.2. Carbon level was least variable (coefficient of variation, CV = 1.9%), while ash level was most variable (CV = 19%). The sum of the mean protein, lipid, carbohydrate and ash levels was 89.9 ± 3.7% of the dry weight. Adding a residual water fraction of 6% obtained from fish, zooplankton and algae (Gnaiger & Bitterlich 1984), leaves only ca. 4% of the total dry weight unaccounted for. This indicates that our analytical methods were satisfactory, including the indirect approach to estimation of protein content (see 'Materials and methods').

The biochemical composition of *Parasagitta elegans* showed clear seasonal patterns (Fig. 1A–F). The lipid level was above the mean from April to August 1997, decreased below the mean from October 1997 to May 1998 and increased again in July 1998. The protein level was below the grand mean from April to July 1997, increased above the mean from August 1997 to April 1998 and decreased in May and June 1998. Carbohydrate was mostly above the mean from April to July 1997, decreased below the mean from August 1997 to April 1998 and increased from April to June 1998. Ash level was mostly above the mean from April to October 1997 with a sharp increase in August and October and a decrease from November 1997 to June 1998. Carbon was below the mean from April to October 1997, increased above the mean from November 1997 to May 1998 and decreased in June 1998. The C/N ratio was above the mean from April to July 1997, decreased below the mean from July 1997 to February 1998 and increased from April to June 1998.

When the data are displayed as CUSUMS, clear seasonal variation in the biochemical composition becomes apparent (Fig. 1G–L). The positive slope in the CUSUM of each biochemical constituent indicates the period in which the biochemical level was higher than the grand mean, and the negative slope when the level was lower than the grand mean. The smoothed CUSUM time-series reveal obvious similarities in the seasonal variability of lipid, carbohydrate and the C/N ratio, and clear inverse relationships between these three and protein, and between ash and carbon.

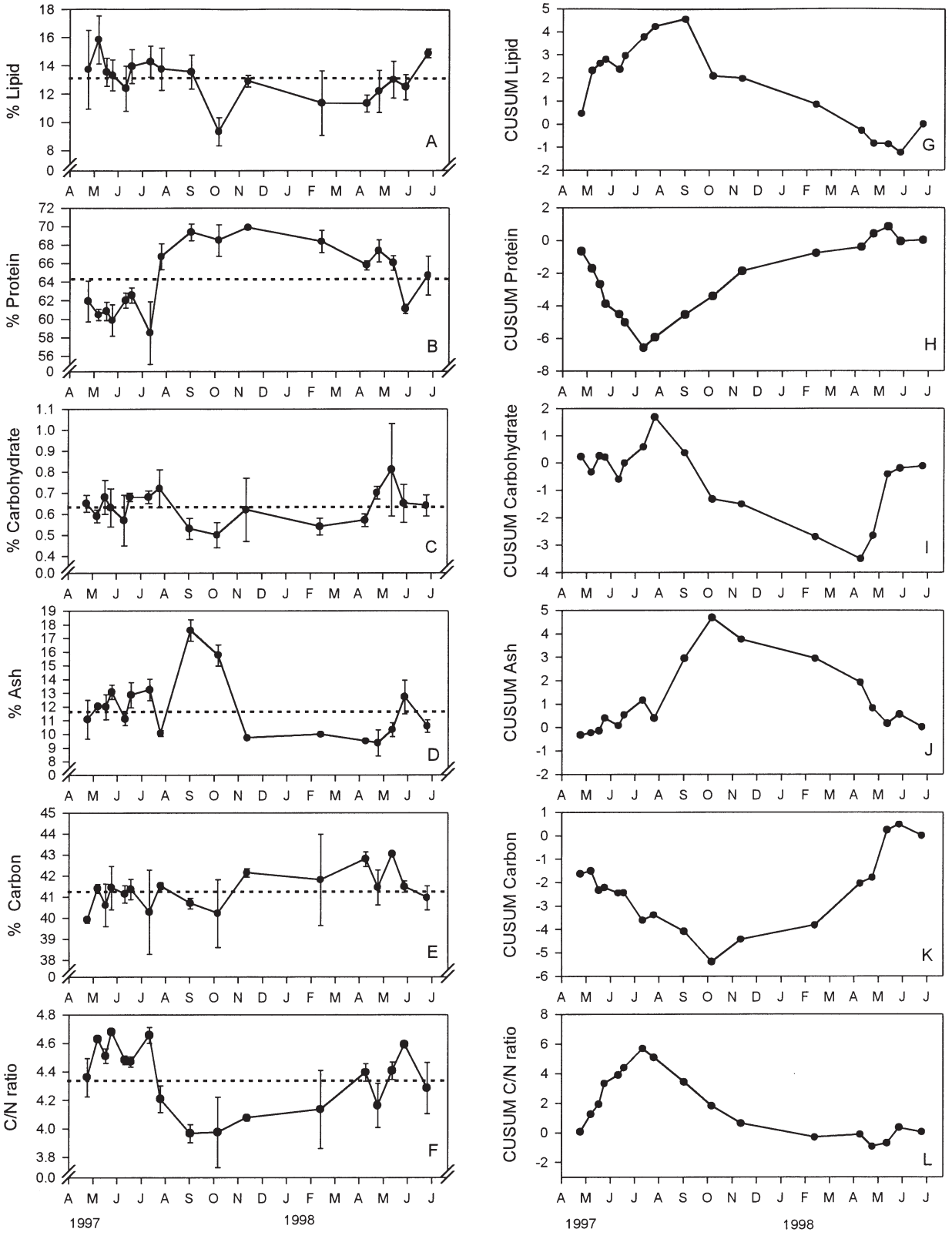

Fig. 1. *Parasagitta elegans*. Biochemical levels (A–F) and cumulative sums of normal standard deviates of the biochemical levels (G–L) from April 1997 to June 1998. Biochemical levels expressed in percent dry weight. Dashed lines represent means; error bars represent analytical variance among replicate pools of chaetognaths taken from single tow

Biochemical composition and reproductive cycle

There was a clear seasonal pattern in the life-history stage composition of hyperbenthic *Parasagitta elegans*. Large mature Stage III individuals dominated the samples from late May through mid-July 1997 and in late May 1998, making up 55 to 90% of all individuals (Fig. 2). From June to October 1997, there was a relative increase in the frequency of immature Stage I individuals, which increased from ca. 10 to 80%. These Stage I individuals clearly metamorphosed into Stage II juveniles between November 1997 and April 1998, when Stage II comprised ca. 80% of the total sample. There was relatively rapid maturation of Stage II into Stage III individuals during April and May 1998. Thus the samples were dominated by Stage III in May and June, Stage I in October and November, and Stage II in February and April.

Correlations between the CUSUMs of the relative proportion of mature Stage III individuals and the biochemical composition show strong relationships between temporal variations in the reproductive cycle and biochemical composition of *Parasagitta elegans* (Fig. 3). Levels of lipid, carbohydrate and the C/N ratio were positively correlated with the percent of Stage III individuals (Fig. 3A,C,F). The level of protein was negatively correlated with the proportion of mature individuals (Fig. 3B). The levels of ash and carbon were not significantly correlated with the relative proportion of mature chaetognaths (Fig. 3D,E). These data suggest that during maturation in the spring and summer, *P. elegans* does not increase its total organic matter (i.e. carbon) as a proportion of dry weight, but only changes its biochemical composition by increasing the proportion of lipid and carbohydrate and decreasing the proportion of protein.

Biochemical levels and abundance of mature copepods

It should be noted that the abundance of copepods reported in this study is an underestimate, since we used a plankton net with a relatively large mesh size (500 µm) to be consistent in the collection of zooplankton from the hyperbenthic zone and the water column. Nevertheless, the abundance of major species of adult copepods varied seasonally (Fig. 4). The abundances of adults of the genera *Calanus*, *Pseudocalanus*, and *Metridia* were high in May and June of 1997 and 1998. There was a sharp increase in the abundance of adult *Temora* spp. in November 1997; this sudden increase is not likely to be an outlier, since this increase occurred in all 3 depth layers, i.e. in 2 different net tows in the water column as well as in the hyperbenthic sledge tow (data not shown). The total abundance of adult copepods was well above the grand mean in May and June of 1997 and slightly above the mean in April and May of 1998. The number of adult copepods in the spring was higher in 1997 than in 1998, and this interannual variation was largely attributable to *Pseudocalanus* species.

The temporal variation in the abundance of adult copepods was highly correlated with the biochemical levels of *Parasagitta elegans* (Fig. 5). The abundance of total adult copepods was positively correlated with lipid and carbohydrate levels and with the C/N ratio (Fig. 5A,C,F), but negatively correlated with protein levels (Fig. 5B). No correlations were found with the levels of ash and carbon (Fig. 5D,E).

DISCUSSION

Seasonal variation in biochemical composition

Although seasonal variability in the biochemical composition of chaetognaths has been reported previously, causal mechanisms have remained elusive. In Biscayne Bay, Florida, USA, *Sagitta hispida* had decreased levels of protein and increased levels of lipid

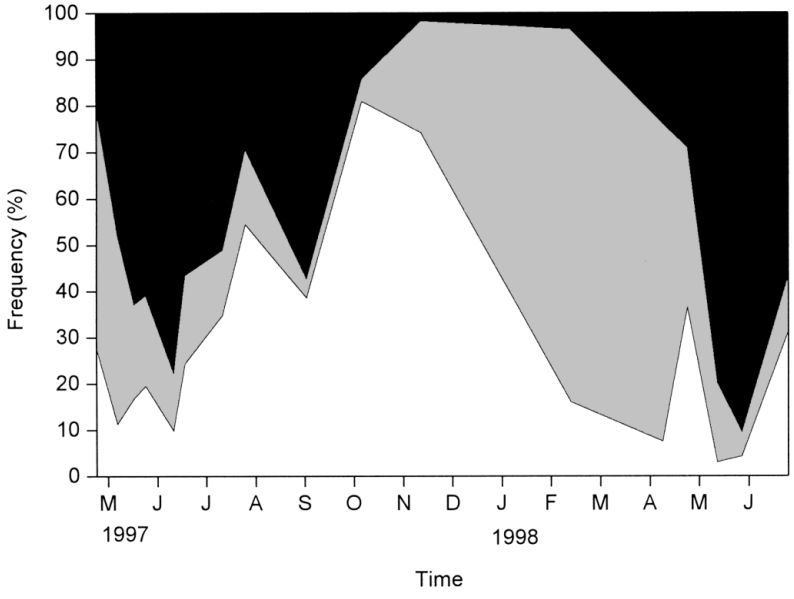

Fig. 2. *Parasagitta elegans*. Annual reproductive cycle, showing relative frequency distributions of life-history Stages I to III (see 'Materials and methods' for stage definitions). □: Stage I, ▨: Stage II, ■: Stage III

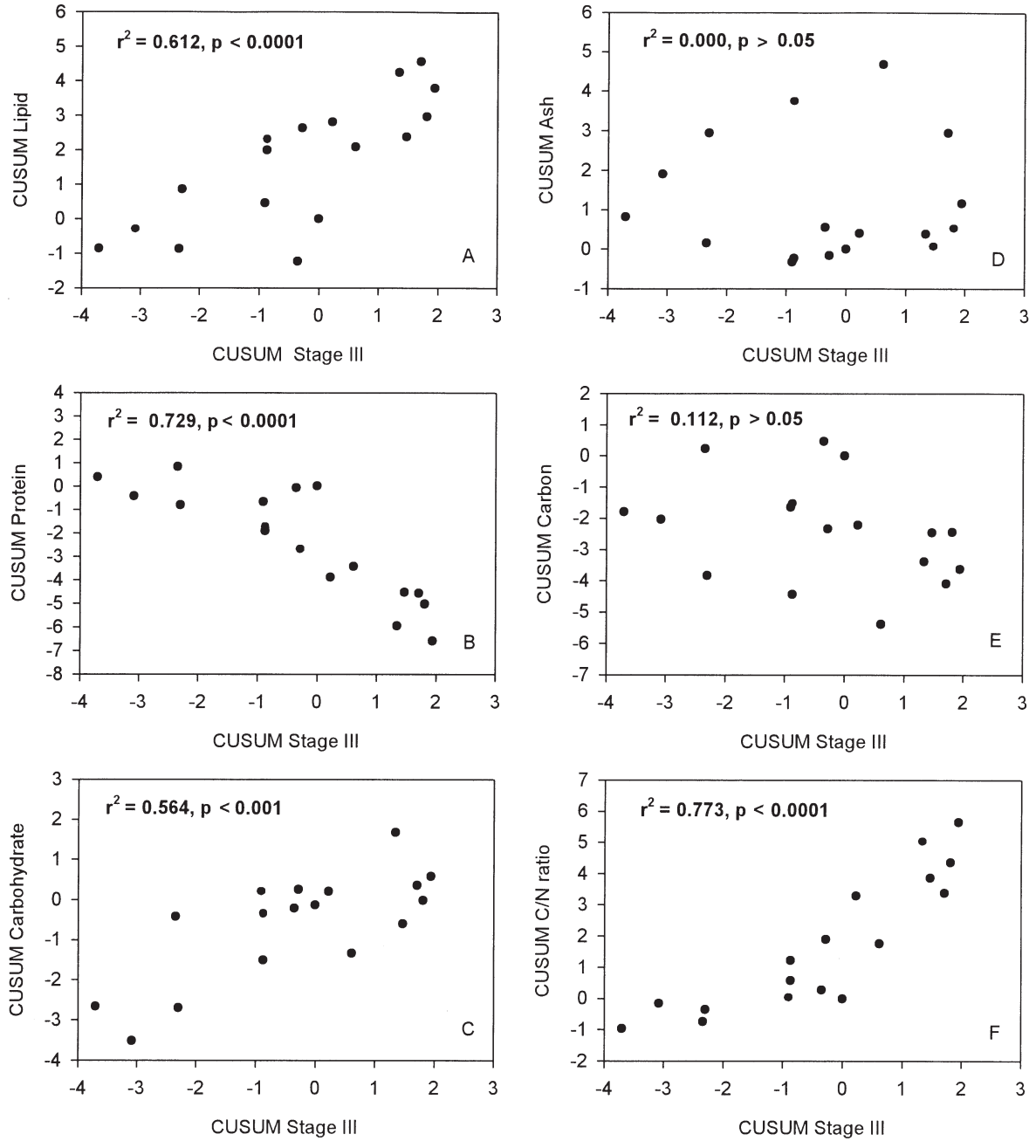

Fig. 3. *Parasagitta elegans*. Correlations between cumulative sums of normal standard deviates of the relative proportion of mature Stage III individuals in the tows and (A) lipid, (B) protein, (C) carbohydrate, (D) ash, (E) carbon, (F) C/N ratio. r^2 = coefficient of determination, p = significance at 95% level (n = 17)

and ash during spring and fall (Reeve et al. 1970). This seasonal pattern could not be explained by the reproductive cycle of *S. hispida*, which has a lifespan of a few weeks and, as a species, reproduces continuously throughout the year. The copepods that are the major prey of *S. hispida* also reproduce continuously, indicating that food availability is not the cause of seasonal biochemical variation in *S. hispida*. Furthermore, the biochemical composition of *S. hispida* remained constant even when individuals were starved for 25% of the generation time. However, the biochemical changes appear to be related to salinity fluctuation (30 to 35‰), protein decreasing and ash increasing as salinity rises. This salinity effect is also found in other gelatinous zoo-

plankton such as hydromedusae and scyphomedusae (Larson 1985, Wright & Purcell 1997, Hirst & Lucas 1998). When these zooplankton are exposed to higher salinity, they increase their bound water, resulting in an increase in dry weight; they also increase their ash weight to maintain buoyancy by selectively exchanging ions (Robertson 1949, Bidigare & Biggs 1980). Therefore, the decrease in the protein level of *S. hispida* at higher salinity is probably due to an increase in bound water and, subsequently, dry weight. *S. hispida* may also control its buoyancy by increasing its ash content when exposed to higher salinity.

In Korsfjorden, Norway, *Eukrohnia hamata* from below 300 m had increased levels of protein and ash in the spring and increased levels of lipid in the fall and winter (Båmstedt 1978). However, this pattern was not related to its seasonal reproductive cycle, since the high lipid levels were also present in immature stages and there were no significant correlations between biochemical composition and body size, which was used as an indicator of maturity. Furthermore, the observed variability in biochemical composition could not be explained by physical variability, since temperature and salinity were relatively constant below 300 m in Korsfjorden. Therefore, food availability is considered to be the most likely factor influencing seasonal changes in the biochemical composition of *E. hamata* (Båmstedt 1978).

In contrast to these previous studies, seasonality in the biochemical composition of *Parasagitta elegans* from the hyperbenthic zone of Conception Bay is clearly a function of both the reproductive cycle and (perhaps) food quality. Lipid and carbohydrate levels increase as *P. elegans* makes the transition from Stage II to Stage III in the spring and summer. These changes are probably affected by food quality rather than food abundance because they occur when large, mature, energy-rich copepods appear in the spring and summer rather than when the total abundance of copepodites increases in the fall (Davis 1982, Myers et al. 1994).

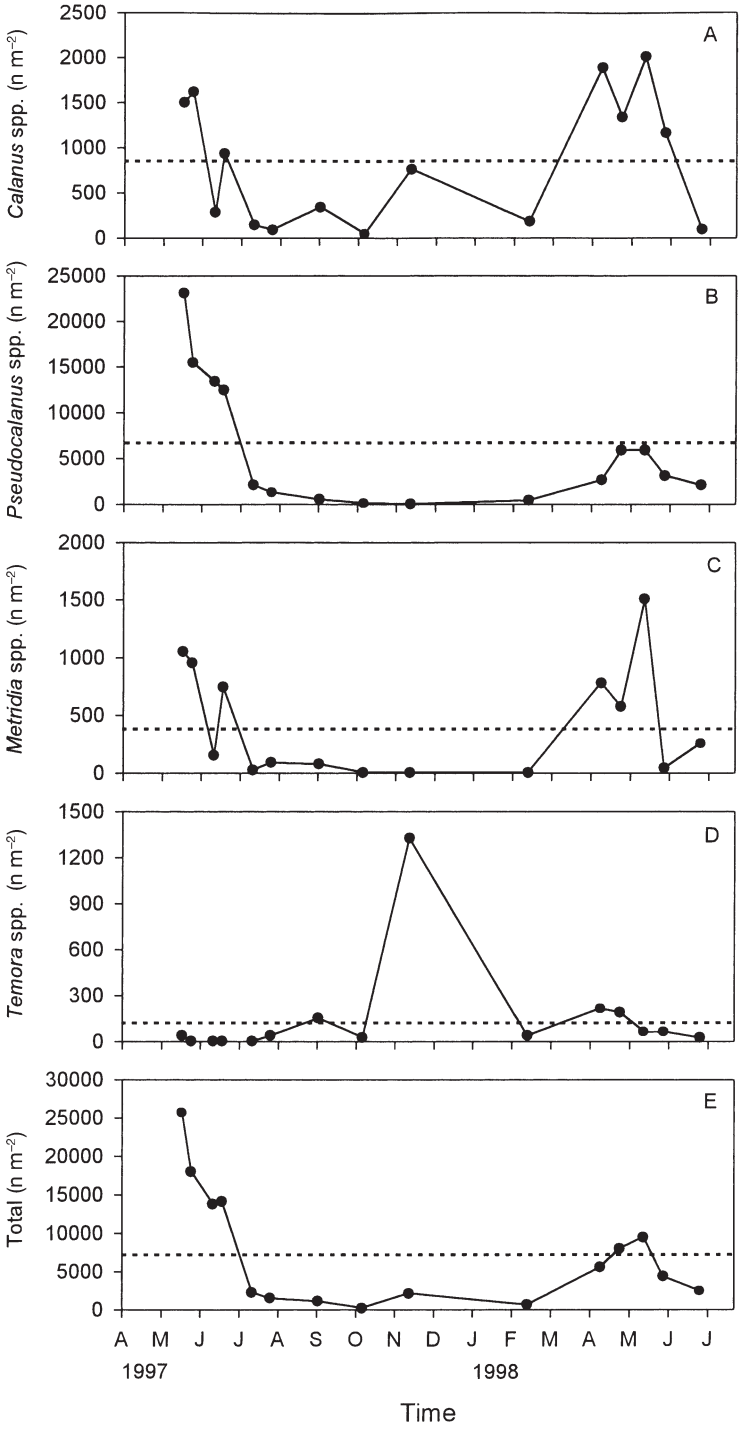

Fig. 4. Abundance of CVI female copepods from May 1997 to June 1998. (A) *Calanus* spp., (B) *Pseudocalanus* spp., (C) *Metridia* spp., (D) *Temora* spp. (E) Total CVI female copepods. Dashed lines represent the means

In Conception Bay, our evidence indicates that energy transfer from primary producers to secondary and tertiary consumers is tightly and temporally coupled. As the spring bloom progresses in April and May, the abundance of mature copepods increases (Fig. 6). Although we have limited interannual data for comparison, there appears to be a relationship between the intensity of the spring bloom and the

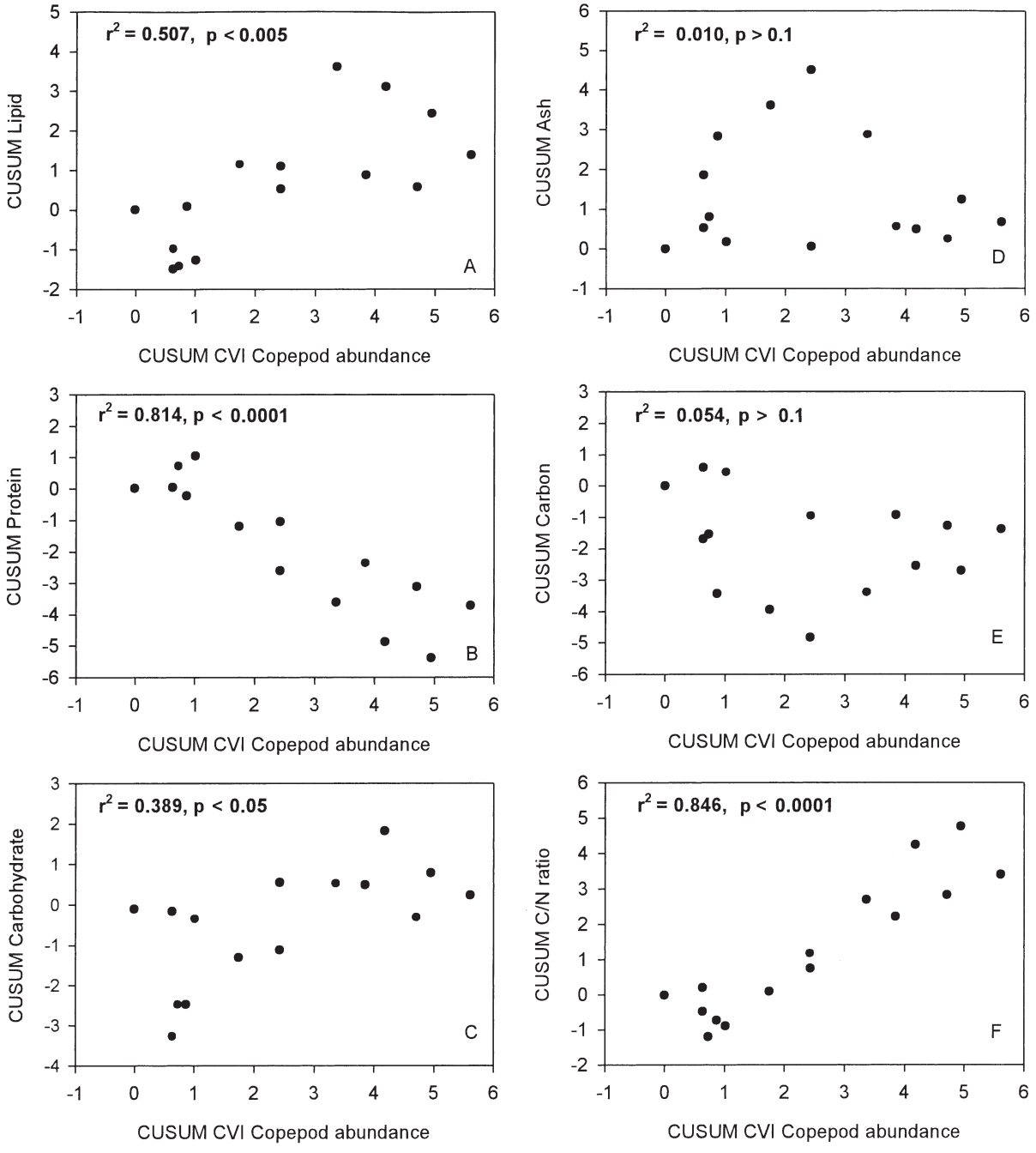

Fig. 5. Correlations between cumulative sums (CUSUM) of normal standard deviates of total female CVI copepods and the following characteristics of the chaetognath *Parasagitta elegans:* (A) lipid, (B) protein, (C) carbohydrate, (D) ash, (E) carbon, (F) C/N ratio. r^2 = coefficient of determination, p = significance at 95% level, n = 15. Two sets of data are missing, since no copepod abundance data were collected on 23 April and 6 May 1997

abundance of mature copepods. More copepods matured in the spring of 1997, when the intensity of the phytoplankton bloom was higher, than in 1998 when the bloom was less intense (Fig. 6). Responding to the increase in the energy in the lower trophic levels, *Parasagitta elegans* also increases its levels of lipid and carbohydrate and undergoes sexual maturation in the spring. More specifically, the time lags between the peaks in phytoplankton, mature copepods and mature chaetognaths are ca. 3 wk (Fig. 6).

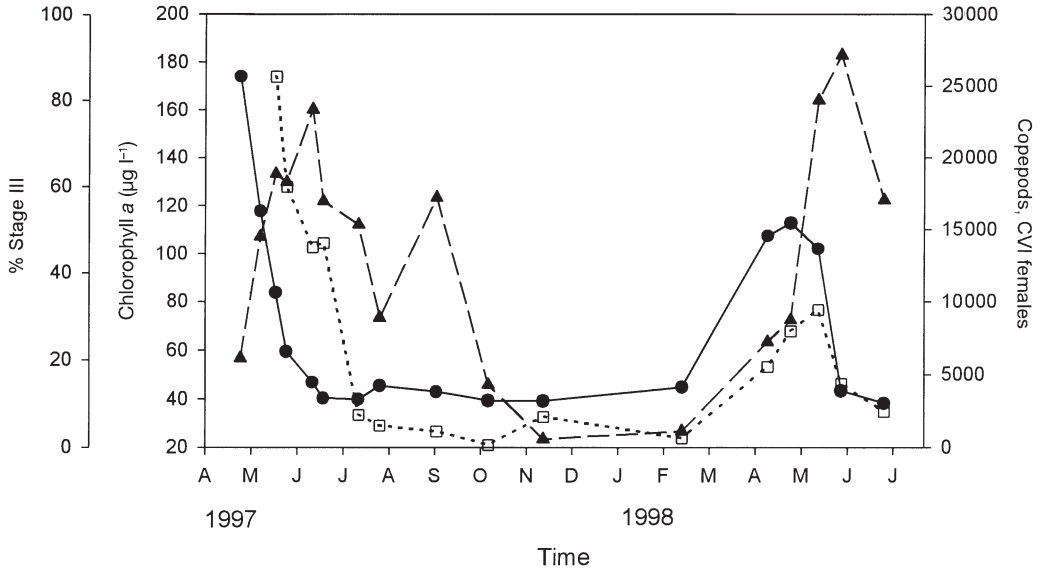

Fig. 6. Concentration of chlorophyll *a*, abundance of female CVI copepods, and relative proportion of mature Stage III *Parasagitta elegans* from April 1997 to June 1998. RFU (relative fluorescence unit) readings from *in situ* fluorometer at 1 m intervals were converted into chlorophyll *a* values and integrated from 0 to 200 m. Calibration equation used to convert RFU to chlorophyll *a* was $y = 0.3983x + 0.2815$, $r^2 = 0.7302$, $p < 0.001$, n = 244, standard error = 1.6374, $F = 654.892$. (●) Chlorophyll *a*; (□) female copepods (Stage CVI); (▲) % Stage III *P. elegans*

Summary

According to Torres et al. (1994) and Hagen (1999), polar zooplankton generally fall into 1 of 3 categories of energy strategies. Type 1 represents overwintering zooplankton, such as herbivorous copepods, which accumulate large lipid deposits as wax esters and enter diapause. Extreme metabolic reduction and reproduction early in the season is found in the overwintering zooplankton. Type 2 represents zooplankton such as euphausiids, hyperiid amphipods and salps , which do not enter true dormancy during winter, but reduce metabolism and metabolize stored triacylglycerols. They feed opportunistically and reproduce when conditions are favorable. Type 3, such as carnivorous copepods (Euchaeta), decapods, mysids, gammarid amphipods and chaetognaths show no metabolic reduction during the winter and have a prolonged breeding season.

The energy strategy of chaetognaths in the hyperbenthic zone of boreal waters such as Conception Bay differs from the energy strategies of polar zooplankton. *Parasagitta elegans* does not overwinter, since it grows at a constant rate throughout the year (Choe & Deibel 2000). Since growth rates and hyperbenthic water temperatures are both constant throughout the year, we conclude that growth is not food-limited. Metabolic reduction probably does not occur in actively growing individuals during winter. Nevertheless, *P. elegans* appears to require additional energy from the spring phytoplankton bloom to achieve sexual maturity, since it accumulates lipid immediately after the spring bloom and utilizes it for reproduction.

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