THE SEASONAL BIOCHEMICAL COMPOSITION OF THE CHAETOGNATH Parasagitta Elegans IN CONCEPTION BAY, NEWFOUNDLAND IN RELATION TO POPULATION DYNAMICS AND TROPHODYNAMICS

NAMI CHOE

INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

Bell & Howell Information and Learning
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
800-521-0600

THE SEASONAL BIOCHEMICAL COMPOSITION OF THE CHAETOGNATH *PARASAGITTA ELEGANS* IN CONCEPTION BAY, NEWFOUNDLAND IN RELATION TO POPULATION DYNAMICS AND TROPHODYNAMICS

by

Nami Choe

A thesis submitted to the

School of Graduate Studies

in partial fulfillment of the

requirements for the degree of

Master of Science

Department of Biology, Faculty of Science

Memorial University of Newfoundland

August 1999

St. John's Newfoundland

Abstract

The seasonal biochemical composition of *Parasagitta elegans* in the water column and benthic boundary layer of Conception Bay, Newfoundland was documented from 1997 to 1998. The seasonal variation in the biochemical levels of *P. elegans* primarily reflected the reproductive cycle. Protein and ash levels increased and lipid and carbohydrate levels decreased when the animals reproduced in the fall. The opposite trends occurred when the animals matured in the spring and summer. Feeding may have caused minor differences in biochemical composition between the spring of 1997 and 1998. Protein level was higher and ash and carbohydrate levels were lower in the spring of 1998. The proportion of *Calanus* spp. in the diet was significantly higher and the abundance of *Calanus* spp. increased earlier in the spring of 1998. This is the first study of the population dynamics, distribution, feeding and biochemical composition of chaetognaths from the benthic boundary layer.

Acknowledgements

I deeply appreciate Dr. Don Deibel for his enthusiasm, patience and guidance throughout the project. I thank Drs. Ray Thompson, Grant Gardner, Erik Thuesen and Paul Snelgrove for their critical comments and editorial help. I also thank Dr. Ray Thompson for the use of his laboratory and equipment. Mike Riehl has given me countless help in the field and laboratory. Sample collection would have been impossible without the crew of the R.V. Karl and Jackie II, Mike Riehl, Vivian Bushell and Dr. Don Deibel. Thanks to Betty Hatfield for her concern and help during the biochemical analyses. Sing Hoi Lee counted the water column copepods and Vivian Bushell counted the benthic boundary layer copepods. Dr. Nick Mumm provided preliminary data and shared his ideas with me. Dr. Vidar Øresland confirmed the taxonomy of chaetognaths and provided me many comments during the feeding study. Hong Chen helped in solving statistical problems. This study was supported by an NSERC Collaborative Project Grant to Don Deibel et al. and a NSERC Research Grant to Don Deibel and by a Graduate Fellowship from the Memorial University of Newfoundland.

Special thanks to Misuk Yoon and Panseok Yang for valuable friendships and all other friends in St. John's for laughs and unusual times. Joyce Kim and Dr. Duk Chu Kim gave me kind advice when I needed it most. Harold and Milly Hammond have been my great singing pals. I would like to thank my family for their love and support and I dedicate this thesis to my personal hero, my Mother.

Table of Contents

List of Tables

List of Figures

List of Appendices

Chapter 1. General Introduction

1.1 General description of chaetognaths

Chaetognaths are found throughout coastal waters and open oceans, constitute 5-15% of zooplankton biomass and are important predators on copepod communities (Welch et al. 1996). They are often found to be the most abundant zooplankton after copepods and are known as indicator species of water masses.

The chaetognath has an elongated, fluid-filled, transparent body, which is a tube of locomotor musculature inside a tough basement membrane covered with a multilayered epidermis. Thus the musculature operates on a hydroskeleton. Chaetognaths bear one or two pairs of lateral fins and a tail fin, and are named from their large cephalic grasping spines. Their common name, arrow worms, describes both their body form and their rapid darting movements (Fig. 1.1). Overall length ranges from 2-120 mm. A rounded and somewhat flattened head bearing grasping spines or hooks, teeth, vestibular organs, and a ventral mouth is separated by a transverse septum from a long muscular trunk. The gut extends through the trunk, terminating at a ventral anus just anterior to a second transverse septum, which divides the posterior trunk region from the tail. Paired female reproductive organs lie in the trunk; the male reproductive system is situated in and on the tail. Conspicuous ciliary fan, or fence, receptor organs are seen arrayed on the head, trunk, tail and even fins of living specimens. On the posterior dorsal surface of the head, behind the eyes, there is a ciliary loop, or 'corona ciliata', which extends posteriorly onto

the trunk in many species (Bone et al. 1991).

Chaetognaths are protandric hermaphrodites - the testes mature before the ovaries. Fertilization is internal and the spawning periodicity is species-dependent. Many warm-water species and populations sampled in areas of strong water mass mixing often breed over all or a large part of the year (Alvariño 1965), whereas cold-water species breed less often. Generation length varies with temperature and species (Bone et al. 1991). Multiple cohorts may be produced by a single adult generation, leading to a greater number of generations where spawning seasons are longer (Øresland 1985).

1.2 Benthic Boundary Layer (BBL)

The benthic boundary layer can be defined in several ways. Physically, it is the layer of water near the bottom where the friction of water moving over the seafloor creates physical mixing of the bottom water and causes the resuspension of sediment and flocculent matter. The BBL can extend from 10 to 100 m above the bottom (mab) depending on the water depth and current speed (Wishner and Gowing 1992). Turbulence in this layer can result in resuspension of bottom sediments. Heavy inorganic particles remain close to the seafloor, but light, organic particles can reach maximum concentrations some distance above the bottom (Lalli and Parsons 1993).

Biologically, the BBL is that portion of water column near the bottom where organic matter from the upper mixed layer settles and supports the production of near-bottom dwelling plankton. In the deep sea, many species of benthopelagic zooplankton inhabit this region and the zooplankton biomass close to the bottom can be higher than the

biomass above (Wishner 1980, Angel and Baker 1982, Smith 1982). In a study done in the San Diego Trough at depths from about 1000 to 4700 m, benthopelagic plankton biomass decreased exponentially with depth but the biomass at 10 mab was greater than that 100 m above bottom (Wishner 1980). In the northeast Atlantic, where the maximum depth is about 4000 m, biomass distribution was similar (Angel & Baker 1982). Enrichment of benthopelagic zooplankton has also been reported from continental shelf waters. Zouhiri and Dauvin (1996) observed that the BBL in the western English Channel (75 m deep) was rich in benthopelagic zooplankton. In Conception Bay, Newfoundland, the BBL is rich in copepods, chaetognaths, euphausiids, fish larvae, amphipods and mysids (Bushell et al. unpublished data). The chaetognath *Parasagitta elegans* is one of the most abundant zooplankton, ranking third behind copepods and amphipods in abundance.

1.3 Objectives of the study

Parasagitta elegans is the most abundant chaetognath in Newfoundland waters (Davis 1982, 1986), and occurs throughout the year in Conception Bay, Newfoundland. According to preliminary results from July 1996, small, juvenile *P. elegans* occurred in the upper water column and large, adult animals occurred deeper (Mumm, unpublished data). This pattern of vertical distribution has been observed in other places (King 1979, Øresland 1985), but my results included an interesting new observation. I found that the density of *P. elegans* in the BBL was higher than the density in the water column by several orders of magnitude. Further investigations are needed to understand the physiology, ecology and population dynamics of these BBL chaetognaths.

The objectives of this study were to determine and compare the seasonal biochemical composition of *Parasagitta elegans* in the BBL and water column of Conception Bay, Newfoundland, from 1997 to 1998. Population dynamics and feeding of *P. elegans* were studied to understand the causes of the seasonal variation in biochemical composition.

1.4 Hypotheses: Detailed questions

The biochemical composition of zooplankton in various areas has been studied to understand their growth, metabolism, trophodynamics and energetics (Beers 1966, Ikeda 1972, Mayzard & Martin 1975, Båmstedt 1978, Båmstedt 1981, Falk-Peterson 1981, Percy & Fife 1981, Yen 1983, Gorsky et al 1988, Ikeda & Skjoldal 1989, Donnelly et al. 1994, Bailey et al. 1995). These studies generally include the proximate (protein, lipid, carbohydrate) and elemental (C, H, N) composition of wet, dry and ash-free dry body tissues of zooplankton.

1.4.1. Seasonal variation in the relationship between biochemical composition, maturity and body size

If the biochemical composition of *Parasagitta elegans* from water column and BBL animals varies seasonally, the following hypotheses need to be tested. The biochemical content of *P. elegans* may depend upon reproductive maturity and body size. One cannot assume that reproductive maturity of chaetognaths depends strictly on body size, since length at maturity may vary depending on environmental factors such as temperature and food availability. Do the animals store protein or lipid for later

reproduction? Do animals of various sizes have a different biochemical composition? The animals living in the water column and the BBL may differ in biochemical composition. To answer the questions, basic knowledge of how *P. elegans* lives in Conception Bay must be obtained. The vertical distribution and population dynamics of *P. elegans* were studied from April, 1997 to June, 1998, and are reported in Chapter 2. The biochemical study results are reported in Chapter 4.

1.4.2. Seasonal variation in the biochemical composition vs. feeding and food availability

The next set of hypotheses deals with feeding. *P. elegans* is known to feed primarily on copepods (Sullivan 1980, Feigenbaum 1982, Øresland 1987, Falkenhaug 1991, Alvarez-Cadenza 1993). The biochemical content of *P. elegans* may depend on how often the animals feed. If the number of prey per chaetognath (NPC) of *P. elegans* depends on the abundance of prey, then the biochemical content may be related to prey abundance. Alternatively, food is not a limiting factor for chaetognaths in Conception Bay and NPC is independent of prey abundance.

The diet of *P. elegans* may change seasonally and could be an important factor affecting its biochemical composition. For example, chaetognaths may not depend on only copepods throughout the year. They may feed cannibalistically or on other gelatinous animals, such as appendicularians, which become abundant in Newfoundland coastal waters during spring and summer (Mahoney & Buggeln, 1983; Deibel, pers. comm.). If copepods are the main diet of chaetognaths, then consumption of different species of

copepods may change the biochemical composition. In Conception Bay, adult *Calanus glacialis* live in the BBL and *Calanus finmarchicus* live in the water column above (Deibel, unpubl.). *Calanus glacialis*, being the larger copepod, may provide more efficient nourishment to chaetognaths compared to *Calanus finmarchicus*. *P. elegans* living in the water column may consume primarily *C. finmarchicus* and other small copepods such as *Pseudocalanus* sp. while *P. elegans* living in the BBL may consume primarily *C. glacialis*. Feeding results are presented in Chapter 3.

Conception Bay, a fjord over 300 m in depth and opening to the Atlantic Ocean (Fig. 1.2), is well suited for study of seasonal biochemical composition of *P. elegans*. The east coast of Newfoundland is dominated by the Labrador Current, which enters Conception Bay as a tongue of very cold water (-1.5°C to -1°C) at a sill depth of 170 m. Below the thermocline (50-80 m), water temperature is between 0 and -1.5°C throughout the year (Taggart & Leggett 1987). If the animals stay below the thermocline, they are not affected by temperature change. This is advantageous for the study since temperature variation can be disregarded as a factor which affects seasonal biochemical composition of *P. elegans*. Whether the animals collected in the BBL migrate into upper, warmer waters on daily or seasonal time scales is unknown, and was investigated in this study.

The main hypotheses of this study are as follows;

1. The population dynamics and distribution of *Parasagitta elegans* change seasonally.
2. The composition and availability of prey for *P. elegans* and the number of prey per chaetognath change seasonally.

3. The biochemical composition of *P. elegans* changes seasonally.
4. The biochemical composition of *P. elegans* depends on stage of maturity, body size and feeding state.

Fig. 1.1 Schematic diagram of chaetognath (*Parasagitta*).
a, anus; al, Alveolar tissue; e, eye; fg, female gonad; gd, gut diverticle; ga, grasping spines; lf, lateral fin; t, testis; tf, tail fin; vg, ventral ganglion; vs, seminal vesicle (Bone et al. 1991)

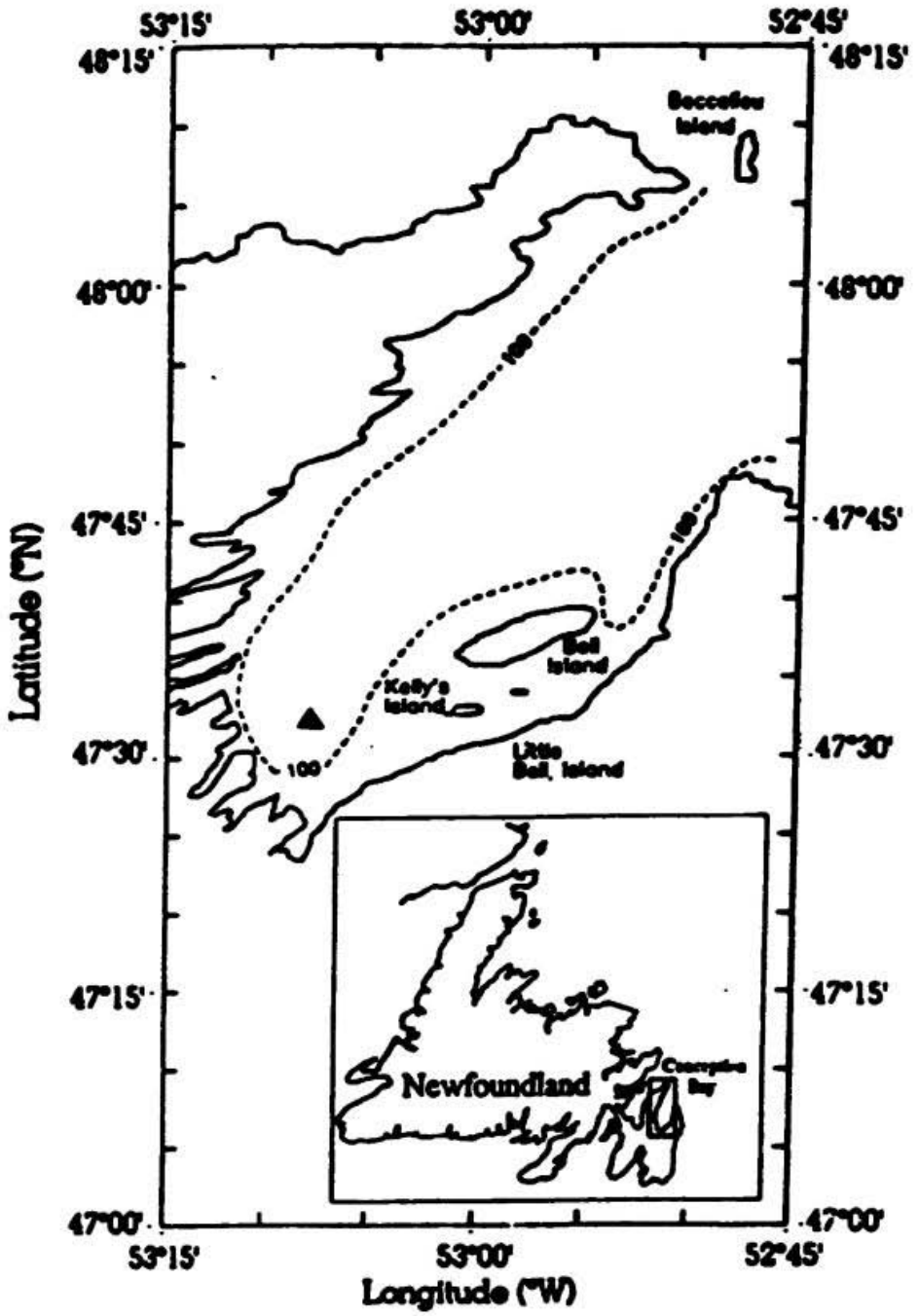

Fig. 1.2 Map of Conception Bay, Newfoundland. Study site is indicated (▲).

Chapter 2. Distribution and Population Dynamics of *Parasagitta elegans* in Conception Bay, Newfoundland

2.1 Introduction

2.1.1 Life cycle and generation time

Chaetognaths are protandrous hermaphrodites, i.e. the testes mature before the ovaries (Hyman 1959, Dunbar 1962, Ghirardelli 1968, Reeve 1970a, Strathmann and Shinn 1987), but there has been considerable disagreement over whether they self-fertilize or cross-fertilize. A number of authors have induced self-fertilization in *Parasagitta setosa* (Dallot 1968), *Sagitta hispida* (Reeve 1970a), *P. elegans* (Pearre unpublished observation), *Sagitta crassa* (Nagasawa 1987), and *Spadella cephaloptera* (Ghirardelli 1968). Others have argued that cross-fertilization is obligatory in nature because of physical difficulties in bringing sperm to the seminal vesicle or because of evolutionary considerations (Alvariño 1983, Reeve and Walter 1972).

Chaetognaths spawn over a prolonged period. Jakobsen (1971), King (1979) and Conway and Williams (1986) stated that *P. elegans* spawn several times over a period of months. This protracted spawning makes it difficult to distinguish individual ages, spawning times and stocks. Larval *Parasagitta* are planktonic, generally remaining near the water surface (Bone, Kapp and Pierrot-Bults, 1991). The newly hatched larvae lack anterior fins, caudal septum, anus, eyes and head armature (chaetae). They start feeding within one or two weeks. Post-larval growth is straightforward. Most body sections

increase in direct proportion to overall length, except that the section behind the caudal septum becomes relatively shorter as the animal grows (Bone, Kapp and Pierrot-Bults, 1991).

Numerous studies on the population dynamics of *Parasagitta elegans* indicate that the generation time depends mostly on temperature. Russell observed a generation time of 43 days for *P. elegans* near Plymouth, where the mean temperature was 16°C (Russell 1932). In Ogac Lake, Baffin Island where the temperatures are -1 to 8°C, a 1 year life cycle was observed (McLaren 1969). Dunbar (1962) observed a generation time of 2 years in Canadian Arctic, where water temperatures do not exceed 2°C. Welch et al. (1996) reported a generation time of 2 years for *P. elegans* in the Canadian high Arctic, where the mean annual temperature was -1.5°C.

2.1.2. Distribution of *P. elegans* in the ocean

Parasagitta elegans (*Sagitta elegans* in older literature), the best-known chaetognath in the world, is found in Arctic and subarctic regions and extends into the northern part of the Atlantic and Pacific Oceans, where water temperatures range from -1.5°C to 21.0°C (Alvariño 1965). Studies of life history and vertical distribution of *P. elegans* indicate that the population structure and patterns of vertical distribution and migration reflect the stage of maturity and size of the individuals. Generally, the older stages of *P. elegans* are found at greater depths than the younger stages (Kotori 1972, Sameoto 1987, Welch et al. 1996). Conway and Williams (1986) observed that the smallest *P. elegans* in the Celtic Sea were found in near-surface waters and did not

migrate, but as their lengths increased they occupied greater depths and a portion of the population displayed diel vertical migration. King (1979) observed that small *P. elegans* in Dabob Bay, Washington were non-migratory and distributed in the top 100 m but that the breeding stages were restricted to a layer between 50 and 100 m during the day and migrated to the surface layer at night, enhancing the probability of successful reproduction.

2.1.3. Objectives of the study

According to a study of the life history of *P. elegans* in central Long Island Sound, biomass was considered to be underestimated because the net tow from the top to the bottom of the water column did not successfully collect those adult animals which live very near the sediments of neritic waters (Tiselius and Peterson, 1986). The authors suggested the use of a special sampling device such as a high volume pump or an epibenthic sled to avoid the underestimation of biomass. Øresland (1987) concluded that good quantitative estimates of the abundance of chaetognaths of Gullmarsfjorden must consider the possible occurrence of *P. elegans* close to the bottom. In the present study, the abundance and biomass of *P. elegans* in the water column and in the benthic boundary layer were estimated to determine if the exclusion of hyperbenthic chaetognaths in other studies could have resulted in considerable underestimation.

The main purpose of this chapter is to understand the population densities, growth and reproduction of *P. elegans* in Conception Bay, Newfoundland from 1997 to 1998. The specific questions addressed are;

- What was the abundance and biomass of *P. elegans* in the water column and BBL?

- Were there ontogenetic and diel vertical migrations of *P. elegans* in Conception Bay?

- When did *P. elegans* reproduce?

- How many cohorts were produced?

- What was the individual growth rate ?

- What was the generation time of *P. elegans*?

2.2 Methods

2.2.1 Sample collection

Specimens of *Parasagitta elegans* were collected from April, 1997 to June, 1998 at Station 5 (47° 32.2' N, 53° 07.9' W), Conception Bay, Newfoundland (Fig. 1.2). The animals in the pelagic layer were collected from 0-50 m, 50-175 m and 175-225 m depth strata using a 500 μm mesh, opening and closing Tucker trawl with a TSK flowmeter. Towing time ranged from 3 to 16 min. The animals in the benthic boundary layer were collected 0.5 m to 1 m off the bottom using a hyperbenthic sledge fitted with a 500 μm mesh net and a TSK flowmeter (Fig. 2.1). The sledge was equipped with a butterfly-valve door held closed by a length of surgical tubing. 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 behind the boat to indicate whether the door was open or closed. The acoustic transmitter (Vemco Inc. Nova Scotia) on the sled also relayed depth and temperature information to the boat in real time. The sledge was dragged at 1.0 to 1.5 knots for 17 to 25 min. The samples were immediately preserved in 4% buffered

formaldehyde. The water column layer between 225 m and the bottom of the Station 5 is approximately 10 m. This layer was not sampled with a Tucker trawl because it could be damaged and clogged with mud and debris from the bottom.

A single tow was done at each time point. Day and night samples were collected to observe the vertical migration pattern and feeding behavior on May 23, 1997 and June 23, 1998. The samples were collected every two weeks during the spring and every month during other seasons. The purpose of frequent sampling during the spring was to closely investigate how the sinking spring phytoplankton bloom could affect the zooplankton in the BBL. Only few samples were collected during the winter due to harsh weather conditions. The sampling dates and times are recorded in Table 2.1, 2.2 and 2.3.

2.2.2. Sample analysis

The gonad maturity of preserved *P. elegans* was recorded and classified into three reproductive stages under a M5 Wild stereo microscope at 25X magnification (Sameoto 1987):

Stage I	Ovaries are invisible 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.

The length of each animal was measured from head to tail, excluding fins, to the nearest mm and the animals from split samples were counted to determine abundance. The total numbers of counted animals from each sample are reported in Table 2.1-2.3. Frequencies

for body size and maturity stage of *P. elegans* were plotted and cohort analysis was applied by fitting a nonlinear Gaussian function to the modes of the distributions (Sameoto 1971, 1973).

For biomass calculation, the dry weight and carbon content were obtained from the animals in different size groups. Formalin preserved specimens were not used to obtain the dry weight and carbon content. To obtain dry weight, live animals of different sizes were rinsed in distilled water and frozen at -80 °C. The body lengths of analyzed animals ranged from 18 to 50 mm, and the size interval was 1 or 2 mm. Frozen tissue was dried in a lyophilizer for 2 days, then weighed to the nearest 0.1 mg. Carbon content was measured with a Perkin-Elmer CHN analyzer (model 2400) standardized with acetanilide. The CV of the carbon measurements from acetanilide was within 0.5 % of known theoretical percentage (i.e., 71.1 % of carbon in acetanilide). Linear and non-linear regression were applied to the data using Origin, Data Analysis & Technical Graphics (Microcal Software, Inc.).

2.3 Results

2.3.1 Abundance and biomass of *P. elegans* in the water column and BBL

The mean annual abundance of *P. elegans* in the 50-175 m stratum was 2 ± 2 m^{-3} and in 175-225 m stratum was 5 ± 6 m^{-3} (Table 2.4). Too few animals were caught for reliable counts in the 0-50 m stratum with a 500 µm mesh Tucker trawl net. The animals in the BBL were more concentrated, with a mean abundance of 24 ± 19 m^{-3}. On an areal basis, the annual mean abundance from 50-225 m was 478 m^{-2}. Sampling from the BBL

represented 1 m off the bottom; therefore, the abundance was 24 m^{-2} which constitutes 5 % of the total abundance in < 0.5 % of the total water column. The actual BBL may extend up to 5 to 10 m off the bottom (Deibel, pers. comm.). If this is the case, the mean abundance in the BBL could range from 121 m^{-2} or 241 m^{-2}, 20 % to 33 % of the total abundance. In the water column, there were seasonal variations in areal abundance (Fig. 2.2). Abundance in the 50-175 m stratum increased to a maximum from August to November. In the 175-225 m stratum, the abundance was consistent excepting a sharp increase during February. No pattern in the variation of abundance was observed in the BBL (Fig. 2.2).

Dry weight of *P. elegans* increased with body length and can be expressed with the equation, $Log_{10}Y = 3.24\ Log_{10}X - 4.19$ ($r^2 = 0.96$, n=56) where Y is dry weight (mg) and X is the body length (mm) (Fig. 2.3). Carbon content of the animals as a function of dry weight can be expressed with the linear equation, $Y = 0.43\ X - 0.02$ ($r^2 = 0.98$, $n = 72$) where Y is the carbon content (mg) and X is the dry weight (mg) (Fig. 2.4). Using the derived equations and the size measurements of the collected animals, biomass in each water column stratum and in the BBL was calculated in terms of dry weight and carbon (Table 2.4). The mean annual biomass in the 50-175 m stratum was 285 ± 454 mg $\cdot$ m^{-2} (dry weight) and the biomass in the 175-225 m stratum was 383 ± 380 mg $\cdot$ m^{-2}. The mean annual areal biomass in the BBL was 203 ± 198 mg $\cdot$ m^{-2}, which constitutes 23 % of the total biomass in the bay. If the BBL extends up to 5 to 10 m from the bottom, the biomass in the BBL could range from 60 to 75 % of the total biomass in the bay. High

biomass occurred during fall and winter in the water column (Fig. 2.5). No pattern in the variation of biomass was observed in the BBL (Fig. 2.5).

2.3.2. Body size and maturity stage frequency distributions

Since the entire water column was not sampled at once but sampled separately from two depth strata, only general points can be made about size and maturity distributions of *P. elegans* in the entire water column from 50-225 m. In the 50-175 m stratum, immature animals (stage 1 and 2) with body lengths < 30 mm were abundant throughout the entire year (Fig. 2.6). In the 175-225 m stratum, most of the animals were immature and less than 40 mm long (Fig. 2.7). Animals less than 10 mm long were not retained by the 500 μm mesh net. Stage 1 animals dominated from late summer to winter in both depth strata, indicating that reproduction occurred in late summer and fall (i.e., after July 23 in 1997).

Body size and maturity stage data from the BBL are shown in Fig. 2.8. Larger and mature animals greater than 40 mm lived only in the BBL. One to two modes of size classes were present. Four cohorts were found from 1997 to 1998 by observing the size modes and ovary maturity data. Cohort 1 matured from stage 2 to 3 from April to June, 1997, reproduced and then disappeared after June. Cohort 3, progeny of cohort 1, appeared in June. Cohort 2 matured from stage 1 to 3 from April to June and reproduced from July to October. This observation was supported by the fact that the matured ovary of cohort 2 was continuously regenerating into stage 1 from July to October. Cohorts 2 and 3 continued to grow and mature into stage 3 by June, 1998. Cohort 4, possibly

progeny of cohort 2, appeared in the BBL from November and continued to mature.

The mean body sizes of the three cohorts present from 1997 to 1998 were plotted (Fig. 2.9) and a growth curve was fitted to the data by applying the logistic function. Three cohorts represented in Figure 2.9 are cohort 1, 2 and 4. The distribution of cohort 3 coincided with cohort 2. Therefore, cohort 3 was not used for the calculation of growth rate and generation time. The mean length of all three cohorts increased with time. The equation which describes the mean length of *P. elegans* as a function of time is $Y = -46.893/(1+(X/509.1)^{1.368}+65.522$ ($n = 21$), where Y is the mean length in mm and X is the time in days. The individual growth rate from this equation is 25.3 mm $\cdot$ yr^{-1} $\cdot$ $individual^{-1}$, or 2.28 mg dw $\cdot$ yr^{-1} $\cdot$ $individual^{-1}$ (i.e., 1.0 mg C $\cdot$ yr^{-1} $\cdot$ $individual^{-1}$). The growth curve starts from a mean length of 18.6 mm and ends at 43.2 mm. According to the growth curve, the generation time of *P. elegans* is at least 560 days. Since the cohort with mean length less than 18.6 mm was not sampled, the time required for the growth to 18.6 mm is not known.

2.3.3 Diel vertical distribution

The body size and maturity stage frequency distributions of *P. elegans* on June 23, 1998, indicated that stage 3 animals moved into the BBL and stage 1 animals moved out of the BBL during the day (Fig. 2.10). During the night, stage 3 animals moved out of the BBL and stage 1 animals moved into the BBL. This observation was supported by the fact that the abundance of animals in the BBL during the day and night was approximately the same (i.e., 50.8 m^{-3} during the day and 49.2 m^{-3} during the night). Stage 3 animals

seemed to migrate upward at night because more stage 3 animals appeared in the 50-175m stratum at night. The body size and maturity stage distributions of *P. elegans* on May 23, 1997, also indicated that stage 3 animals occupied the BBL during the day and stage 1 animals were present mostly in the BBL during the night (Fig. 2.11).

2.4 Discussion

2.4.1. Distribution

This is the first report of the population dynamics of chaetognaths which includes animals from the BBL. Total abundance could be underestimated by 5 to 33 % and total biomass by 23 to 75 % if animals from the BBL were excluded from this study. The abundance and biomass of *P. elegans* increased during fall and winter in the water column since mature animals in the BBL reproduced during that time.

Since only a single sample was obtained at each time point, it may be questionable whether temporal variation in abundance can be discussed. However, based on the previous studies on replicability of zooplankton sampling, a single tow is valid for the study of zooplankton distribution (Gardiner 1931, Cassie 1968, Wiebe and Holland 1968). Hesthagen and Gjermundsen (1977) tested the precision of sampling the hyperbenthic zooplankton with Beyer's closing net attached to a hyperbenthic sledge and concluded that the gear samples the hyperbenthos with a high degree of replicability.

It is believed that spawning occurs in deep water (Kramp 1939, David 1958), since sexually mature individuals are usually only found there and the eggs hatch as they rise to the surface. Previous studies on *Parasagitta elegans* showed that small, young stages

were found in the upper layers of the water column and as they matured they were found at deeper levels (Jakobsen 1971, Sameoto 1971, Zo 1973, Cheney 1985, Øresland 1985, Conway and Williams 1986, Tiselius and Peterson 1986, Sameoto 1987). This study agrees with the others, since large stage 3 animals were mostly present in the BBL.

Diel migration of *P. elegans* was observed from the BBL to the upper 50-175m stratum. The migration seemed to be performed by all stages of animals in this study, whereas other studies concluded that only the larger, mature animals actively migrate upward during the night. The size and maturity stage distributions of *P. elegans* from the BBL indicated that stage 3 animals of all sizes moved into the BBL during the day and moved out during the night. Stage 1 animals moved out of the BBL during the day and into the BBL during the night. Zo also (1973) observed that adult *P. elegans* occurred at greater depths than did young animals during daylight. King (1979) reported that stages 2 and 3 of *P. elegans* underwent vertical migrations at different seasons. According to Conway and Williams (1986), stage 3 animals are capable of diel vertical migration.

2.4.2. Population dynamics

P. elegans matured during the spring and summer, when *Calanus* spp. were abundant, and reproduced during the fall (cf., Fig. 3.3 in Chapter 3). In Conception Bay, the annual maximum of *Calanus* nauplii occurs in the fall (Davis 1982). In other studies, the recruitment of chaetognaths either coincided with or followed an increase in copepod biomass. The first major production of eggs of *P. elegans* in Bedford Basin, Nova Scotia, occurs in spring, with each subsequent increase in egg production occurring immediately

after an increase in copepod biomass (Sameoto 1973). King (1979) observed that the maturation of *P. elegans* in Dabob Bay, Washington, during spring coincided with the development of the first large spring cohort of small herbivorous copepods. According to Welch et al. (1996), young-of-the-year recruitment of *P. elegans* in the Canadian high Arctic coincided with the occurrence of copepod nauplii.

Chaetognaths are generally known to be semelparous - to spawn once and then die (Kuhl 1938, Alvariño 1965, McLaren 1969, Jakobsen 1971, Sameoto 1971). However, Reeve (1970 a) documented continuous growth of *Sagitta hispida* during the egg-laying period in the laboratory, and Nagasawa (1984) confirmed this in *S. crassa*. Michael (1919), Thompson (1947), Ghirardelli (1951), Furnestin (1953), Owre (1960), Boltovskoy (1975), and Koszteyn (1983) have reported from field data that *S. enflata* appears to go through two or more complete spawning cycles at different body sizes. Although no laboratory observations are available on egg-laying in *P. elegans*, results obtained from the Celtic Sea suggest that they spawn several times (Conway and Williams, 1986). *P. elegans* in the BBL of Conception Bay does not seem to be semelparous. When animals from cohort 2 reached maturity at 30 mm, they spawned once during late summer and fall and continued to grow and mature. If the sampling had continued, mature animals from cohort 2 at 45 mm could have been observed to spawn once more then die.

Size at maturity changes as a function of temperature. In general, chaetognaths mature at larger sizes at lower temperatures (McLaren 1963, Sameoto 1971, 1973, Reeve and Walter 1972, Zo 1973). The only other study of chaetognath populations from

sub-zero water was by Welch et al. (1996). In their study, the size at maturity of *P. elegans* reached 45 mm in the Canadian high Arctic where the mean annual temperature is about -1.5 ° C. In the present study, the size at maturity of *P. elegans* reached 52 mm in Conception Bay where the mean annual temperature below the thermocline is -1.0 ° C. A larger size at maturity was found in Conception Bay because animals from the BBL were included. In Welch et al.'s study, tows were made from 0 to 100 m over a 107 m water column, and may have missed the mature animals larger than 45 mm living near the bottom. However, this comparison may not be valid since other factor such as food availability, which influence growth and fecundity, could be different in the Canadian high Arctic and Conception Bay.

The growth rate of *P. elegans* from the BBL in Conception Bay was continuous throughout the year, although the temperature was below zero. The growth rate of *P. elegans* in St. Margaret's Bay, Nova Scotia, increased as the temperature increased but growth almost stopped when the mean temperature reached its annual minimum (1 to 2 °C) (Sameoto 1971). Sameoto (1973) later found that the growth rate of *P. elegans* in Bedford Basin, Nova Scotia, increased as the mean water temperature increased in summer. In the Canadian high Arctic, *P. elegans* grows continually without interruption or slowdown throughout the year, despite temperatures reaching the freezing point of seawater (Welch et al. 1996). The growth rate of *P. elegans* in Bedford Basin was not constant, since temperature fluctuated throughout the year. The growth rate of *P. elegans* in the Canadian high Arctic (mean annual temperature -1.5 °C), was 2.03 mg

dry weight · individual^{-1} · yr^{-1} (Welch et al. 1996, calculated from the growth curve equation). The growth rate of *P. elegans* in Conception Bay was 2.28 mg dry weight · individual^{-1}· yr^{-1}. Similar growth rates in both places is probably attributable to similar temperatures.

Generation time varies inversely with temperature. Sameoto (1971) found that the generation time of *P. elegans* varies from 3 to 7 months, depending inversely upon temperature, which ranged from 3.5 to 9.1 °C in his study. King (1979) reported one or possibly two generations per year from a population in Dabob Bay, Washington, where temperature ranges from 4.9 to 21.7 °C and generation time is 4-5 months. *P. elegans* has three spawning periods during the year, and generation time is 6-10 months at Ocean Station P in the subarctic Pacific, where temperature ranges from 6 to 14 °C (Terazaki and Miller, 1986). In the Sea of Japan, where the temperature ranges from 0-25 °C, there are two principal spawning periods each year and the generation time is 10-12 months (Terazaki, 1993). In the Canadian high Arctic, where the mean annual temperature is about -1.5 °C, there are three cohorts of *P. elegans* and the generation time is 23 months (Welch et al, 1996) although this could be an underestimate. The largest mean size of the first cohort may not have been found since large mature animals in the BBL were not sampled. In Conception Bay, where the temperature below the thermocline is -1 °C all year, there are four cohorts of *P. elegans* and the generation time is at least 19 months. This value is also an underestimate, because the growth curve was calculated for animals larger than 18.6 mm.

2.5. Summary

The mean annual abundance of *Parasagitta elegans* was 477.6 m^{-2} in the water column (50-225 m) and 24.1 m^{-2} in the BBL of Conception Bay, Newfoundland. The mean biomass was 289.2 mg · C · m^{-2} in the water column and 84.7 mg · C · m^{-2} in the BBL which constitutes 23 % of the total biomass in the bay. Larger and mature animals greater than 40 mm lived mostly in the BBL. Smaller and immature animals, less than 30 mm, lived in the water column and the BBL. The population dynamics of *P. elegans* from the BBL was studied since animals of all maturity status were present in the BBL. Four cohorts were found from 1997 to 1998 by observing the size modes and ovary maturity data. Cohort 1 reproduced, probably for the second time, in late spring and died. Cohort 2 reproduced in the fall, regenerated into the immature stage and matured over winter and spring, showing clearly that the animals are not semelparous. The reproduction of cohort 2 followed the recruitment of *Calanus* spp. The estimated growth rate of *P. elegans* was 2.28 mg dry weight · $individual^{-1}$ · yr^{-1} (1.0 mg C · $individual^{-1}$·yr^{-1}) and the generation time was at least 560 days.

Table 2.1 Number of animals analyzed from the BBL samples

Date (N=night)	Time	# counted	# split
Apr. 23, 97	1115	846	full sample
May 6, 97	1145	1057	full sample
May 16, 97	1630	163	1/4
May 23, 97	1520	816	1/4
May 23, 97 N	2240	576	1/2
June 9, 97	1105	292	1/16
June 16, 97 N	2200	428	1/2
July 8, 97	1050	672	1/2
July 22, 97 N	2150	440	1/4
Aug. 28, 97	1115	344	1/16
Oct. 1, 97	2215	474	1/8
Nov. 6, 97	0925	497	full sample
Feb. 5, 98	1030	725	1/8
Apr. 2, 98	1000	578	full sample
Apr. 17, 98	0945	547	1/4
May 5, 98	1000	402	1/16
May 20, 98	1000	552	1/2
June 17, 98	1115	710	1/8
June 23, 98	1555	652	1/8
June 24, 98 N	2245	608	1/8

Table 2.2 Number of animals analyzed from mid-depth (50-175 m) samples. Full samples were analyzed.

Date (N=night)	**Time**	**# counted**
May 16, 97 N	1915	220
May 23, 97 N	1930	280
June 17, 97 N	0225	157
July 8, 97	1510	3
July 23, 97 N	0250	25
Aug. 28, 97	1430	159
Oct. 1, 97 N	0030	83
Nov. 6, 97	1255	708
Feb. 5, 98	1340	5
Apr. 2, 98	1245	70
Apr. 17, 98	1230	45
May 5, 98	1356	59
May 20, 98	1317	11
June 17, 98	1420	3
June 23, 98	1810	16
June 24, 98 N	0050	52

Table 2.3 Number of animals analyzed from near-bottom (175-225 m) samples. Full samples were analyzed.

Date (N=night)	**Time**	**# counted**
May 16, 97 N	2035	104
May 23, 97 N	2150	126
June 9, 97	1515	187
June 17, 97 N	0300	88
July 8, 97	1545	19
July 23, 97 N	0325	23
Aug. 28, 97	1500	90
Oct. 1, 97 N	0200	116
Nov. 6, 97	1348	98
Feb. 5, 98	1353	778
Apr. 2, 98	1330	84
Apr. 17, 98	1305	63
May 5, 98	1315	45
May 20, 98	1240	86
June 17, 98	1345	23
June 23, 98	1740	160
June 24, 98 N	0010	89

Table. 2.4 Mean annual abundance and biomass of *P. elegans* in Conception Bay, Newfoundland from 1997 to 1988

Depth	Abundance	std	N	Abundance	std	N
(m)	(m^{-3})			(m^{-2})		
50-175 m	2	2	14	239	274	14
175-225 m	5	6	14	239	311	14
BBL	24	19	15	24	19	15

Depth	Biomass	std	N	Biomass	std	N
(m)	(mg dry wt · m^{-2})			(mg C · m^{-2})		
50-175 m	285	454	14	123	196	14
175-225 m	383	380	14	166	165	14
BBL	203	198	15	87	85	15

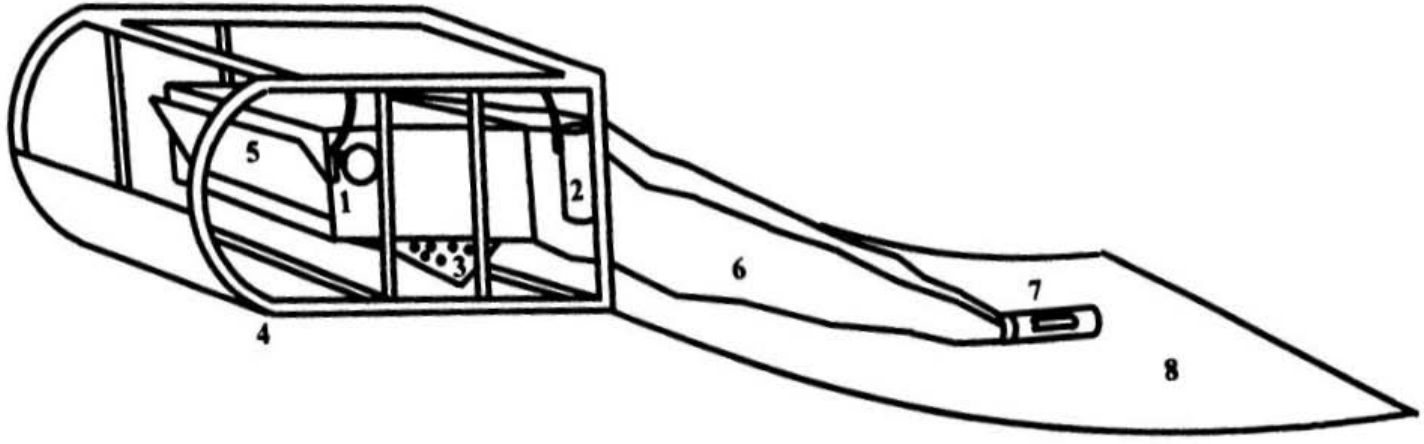

Fig. 2.1 Hyperbenthic sledge

1. Magnetic switch 2. Acoustic transmitter 3. Lever 4. Runner
5. Door 6. Net 7. Cod end 8. Mat

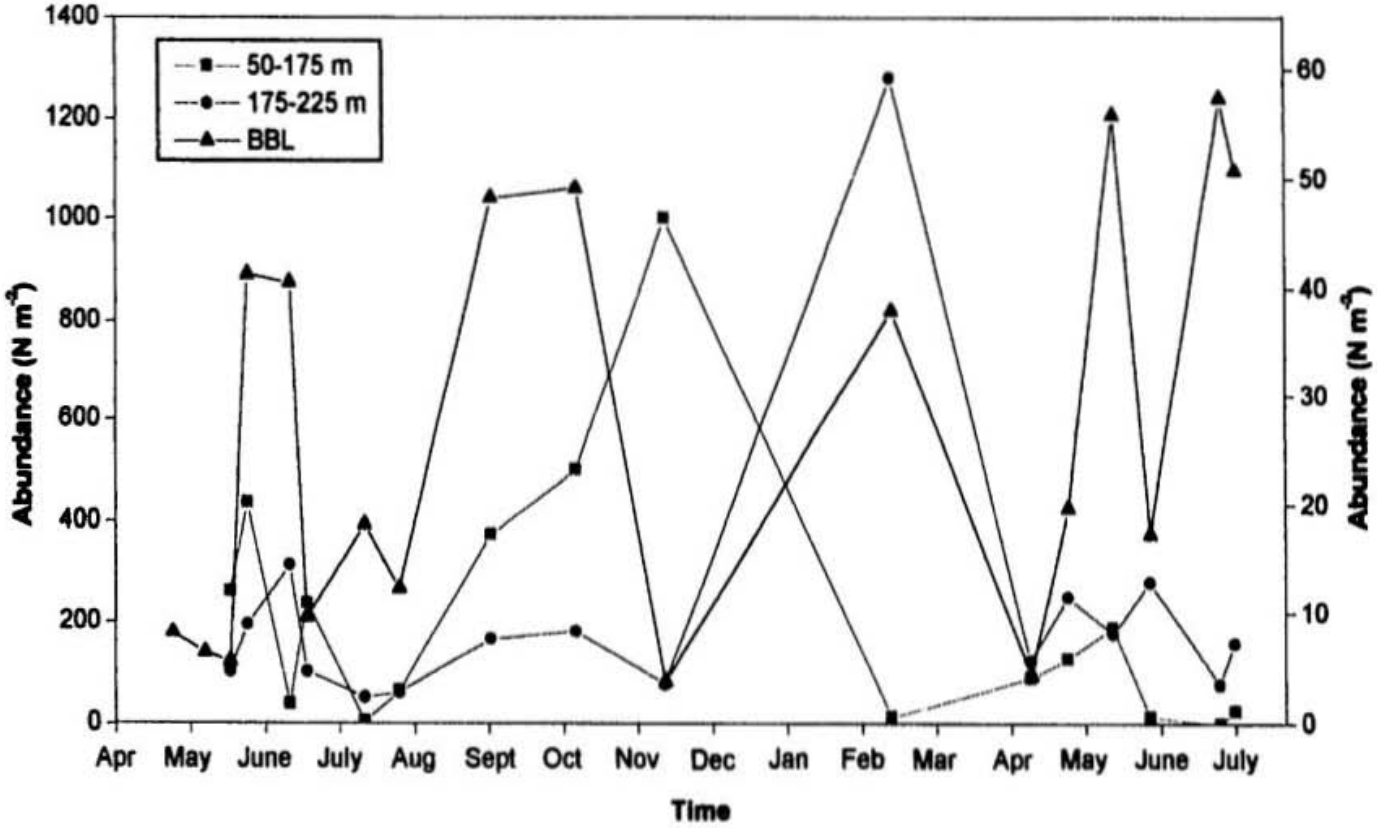

Fig. 2.2 Abundance of *P. elegans* in Conception Bay, Newfoundland from 1997 to 1998
(Left axis indicates abundance in the 50-175 m and 175-225 m strata and right axis indicates abundance in the BBL.)

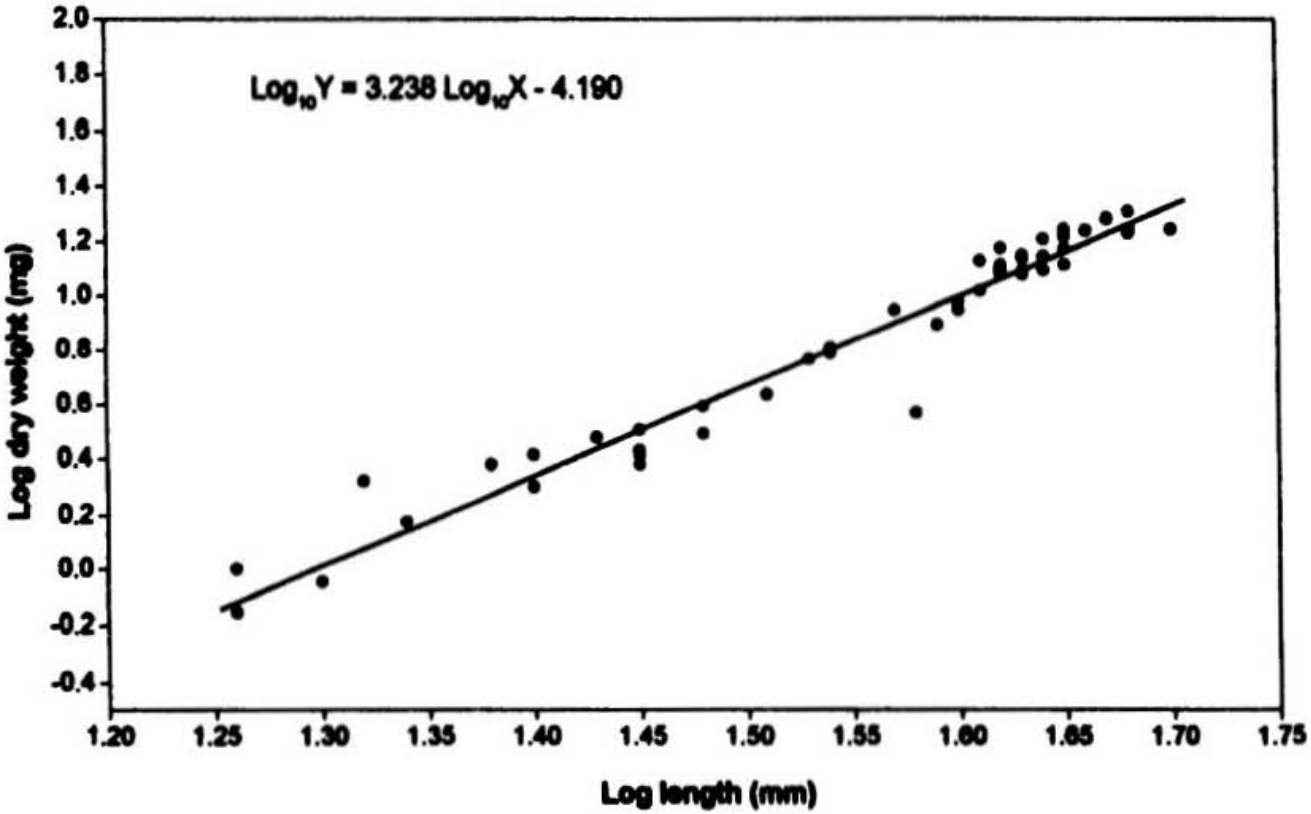

Fig. 2.3 Dry weight versus body length of *P. elegans*
The body lengths of animals range from 18-50 mm, and the length interval is 1 to 2 mm.

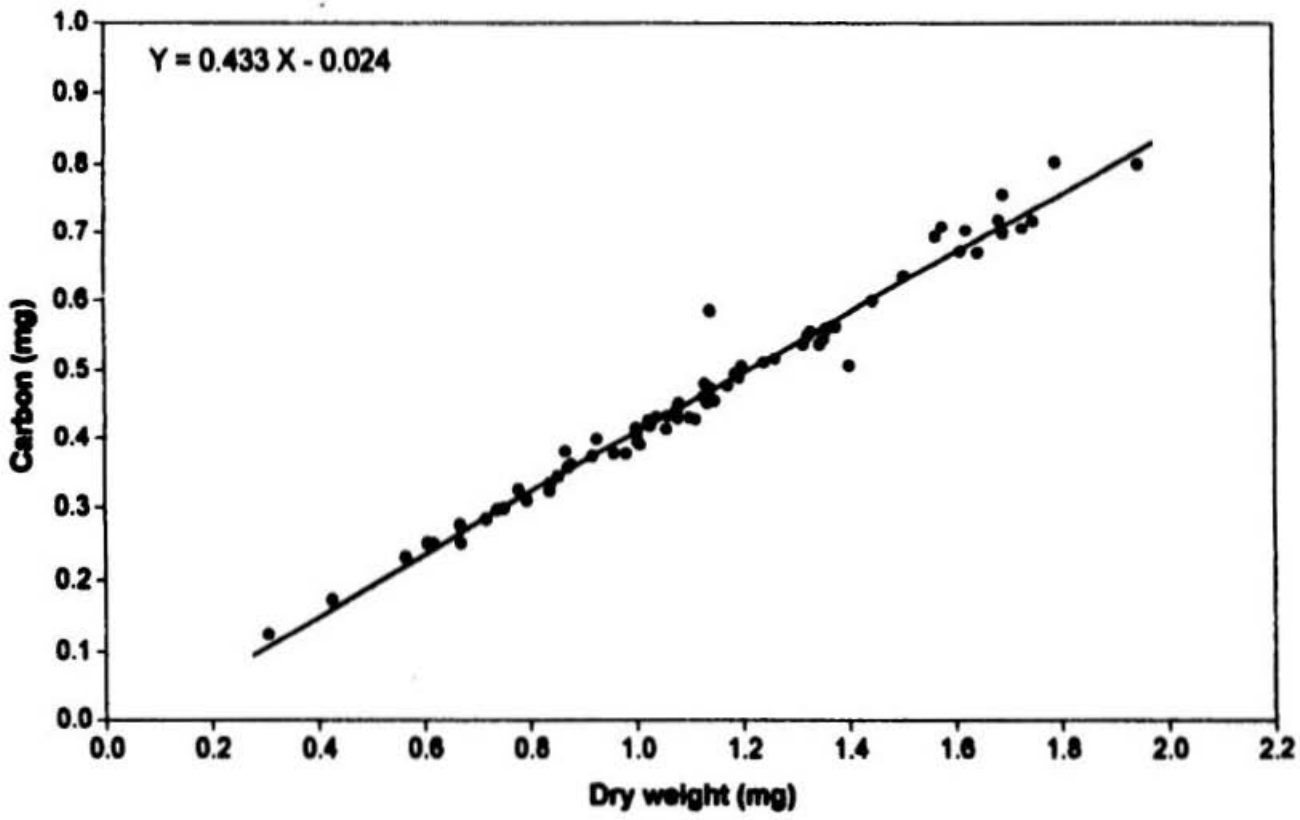

Fig. 2.4 Carbon versus dry weight of *P .elegans*

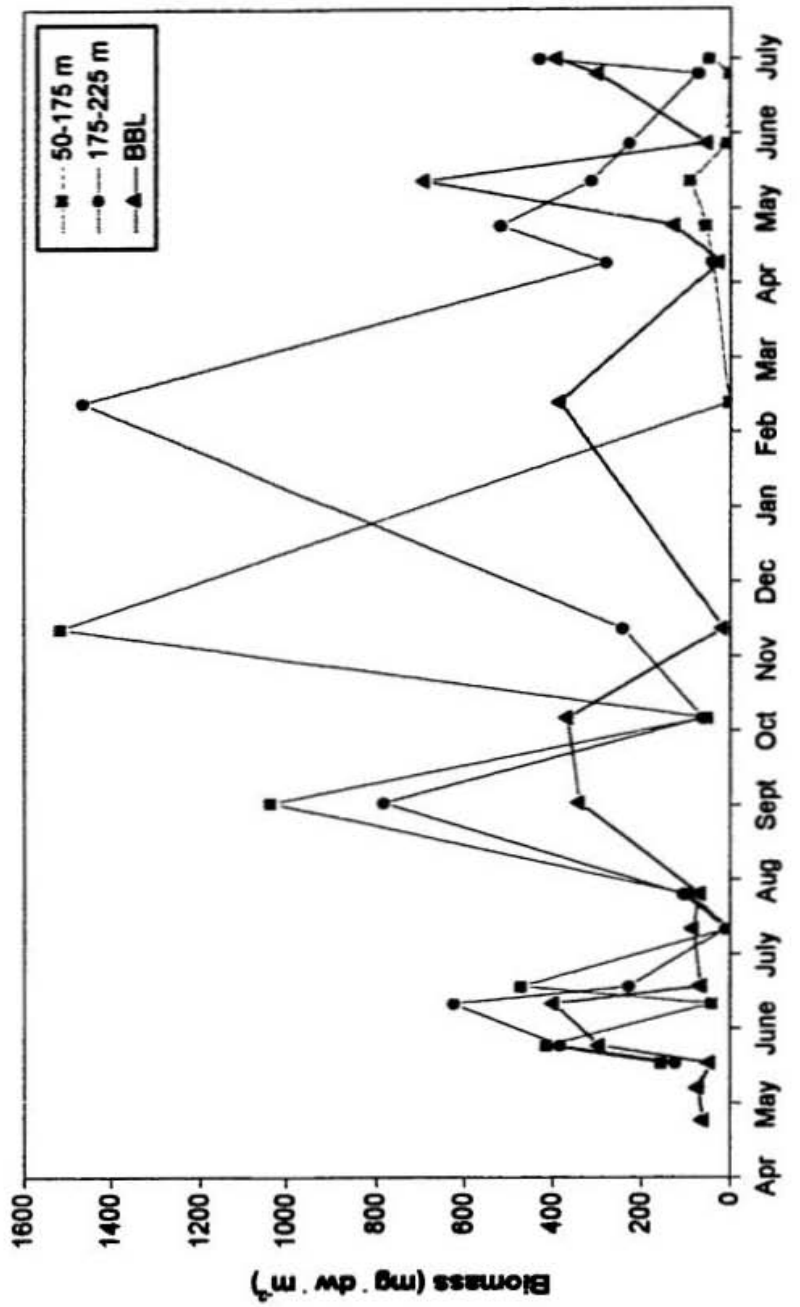

Fig. 2.5 Biomass of *P. elegans* in Conception Bay, Newfoundland from 1997 to 1998

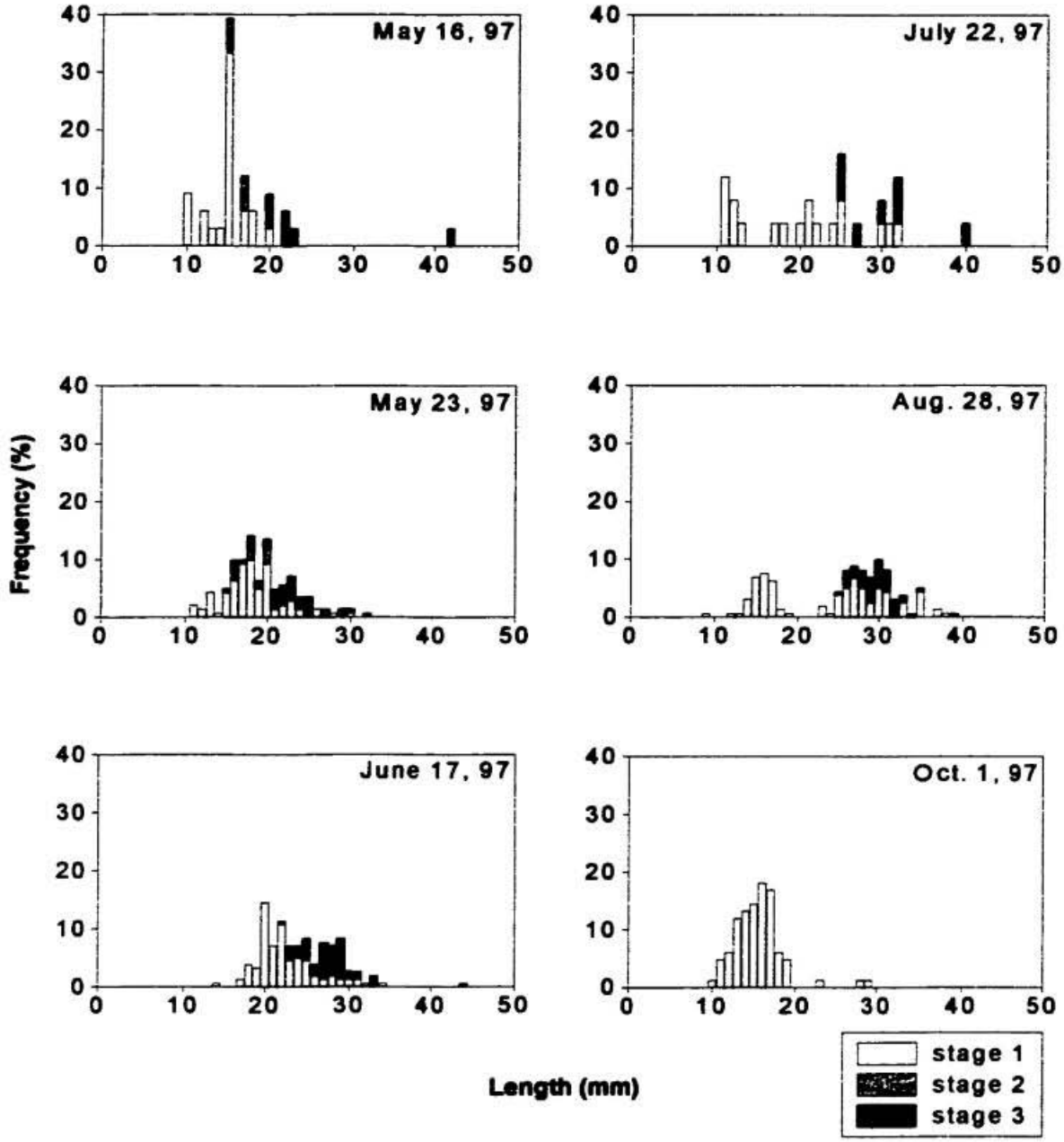

Fig. 2.6 Body size and maturity stage frequency distribution of *P. elegans* in the 50-175m stratum of the water column from 1997 to 1998

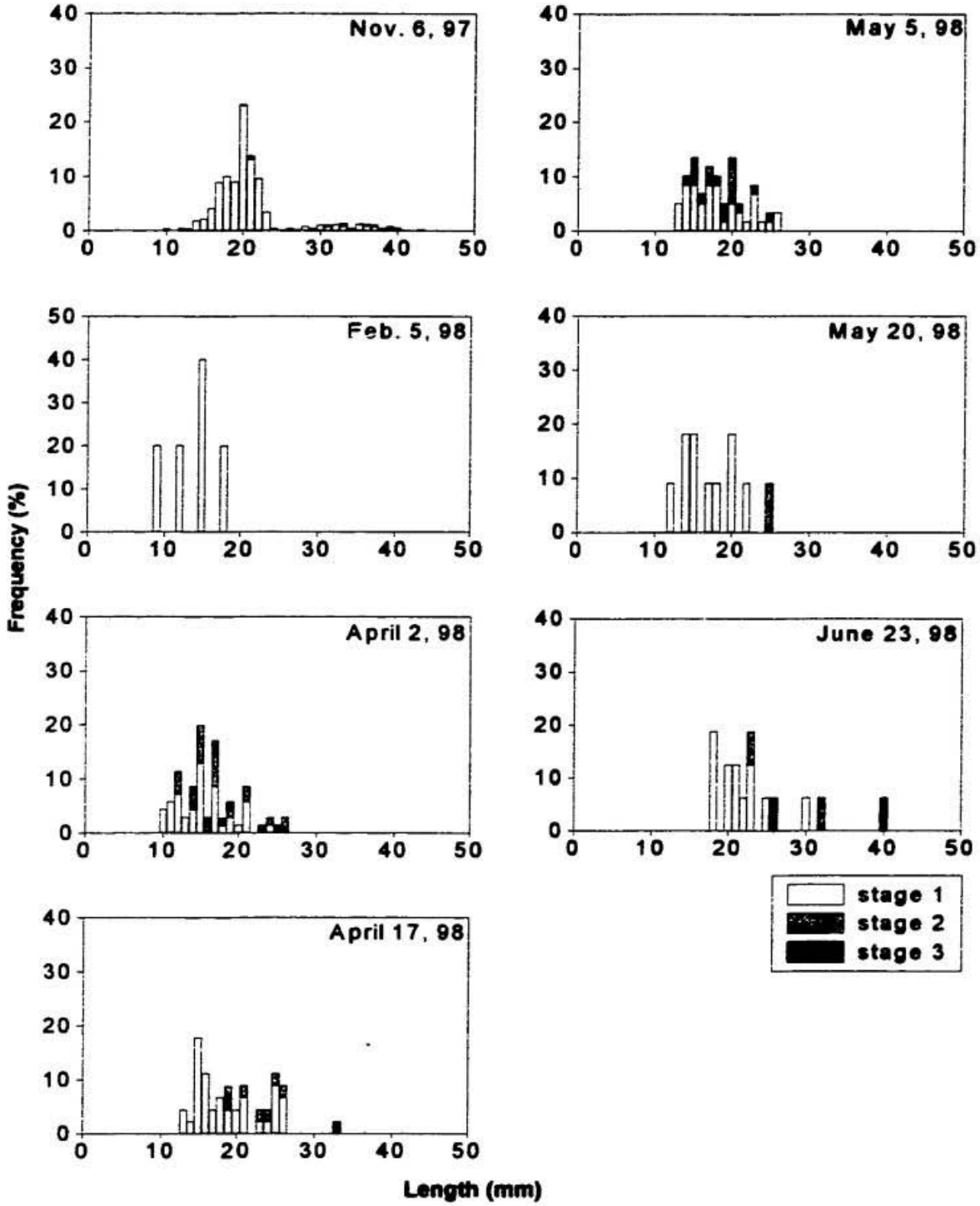

Fig. 2.6 (cont'd) Body size and maturity stage frequency distribution of *P. elegans* in the 50-175m stratum of the water column from 1997 to 1998

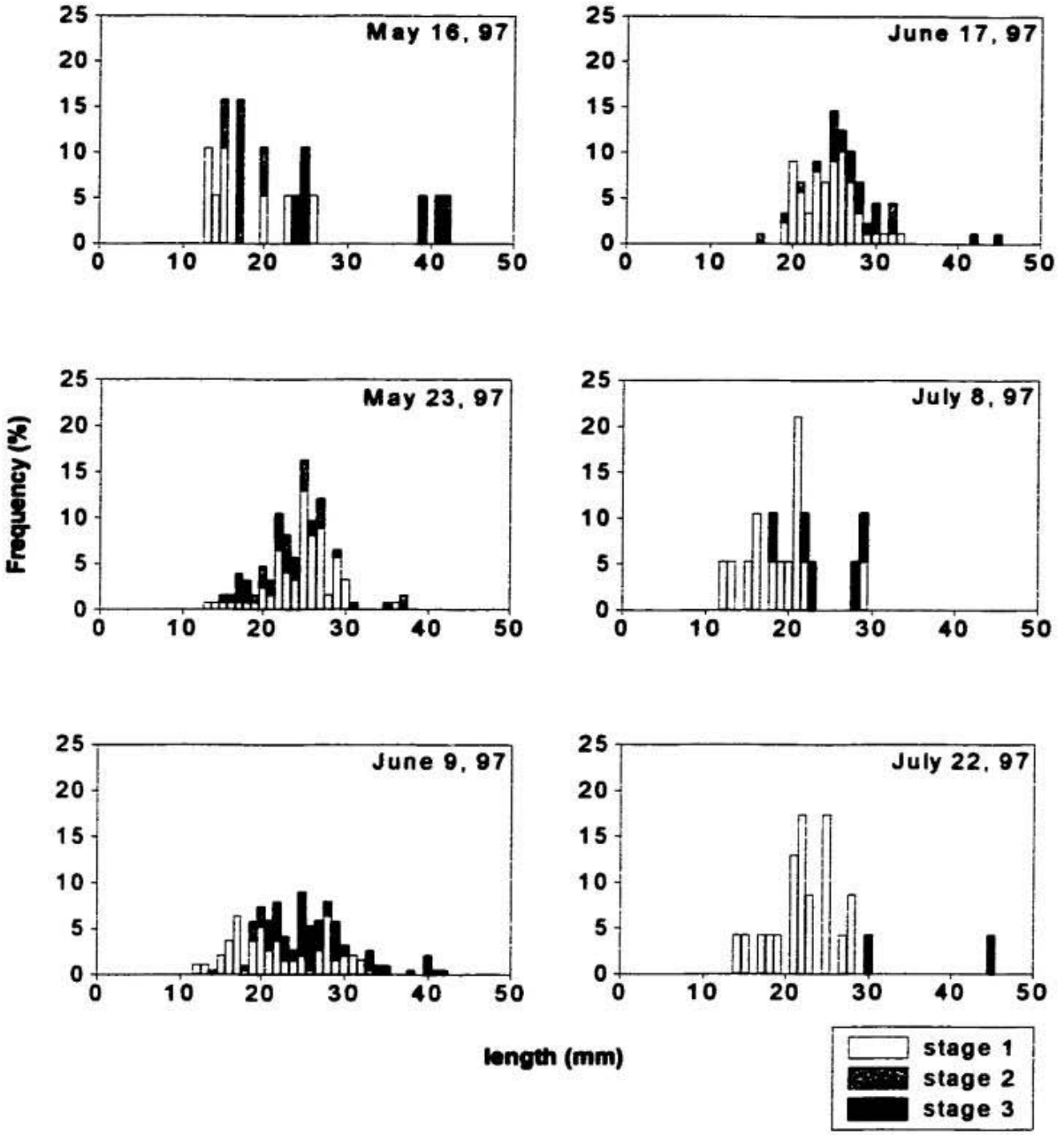

Fig. 2.7 Body size and maturity stage frequency distribution of *P. elegans* in the 175-230m stratum of the water column from 1997 to 1998

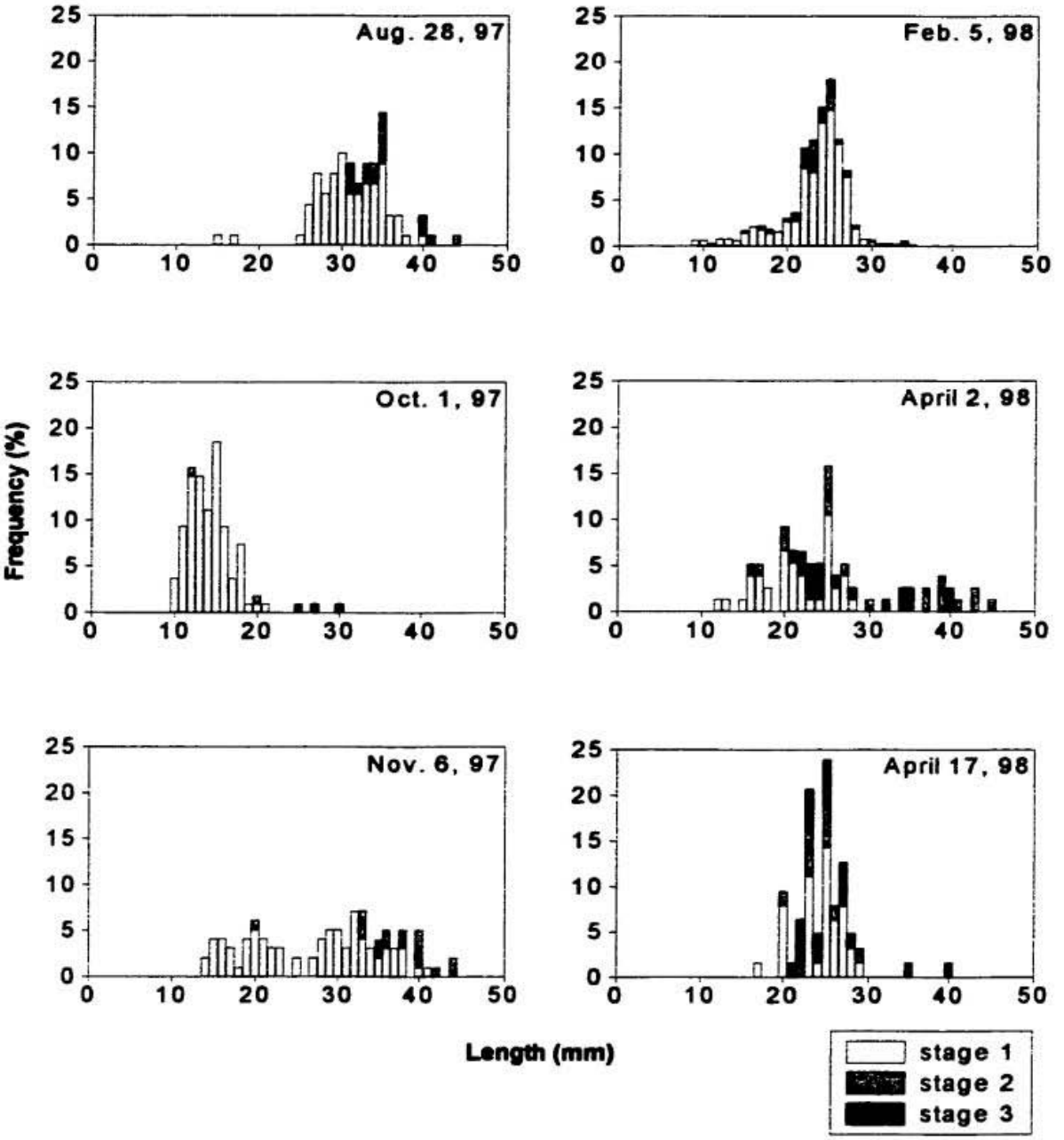

Fig. 2.7 (Cont'd) Body size and maturity stage frequency distribution of *P. elegans* in the 175-230m stratum of the water column from 1997 to 1998

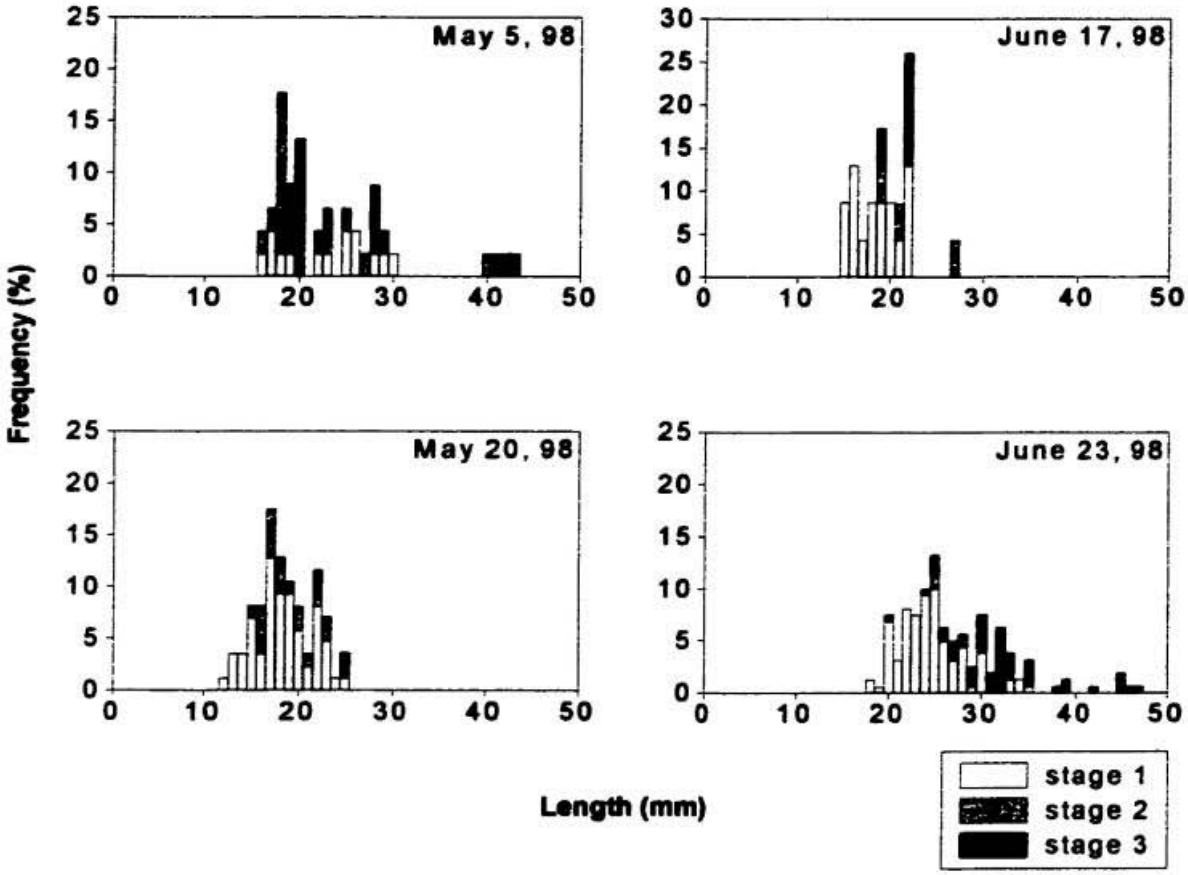

Fig. 2.7 (Cont'd) Body size and maturity stage frequency distribution of *P. elegans* in the 175-230m stratum of the water column from 1997 to 1998

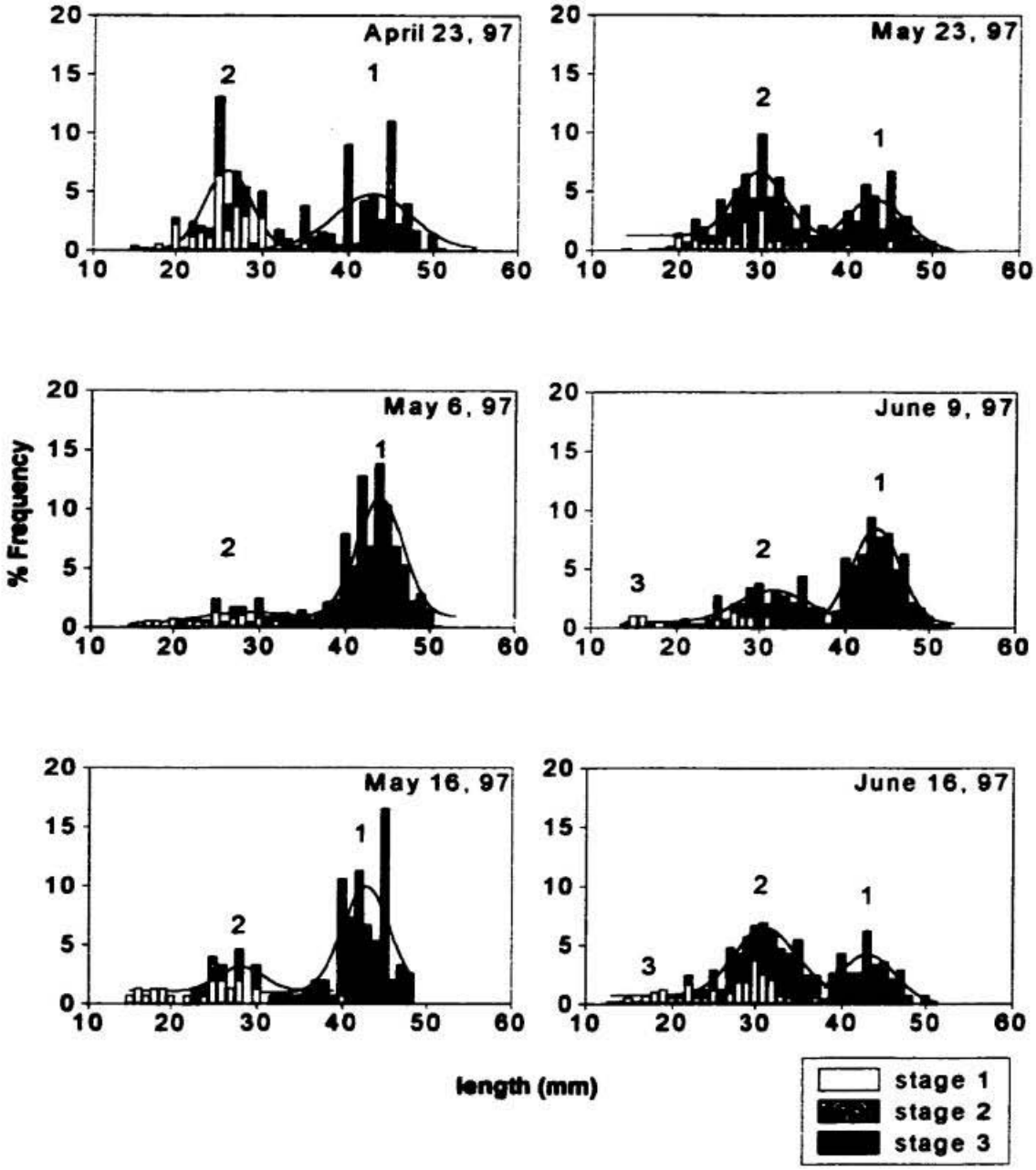

Fig. 2.8 Body size and maturity stage frequency distribution of *P. elegans* in the BBL from 1997 to 1998
(Numbers above the size modes indicate cohorts)

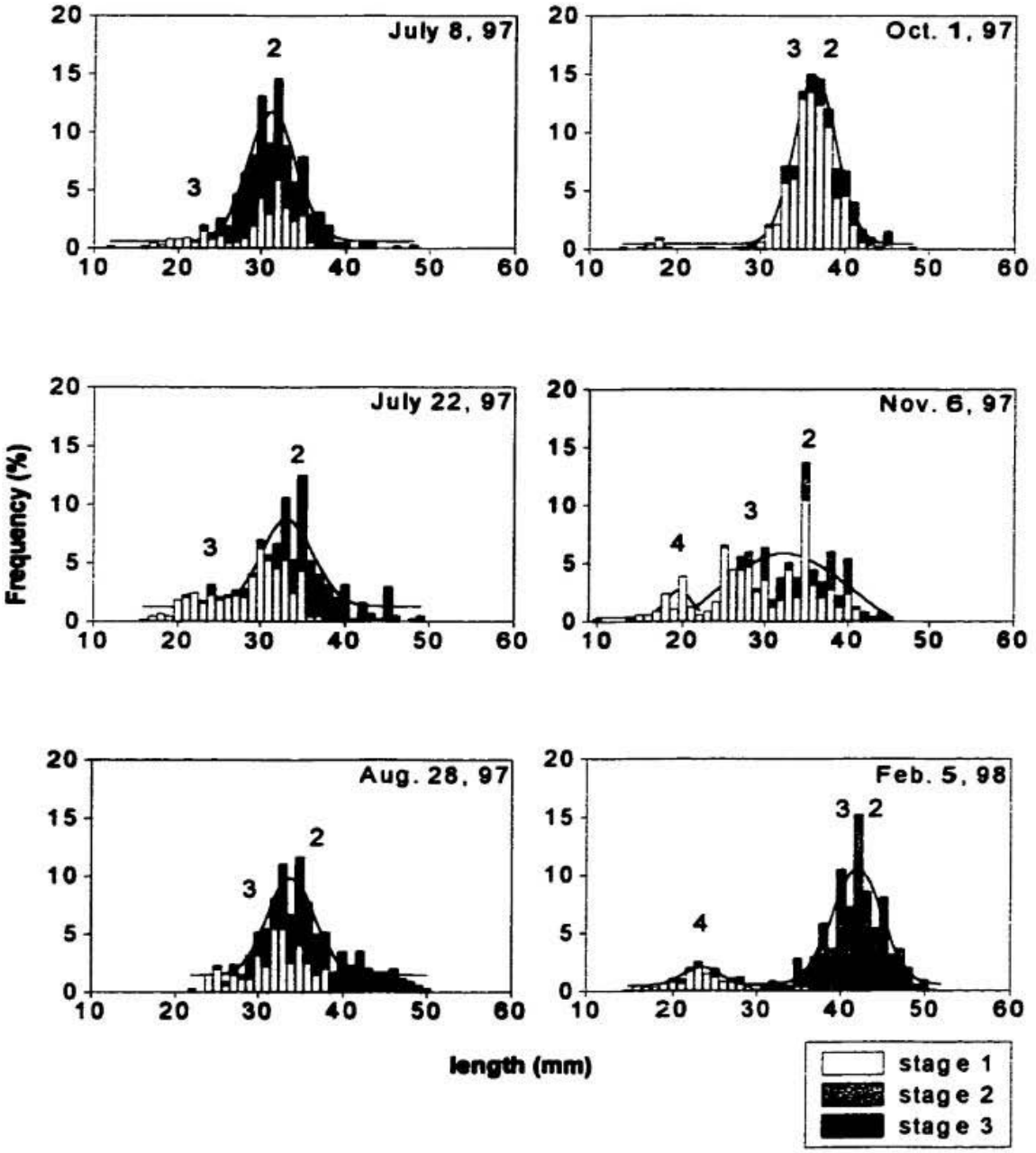

Fig. 2.8 (Cont'd) Body size and maturity stage frequency distribution of *P. elegans* in the BBL from 1997 to 1998 (Numbers above the size modes indicate cohorts)

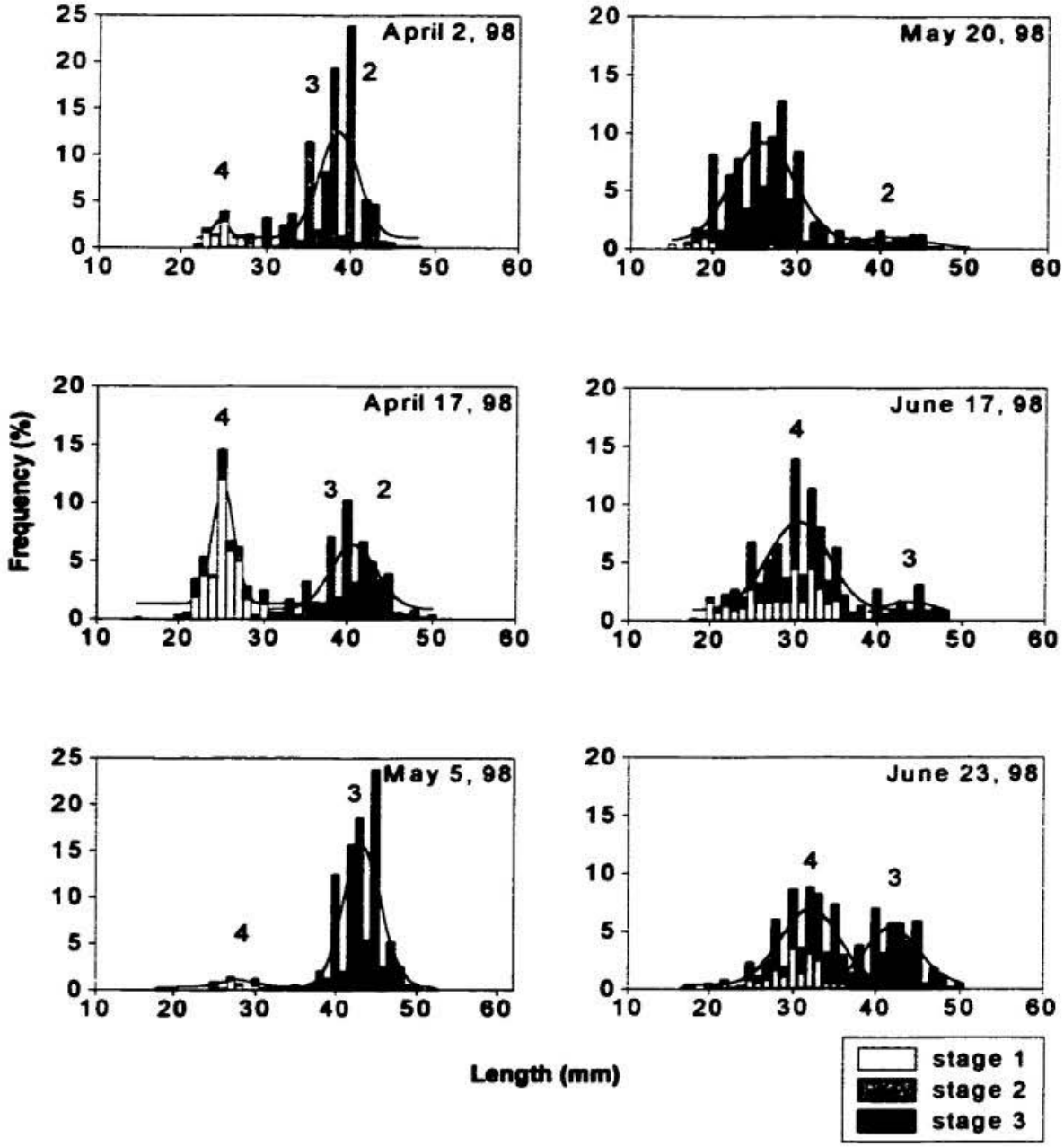

Fig. 2.8 (Cont'd) Body size and maturity stage frequency distribution of *P. elegans* in the BBL from 1997 to 1998 (Numbers above the size modes indicate cohorts)

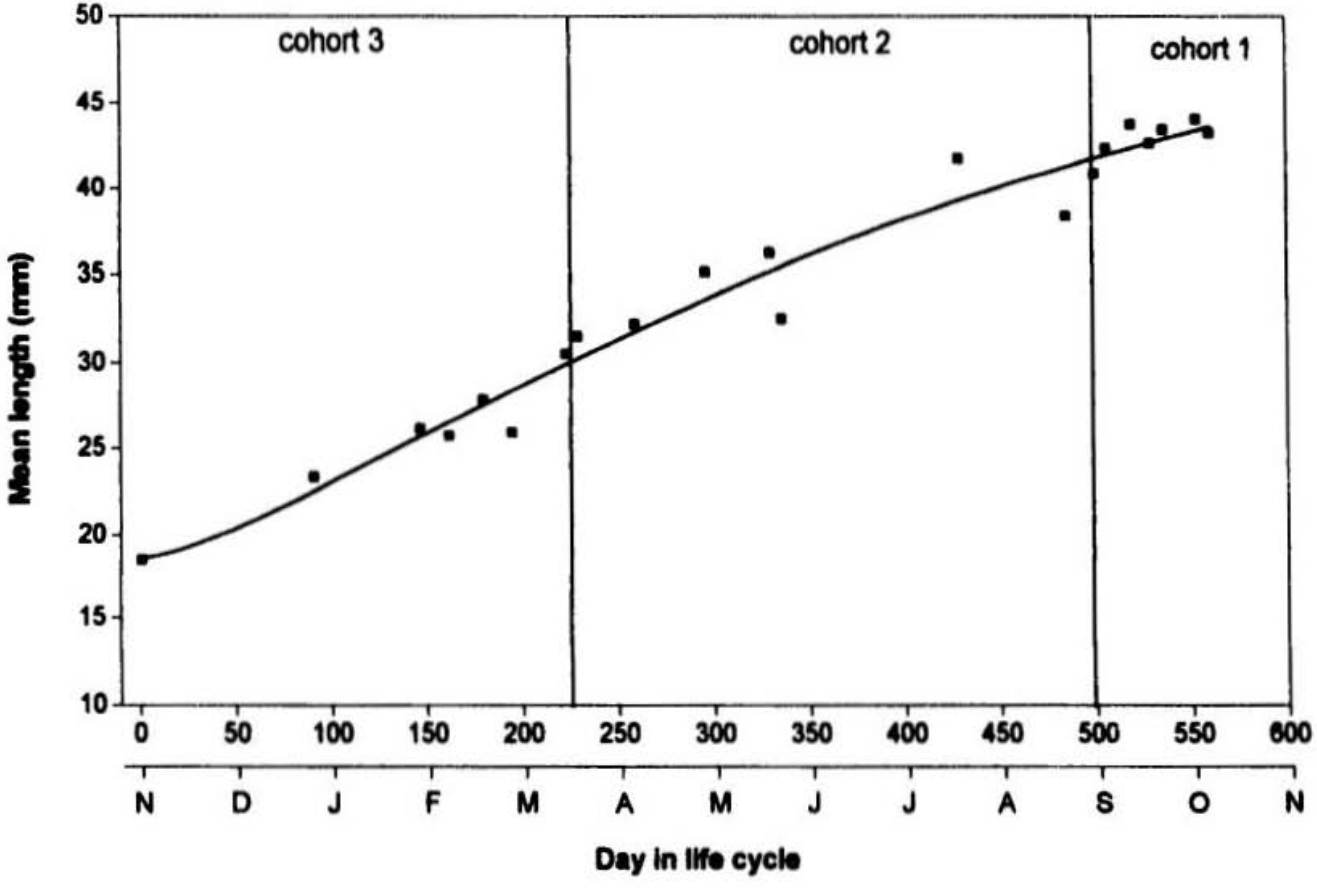

Fig. 2.9 Mean length of *P. elegans* at each cohort in BBL from 1997 to 1998
Each cohort was combined to make one continuous growth curve (Welch et al. 1996).

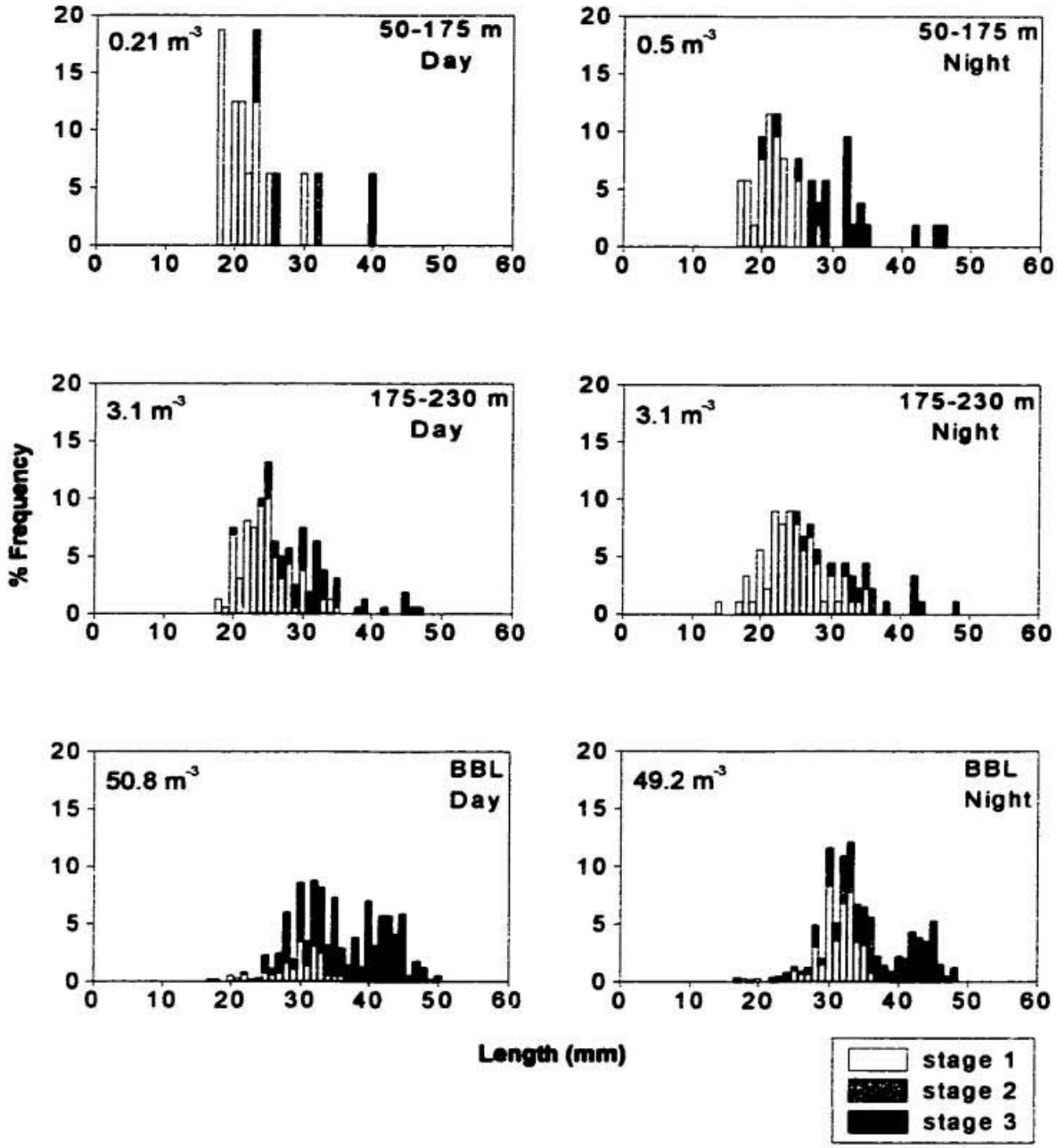

Fig. 2.10 Body size and maturity stage frequency distributions of *P. elegans* during day and night on June 23, 1998

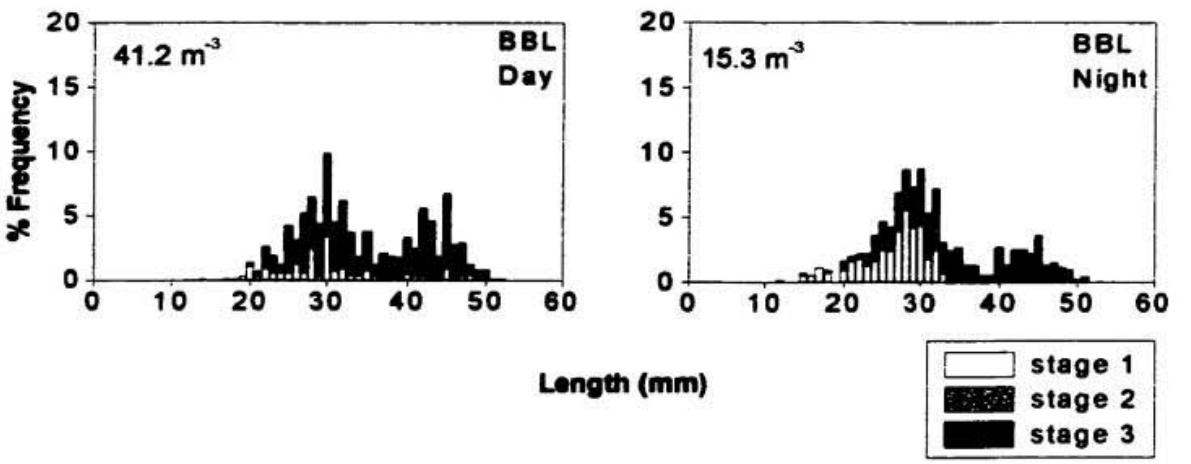

Fig. 2.11 Body size and maturity stage frequency distributions of *P. elegans* in the BBL during day and night on May 23, 1997

Chapter 3. Feeding of *Parasagitta elegans* in Conception Bay, Newfoundland

3.1 Introduction

3.1.1. Feeding of chaetognaths

All species of chaetognaths are strictly carnivorous, the diet consisting mainly of copepods. Other prey includes appendicularians, tintinnids, rotifers and chaetognaths (Szyper 1978, Feigenbaum 1979, Sullivan 1980, Pearre 1981, Kimmerer 1984, Øresland 1987, Falkenhaug 1991, Alvarez-Cadena 1992, Kehayias et al 1996, Marazzo et al 1997). Chaetognath populations may have a substantial grazing impact on copepod biomass. The daily consumption of copepods by *Parasagitta elegans* is 0.2 % in Gullmarsfjorden, Sweden (Øresland 1987), 1.3 % in northern Baffin Bay (Sameoto 1987) and 0.1 % in Canadian high Arctic (Welch et al. 1996). Chaetognaths in general may compete with other organisms in the ocean for the same source of food. Nine species of chaetognaths, mostly *Sagitta enflata*, consume up to 44 % d^{-1} of standing stocks of large copepods that also were prey of large fish larvae off the southeastern U. S. coast, suggesting that chaetognaths consume substantial amount of copepod populations (Baier and Purcell 1997).

Chaetognaths use their grasping hooks and teeth located around the mouth to capture and ingest prey. The two lateral sets of grasping hooks form a basket preventing the escape of prey once caught (Darwin 1844); the grasping hooks also manipulate the prey and force it into the gut. The posterior and anterior teeth and the grasping hooks, are

capable of penetrating the prey (Thuesen and Bieri 1987). When the prey is punctured, the Na^+ channel blocking neurotoxin, tetrodotoxin (TTX), which is synthesized by several species of bacteria, is secreted from the papillae of the vestibular ridge and paralyzes the prey (Thuesen et al. 1988). Once the prey is paralyzed, it is swallowed whole. The ingested prey is wrapped in a peritrophic membrane and passed to the posterior part of the gut by peristaltic movements of the gut wall (Feigenbaum and Marris 1984). Since the prey is swallowed whole, it can be dissected out and easily identified.

3.1.2. Number of prey per chaetognath (NPC)

The NPC may depend on several factors, including size. The NPC of *Sagitta enflata* from the Gulf Stream near Florida increased with size (Feigenbaum, 1979). The NPC was higher in the adults of *S. friderici* and *S. enflata* in Guanabara Bay, Brazil (Marazzo et al. 1997). The NPC may depend on reproductive status. For example, in Guanabara Bay, Brazil, the NPC of *S. friderici* and *S. enflata* was higher in the adult (Marazzo et al, 1997). In the Gullmarsfjorden, Sweden, the feeding rate of *P. elegans* was highest for the breeding generation in spring and lowest for the immature generation in autumn and winter (Øresland, 1987). Time of day might also play a role. Chaetognaths generally feed more often during the night (Rakusa-Suszczewski 1969, Nagasawa & Marumo 1972, Pearre 1973, Szyper 1978, Feigenbaum 1982, Kehayias et al. 1996, Marazzo et al 1997).

The NPC may also depend on prey density. In the laboratory, chaetognaths increased their feeding rate with food concentration until they apparently attained satiation

(Reeve 1980, Nagasawa 1984). Reeve called the food level at satiation the 'critical density' and cited its existence in chaetognaths as evidence that they are not superfluous feeders. In most cases, critical densities determined in the laboratory lie far beyond the range of prey densities in nature, yet some reported natural feeding rates are comparable with maximum laboratory rates (Feigenbaum and Maris 1984). Attempts to correlate chaetognath feeding in nature with prey abundance have generally been unsuccessful (Mironov 1960, Nagasawa and Marumo 1972, Sullivan 1980, Bushing and Feigenbaum and Maris, 1984) because chaetognaths do not necessarily feed at the depth at which they are caught (Pearre 1973) and it is difficult to estimate prey density on a scale important to the chaetognaths (Sullivan 1980). Drits (1981) found an increase in the daily ration of *S. enflata* from 0.65 to 3.2 prey $\cdot$ d^{-1} when copepod density increased from 0.7/1 to 12/1. However, the data were not analyzed statistically. Kimmerer (1984) found that the feeding of *S. enflata* increased with prey abundance in Kaneohe Bay, but levelled off at a copepod density of 200/1.

3.1.3. Objectives of the study

This is the first feeding study of chaetognaths to include the animals from the BBL. Other studies have concentrated on the animals from the surface or the entire water column, excluding the BBL. The most significant observation is that large and mature individuals of *P. elegans* were concentrated in the BBL of Conception Bay. The main purpose of the feeding study was to find out if the seasonal variation in the feeding of *P. elegans* influenced population dynamics and biochemical composition.

Specific questions about the feeding of *P. elegans* in Conception Bay, Newfoundland are:

- Is there a seasonal trend in the NPC and diet of *P. elegans*?
- Does the NPC and diet of *P. elegans* in the BBL and the water column differ?
- Are the NPC and diet of *P. elegans* size-dependent?
- Do the NPC and diet of *P. elegans* depend on reproductive status?
- Does the NPC depend on prey availability?
- What are the estimated feeding rates of *P. elegans*?

3.2 Methods

The water column was sampled with a Tucker trawl net (500 μm mesh) from 50-175 m and 175-225 m. The BBL samples were collected with a benthic sledge (500 μm mesh). Detailed protocols are described in the method section of Chapter 2. Several samples in this study were collected during the night. Day and night samples were collected to observe the vertical migration pattern and feeding behavior on May 23, 1997 and June 23, 1998. The sampling dates and number of animals analyzed are recorded in Table 2.1 , 2.2 and 2.3.

The gut contents of *P. elegans* were examined under a Wild M5 dissecting microscope. The mandibles of digested copepods were dissected from the gut with a pair of sharpened insect mounting pins. The shape and size of the mandibles were determined following descriptions in Falkenhaug (1991). Copepod species were identified by referring to the shapes and sizes of mandibles from specimens collected in Conception

Bay. Gut contents other than copepods and chaetognaths were difficult to determine and were recorded as "unidentified". Parasites were often found in the body cavity outside the gut. Body length and maturity stage of the animals were determined as described in Chapter 2. How often the animals fed was expressed as the number of prey per chaetognath (NPC). The daily feeding rate of *P .elegans* was calculated from equation of Bajkov (1935),

$$FR = \frac{NPC\ (24)}{DT}$$

where NPC is the number of prey per chaetognath and DT = digestion time in hours. The hourly rate was multiplied by 24 to convert to a daily ingestion rate. Digestion time was calculated using the equation of Pearre (1982).

$$DT = 10 \cdot 24^{\,e^{-0.095\,t}}$$

where t = temperature in °C. The feeding rates of the animals living below the thermocline from 50-175 m, 175-225 m and BBL were calculated. Since the temperature in these water column layers is -1 °C all year round, the digestion time was estimated to be 11.3 hours.

I next wanted to determine if the NPC and the diet of *P. elegans* depend on prey availability. Available prey in the water column and the BBL was obtained from the samples collected with a Tucker Trawl and benthic sledge. Since 500 µm mesh nets may exclude small copepods, tows were made with a WP-2 ring net (206 µm mesh, 0.5 m diameter) with a low-speed rotor mechanical flowmeter (General Oceanic model 2030) to

determine which stages of copepods were omitted from the analysis. The sampling dates and depths are recorded in Table 3.1. The abundance of zooplankton and the stages of all the copepods from the water column and the BBL were determined. The data were statistically analyzed using the Statistical Analysis System (SAS Institute, Cary, North Carolina). The comparison between two groups of data were analyzed using t-test and the comparison between several groups of data were analyzed using GLM (General Linear Model).

3.3 Results

3.3.1 Diet of *P. elegans* in the benthic boundary layer (BBL)

The diet of *P. elegans* was relatively constant throughout the year (Fig. 3.1). *Calanus* was the most frequently ingested prey species (median = 41.1 %), while *Pseudocalanus* was the second (median = 14.5 %). *Calanus* seemed to be preferred over *Pseudocalanus* even though *Pseudocalanus* was more abundant than *Calanus* (Fig. 3.2). *P. elegans* mostly ingested *Pseudocalanus* on May 16, 1997 when the abundance of *Calanus* was much lower than *Pseudocalanus*. Within the genus *Calanus*, *C. finmarchicus* and *C. glacialis* were ingested more frequently than *C. hyperboreus* since they were more abundant in Conception Bay (Fig. 3.3). *Calanus* was more frequently ingested during spring than fall and winter. Median % *Calanus* of all prey in the spring of 1997 and 1998 were 22.6% and 21.1 % and 12.4% in the fall and winter of 1997. During November, a high proportion of the diet consisted of *Temora*, even though the concentration of *Temora* was low (Fig. 3.1). Cannibalism occurred year round, with

seasonal maxima in winter.

The diets of small (< 35 mm long) and large (> 35 mm) *P. elegans* were quite different from one another (Fig. 3.4, 3.5). Small chaetognaths fed mostly on small prey such as *Calanus* spp. and *Pseudocalanus* spp. (median = 13.8 % and 26.8 %, respectively). Consumption of *Calanus finmarchicus* and *Calanus glacialis* by small chaetognaths increased during spring then decreased from summer to winter. Small chaetognaths consumed more large *C. finmarchicus* and *C. glacialis* (stage IV-VI) (median = 26.8 %) than small *Calanus* spp. (stage I-III) (median = 17 %). Large chaetognaths fed less on *Calanus* spp. (median = 6.7%) but showed a high degree of cannibalism (median = 30.8 %). They rarely ingested young stages of *Calanus* spp. (stage I-III).

The samples from the 500 μm mesh Tucker Trawl net underestimated the numbers of smaller copepods. A comparison between samples from the 206 μm and 500 μm mesh nets indicated that stages I to III of *Calanus* spp. and all stages of *Pseudocalanus*, *Metridia* and *Temora* were underestimated (Table 3.1). Therefore, standard normal deviates of the copepod abundances were plotted to observe the relative increase and decrease from the mean abundance (Fig. 3.6).

3.3.2 NPC of *P. elegans* in the BBL

The NPC of *P. elegans* in the BBL ranged from 0.02 to 0.20 with mean of 0.08 ± 0.05 (n = 18) from April, 1997 to June, 1998 (Fig. 3.7). The NPC increased during spring and fall. The spring peak of NPC was higher and occurred earlier in 1998. The feeding

rates of *P. elegans* in the BBL ranged from 0.04 to 0.43 prey day^{-1} with a mean of 0.19 ± 0.10 prey day^{-1} ($n = 16$) (Table 3.2).

The NPC depended on the size of the animals (GLM, $p<0.05$, $n > 100$ for each size group pooled from all data). The mean NPCs of small and large animals was 0.11 ± 0.08 % and 0.07 ± 0.04 % respectively, indicating that small animals (< 35 mm length) fed more frequently than did large animals (> 35 mm length), (Fig. 3.8). The seasonal fluctuation in the NPC was obvious in smaller animals. The NPC of small animals increased sharply during spring, decreased during summer and increased during winter. A similar seasonal pattern existed in large animals, except the NPC decreased during winter.

There was no statistically significant difference in the mean NPC among the 3 maturity stages (GLM with pooled data, $p > 0.05$; Fig. 3.9). The mean NPC of stage 1 to 3 were 0.10 ± 0.06, 0.07 ± 0.04 and 0.08 ± 0.05, respectively. The NPC of stage 1 animals increased during spring 1997, decreased during summer, increased gradually during winter and increased sharply during spring 1998. The NPC of stage 2 animals increased during spring, decreased during summer to winter, then increased during the following spring. Stage 3 animals showed a similar trend as in stage 2 animals except there was an abrupt increase during October, 1997. Reliable data on stage 3 animals could not be obtained during winter since the number of stage 3 animals was scarce. The increase of NPC in spring of 1998 was higher than the increase in 1997 for all stages.

The day and night samples from the BBL and water column from April, 1997 to

June, 1998 showed that the NPC during day and night did not differ (t-test, $p>0.05$). Two sets of diel samples on May 23, 1997 and June 23, 1988 also showed that the NPC did not seem to differ during day and night (Table 3.3). Two sets of data were not enough for statistical analysis.

3.3.3 Diet and NPC of *P. elegans* in the water column

Insufficient numbers of animals were collected from the water column for the detailed feeding study. In general the diet of water-column chaetognaths, which were predominantly smaller than 35 mm, consisted primarily of *Calanus* spp. and *Pseudocalanus* spp. (Table 3.4). Similar changes in the diet occurred as in the BBL. During November, the animals fed exclusively on *Temora* when *Temora* was available in the water column (Fig. 3.10, 3.11). Cannibalism was low. Cannibalism did not occur in the animals from the water column strata (Table 3.4). Data from 50-175 m and 175-225 m in 1997 showed that the NPC increased during early summer and decreased during fall then increased again during winter (Fig. 3.7).

3.3.4 NPC of *P. elegans* in the BBL and water column

The NPC depended on depth (GLM, $p < 0.05$) (Fig. 3.7). The NPC in each depth stratum from the surface to BBL indicated that the animals in the shallower depths fed most frequently. The mean feeding rate of *P. elegans* in the BBL was 0.2 ± 0.1 prey d^{-1} (Table 3.2). The mean feeding rates in the 175-225 m and 50-175 m strata were 0.3 ± 0.1 and 0.6 ± 0.3 prey d^{-1}, respectively.

3.4 Discussion

3.4.1 Diet of *P. elegans* in the BBL

P. elegans does not have strict selectivity in its diet because they fed on most of the copepods available in Conception Bay, so *Calanus* spp. and *Pseudocalanus* spp. were the principal prey ingested, since they were the most abundant copepod species in the bay. However, there was some evidence that *P. elegans* preferred *Calanus* although *Pseudocalanus* was the most abundant copepod species in the BBL. The net used for sampling underestimated stages I to III of *Calanus*, all stages of *Pseudocalanus* and *Temora*. Even though the sledge underestimated *Pseudocalanus*, the numbers of *Pseudocalanus* were higher in sledge samples than any other taxon, at least for most times of the year. This fact suggests that *Pseudocalanus* was the most abundant copepod species in the BBL. High ingestion of *Temora* during November may indicate that the availability of *Temora* was high in November. The standard normal deviates of copepod abundance indicated an increase in the abundance of *Temora* in November (Fig. 3.6).

The diet of *P. elegans* in February remains unknown. The chaetognaths fed scarcely on *Calanus* spp. but fed heavily on conspecifics. The proportion of chaetognaths in the diet was from 0 to 57.6 %. Since the mean lengths of each stage of *P. elegans* were not particularly large, size could not explain the intense cannibalism (Fig. 3.12). Copepod availability during February in Conception Bay was relatively low, but was not the lowest observed. Prolonged low availability of food in the winter may have caused low ingestion of *Calanus* spp. and high ingestion of chaetognaths, but only few

zooplankton samples were available in the fall and winter to support the hypothesis.

The most unusual observation in this study is that the highest incidence of cannibalism is seen in chaetognaths ever studied. In this study, the maximum proportion of chaetognaths in the total diet of small *P. elegans* was 33.3 % and the maximum proportion in large *P. elegans* was 82.4%. In other studies, the percent cannibalism of *P. elegans* in shallow water ranged from 0.9 to 4.0 % and the mean body length ranged from 9.0 to 13.4 mm (Stone 1965, Rakusa-Suszczewski 1969, Pearre 1970, Sullivan 1977, Feigenbaum 1979). A low occurrence of cannibalism in larger *P. elegans* (0.6 % NPC, median length ranging from 18 to 28 mm) was reported from Gullmarsfjorden, Sweden (Øresland, 1987). The high incidence of cannibalism of *P. elegans* in the BBL of Conception Bay can be due to the following reasons. First, the animals in the BBL are large compared with the animals living in the upper water column layers. Generally, the length of *P. elegans* in the BBL is divided into two modes. The median length of the smaller mode was about 30 mm and the median length of the larger mode was 45 mm. The animals in the upper water column were smaller than 35 mm all year and they did not display cannibalism. Secondly, the encounter rate of small chaetognaths by the larger chaetognaths in the BBL was probably high since the abundance was exceedingly high. The mean abundance of both in the BBL was 28 ± 20 m^{-3} and in the upper water column 2.8 ± 4.3 m^{-3}.

3.4.2 NPC of *P. elegans* in the BBL

In general, the NPC of *P. elegans* in the BBL was maximal during spring and fall.

This pattern coincides with the seasonal trend in copepod abundance, which has maxima of *Calanus* species in the BBL during spring and fall. *P. elegans* responds quickly to the abundance of *Calanus*, since the spring increase in the abundance of *Calanus* sp. occurred earlier in 1998 (May) than in 1997 (June) and the same pattern was observed in the NPC of *P. elegans*.

3.4.3 NPC and body size of *P. elegans*

Generally, the NPC was highest in smaller chaetognaths (< 35 mm) in the BBL. This result contradicts most published studies of water-column chaetognaths. Øresland (1987) separated *Parasagitta elegans* into old and new generations with median lengths $\geq$ 20 mm and $\leq$ 20 mm. He observed a higher NPC in the large animals and hypothesized that the larger animals may have higher encounter rates with prey due to higher swimming velocities or less discriminating feeding due to higher food requirements for reproduction. Falkenhaug (1991) and Alvarez-Cadena (1993) also found that in the Barents Sea and Irish Sea large *P. elegans* had the highest NPC. Feigenbaum (1979) divided the sub-tropical *Sagitta enflata* into eleven size categories and found that the NPC increased with increasing body length.

However, comparison with other studies may not be valid in this case since other feeding studies of chaetognaths are from the animals living in the water column. *P. elegans* in the BBL is exposed to different conditions than it is in the water column. The differences in the NPC in small and large animals in the BBL are due to the fact that the diets of these two groups of animals are quite different. Low incidences of

cannibalism have been reported from studies of *P. elegans* in the water column from other places (Feigenbaum and Maris, 1984). My study agrees that the animals in the water column show low cannibalism since small animals live there. In the BBL, a high incidence of cannibalism occurred, up to 57.6 % chaetognaths of the total diet (Fig. 3.1). As shown in Figs. 3.4 and 3.5, cannibalism occurred more frequently in larger animals. Since the ingestion of large items such as chaetognaths may increase the digestion time, larger animals may not have to feed often to meet their need for growth and reproduction. Pearre studied cannibalism in chaetognaths and came to the same conclusion and recognized that cannibalism in chaetognaths increased with the size of the predator species (1982). In his study, cannibalism was affected by prey abundance and predator size. He concluded that cannibalism may be energetically necessary for the existence of large species. It should be noted that there could be other causes for the higher NPC in small animals. The body specific metabolic rate could be higher, and the digestion time could be shorter in small animals.

3.4.4 NPC and the maturity stage of *P. elegans*

Previous studies concluded that the NPC increased as the animals matured (Falkenhaug 1991, Alvares-Cadena 1993), but in this study the NPC was higher in immature stage 1 animals, owing to the differences in the size and diet of immature and mature animals. Figure 3.12 shows that the mean length of stage 1 animals was less than 35 mm, except during October, and the mean lengths of stage 2 and 3 was greater than 30 mm except during May. The only difference in the diet of immature and mature

animals is that cannibalism occurred in stages 2 and 3, which may not feed frequently since they ingest large items (Table 3.5). During October, stage 1 fed on chaetognaths since stage 1 animals were unusually large (mean length, 36 mm).

3.4.5 Feeding and time of the day

The feeding activity of *Parasagitta elegans* is known to increase during the night (Wimpenny 1937, 1938; Rakusa-Suszczewski 1969, Pearre 1973, Sullivan 1980, Feigenbaum 1982, Ohman 1986, Øresland 1987). In this study, there was no diel variation in NPC of *P. elegans* in the BBL so the data collected during the day and night were not separated. The day and night samples on May 23, 1997, and June 23, 1998, showed that the diel NPC are almost the same. Perhaps, the time interval between day and night sampling was not long enough. The day data were collected at 15:00 and the night data were collected at 22:00. Since the digestion time of *P. elegans* is estimated to be 11.3 hrs, a 7 hr sampling interval may not be enough to detect a difference in the diel NPC. More frequent sampling during 24 hrs are necessary to observe the diel feeding behavior.

3.4.6 Feeding rates of *P. elegans*

The feeding rates of *P. elegans* in Conception Bay are similar to the feeding rates of *P. elegans* var. *arctica* recorded in the Barents Sea during the early summer of 1983 (Falkenhaug, 1991). The estimated feeding rates ranged between 0.30 and 1.05 prey per chaetognath per day, and the mean temperature was -1.5 °C in the Barents Sea. The reported feeding rates in my study can only be approximations since the following

assumptions could be false. The single NPC data were obtained for each sampling day except May 23, 1997, and June 23, 1998. According to the feeding study of *P. elegans* at different seasons in Gullmarsfjorden, Sweden, variations occurred in the NPC during a 24 hr period. The NPC was higher at night during spring but did not differ during winter (Øresland 1987). For this reason, several NPC values need to be obtained during a 24 hr period for more accurate estimations of NPC.

The digestion time used for the calculation of feeding rate may not be accurate, since temperature is not the only factor affecting the digestion time. Digestion time can vary depending on the type of food ingested by chaetognaths. In most studies, different food categories are assumed to have the same digestion time (Kimmerer 1984, Falkenhaug 1991, Alvares-Cadena 1993). Øresland (1987) estimated that the mean digestion time varied from 9.3 to 4.9 h depending on prey category. In his study, the digestion times with Stage IV to VI *Calanus* spp. were longer than with smaller stages of *Calanus* spp. or other copepod genera. The digestion time can also vary in this study since the diet of *P. elegans* was different often times. In the middle of May 1997, a high portion of the diet consisted of *Pseudocalanus* spp., and the consumption of such smaller copepods could result in shorter digestion time and higher feeding rate than the roughly estimated values. The opposite might be the case during February 1998 when intense cannibalism occurred. Ingestion of large items could result in longer digestion time and lower feeding rate. Therefore, mean NPC and specific digestion time for different food items need to be obtained for true feeding rates of *P. elegans* to be calculated.

3.4.7 Possible sources of error; cod end feeding and defecation

Previous studies reported that chaetognaths are notorious cod-end feeders (Feigenbaum & Maris 1984). Sullivan (1980) found that consumption by *P. elegans* collected in a 183 μm mesh net was 10 to 50 % greater than by specimens collected in a 333 μm mesh net, which retained fewer prey. Chaetognaths can defecate in the cod-end when they are stressed. Baier and Purcell (1997) found that prey loss from the gut contents of different chaetognaths species was substantial, with as much as 50 % of prey lost in tows of greater than 2 min duration. Cod-end feeding, as indicated by prey in the foregut, undigested prey, and non-prey items, was much less important than prey loss (Baier and Purcell 1997). Suggested methods to reduce errors due to cod-end feeding would be minimizing tow duration and reducing prey available in the nets by using nets with larger mesh size.

In this study, the tow times of the water column samples ranged from 8 to 21 min and the tow time of the BBL samples ranged from 37 to 46 min. The mean NPC from the water column tows were 0.24 ± 0.18 and the mean NPC from the BBL tows were 0.08 ± 0.05. Longer tows of the BBL samples may have produced lower NPC. The mean NPC from the BBL tows was significantly lower than that from the water column (Fig. 3.13, t-test, n=26, $p>|t| = 0.02$). Usually the cod end used for the BBL tows were extremely crowded with other zooplankton. This stressful environment may have induced defecation since most of the food items in the gut of chaetognaths were found at the very end of the gut. Cod-end feeding in the BBL samples may not be as important as cod-end defecation

since the cod ends were probably too crowded for the animals to feed and because few prey were found in the foregut. Time-controlled tests are needed to confirm the possible errors.

3.5 Summary

The NPC of *Parasagitta elegans* in the BBL of Conception Bay increased during spring and fall and decreased during summer and winter from 1997 to 1998. The abundance of copepods showed a similar seasonal trend. Small, immature chaetognaths fed more frequently. Small chaetognaths fed mostly on *Calanus* and *Pseudocalanus* spp. and large chaetognaths displayed high cannibalism. The NPC during day and night did not differ. The animals in the shallower depth fed more frequently.

Table 3.1 Abundance of copepods sampled with a Tucker Trawl net (500 μm) and a WP-2 ring net (206 μm)

Date	Depth (m)	Species	Stage	Tucker Trawl $N \cdot m^{-3}$	WP-2 $N \cdot m^{-3}$
June 9, 97	0-50	*Calanus spp.*	1-3	106.2	214.3
		Calanus spp.	4	10.6	14.6
		Calanus finmarchicus	5	0	1.2
		C. finmarchicus	6F	1.5	0
		C. glacialis	5	0.9	0
		C. glacialis	6F	0.3	0
		C. hyperboreus	4	0.3	2.4
		C. hyperboreus	5	0	2.4
		Pseudocalanus spp.	4	0.6	2.4
		Pseudocalanus spp.	5F	3.5	39
		Pseudocalanus spp.	5M	0.3	13.1
		Pseudocalanus spp.	6F	6.8	65.8
		Pseudocalanus spp.	6M	0	1.2
		Metridia longa		0	2.4
		Temora spp.		0	0

Table 3.1 (cont'd.) Abundance of copepods sampled with a Tucker Trawl net (500 μm) and a WP-2 ring net (206 μm)

Date	Depth	Species	Stage	Tucker Trawl	WP-2
(N = night)	(m)			$N \cdot m^{-3}$	$N \cdot m^{-3}$
July 8, 1997	0-175	*Calanus spp.*	1-3	123.9	343.1
		Calanus spp.	4	17.2	12.9
		Calanus spp.	5	0.6	0
		Calanus spp.	6F	0.3	0
		Pseudocalanus spp.	1-3	0.7	512.1
		Pseudocalanus spp.	4	0	121.6
		Pseudocalanus spp.	5F	3.2	11.9
		Pseudocalanus spp.	5M	0.3	21.8
		Pseudocalanus spp.	6F	7.2	6.9
		Metridia longa		0	11.9
		Temora spp.		0.5	3
July 23, 1997	1-160	*Calanus spp.*	1-3	153.4	272.6
		Calanus spp.	4	64.4	14.2
		Calanus spp.	5	0.6	0
		Calanus spp.	6F	0.9	0
		Pseudocalanus spp.	1-3	1.6	483.3
		Pseudocalanus spp.	4	0.3	151
		Pseudocalanus spp.	5F	3.4	24.3
		Pseudocalanus spp.	5M	0.9	35.5
		Pseudocalanus spp.	6F	14.7	28.4
		Pseudocalanus spp.	6M	0	4.1
		Metridia longa		0	51.2
		Temora spp.		0.6	13.2

Table 3.2 Feeding rates of *P. elegans* in Conception Bay from 1997 to 1998

Time	50-175 m	175-225 m	BBL
05/16/97	-	-	0.18
05/23/97	-	-	0.25
06/09/97	-	-	0.12
06/16/97	0.65	0.34	0.13
07/08/97	-	-	0.12
07/22/97	0.51	0.28	0.12
08/28/97	0.27	0.14	0.04
10/01/97	-	-	0.21
11/06/97	0.92	0.37	0.19
02/05/98	-	-	0.09
04/02/98	-	-	0.14
04/17/98	-	-	0.43
05/05/98	-	-	0.29
05/20/98	-	-	0.30
06/17/98	-	-	0.14
06/23/98	-	0.36	0.28
min	0.27	0.14	0.04
max	0.92	0.37	0.43
mean	0.59	0.30	0.19
std	0.27	0.09	0.10

Note: Feeding rates are expressed as number of prey per day per chaetognath.
The Tucker trawl net was used to collect 50-175 m, 175-225 m depth strata samples and the benthic sledge was used to collect the BBL samples.

Table 3.3 NPC of *P. elegans* from the BBL during day and night in a 24 hour period

Date	Time	NPC
May 23, 1997	1520	0.114
May 23, 1997	2240	0.118
June 23, 1998	1555	0.137
June 23, 1998	2245	0.127

Note: NPC denotes number of prey per chaetognath.

Table 3.4 Percentage of prey items found in *P. elegans* from the water column layers

Date	Depth	*Calanus*	*Pseudocalanus*	*Metridia*	*Temora*	chaetognath	unidentified
06/17/97	0-50 m	81.3	12.5	6.3	-	-	-
	50-175 m	62.5	18.8	4.2	-	-	14.6
	175-225 m	26.7	66.7	-	-	-	6.7
07/22/97	0-50 m	35.3	5.9	5.9	23.5	-	29.4
08/28/97	50-175 m	50	30	5	5	-	10
11/06/97	50-175 m	2.7	1.3	1.3	89.6	0.5	4.5
	175-225 m	11.1	-	5.6	77.8	-	5.6
06/23/98	50-175 m	80	20	-	-	-	-
	175-225 m	58.8	17.6	-	-	5.9	17.6

Note: The samples were collected with a Tucker trawl net.

Table 3.5 Percentage of prey items found in *P. elegans* of all stages from the BBL

Date	Stage	*Calanus*	*Pseudocalanus*	*Metridia*	*Chiridius*	chaetognath	unidentified
5/23/97	1	64.3	7.2	-	-	-	28.6
	2	77.3	4.5	4.5	-	4.5	9.1
	3	50.9	9.4	1.9	-	13.2	24.5
7/08/97	1	21.4	35.7	-	-	-	42.9
	2	-	-	-	-	-	-
	3	62.5	25	-	-	-	12.5
10/01/97	1	33.3	8.3	-	11.1	36.1	11.1
	2	-	-	-	-	-	-
	3	30	-	-	10	40	20
2/05/98	1	13.3	40	-	-	33.3	13.3
	2	5.9	11.8	-	-	82.4	-
	3	-	-	-	-	-	-
4/17/98	1	82.4	9.8	-	-	-	7.8
	2	76.9	3.8	-	-	15.4	3.8
	3	55.6	7.4	-	3.8	18.5	14.8
6/17/98	1	62.5	18.8	-	-	-	18.8
	2	-	-	-	-	-	-
	3	76	16	-	-	4	4
6/23/98	1	76	12	-	4	-	8
	2	-	-	-	-	-	-
	3	40	14.5	1.8	-	34.5	9.1

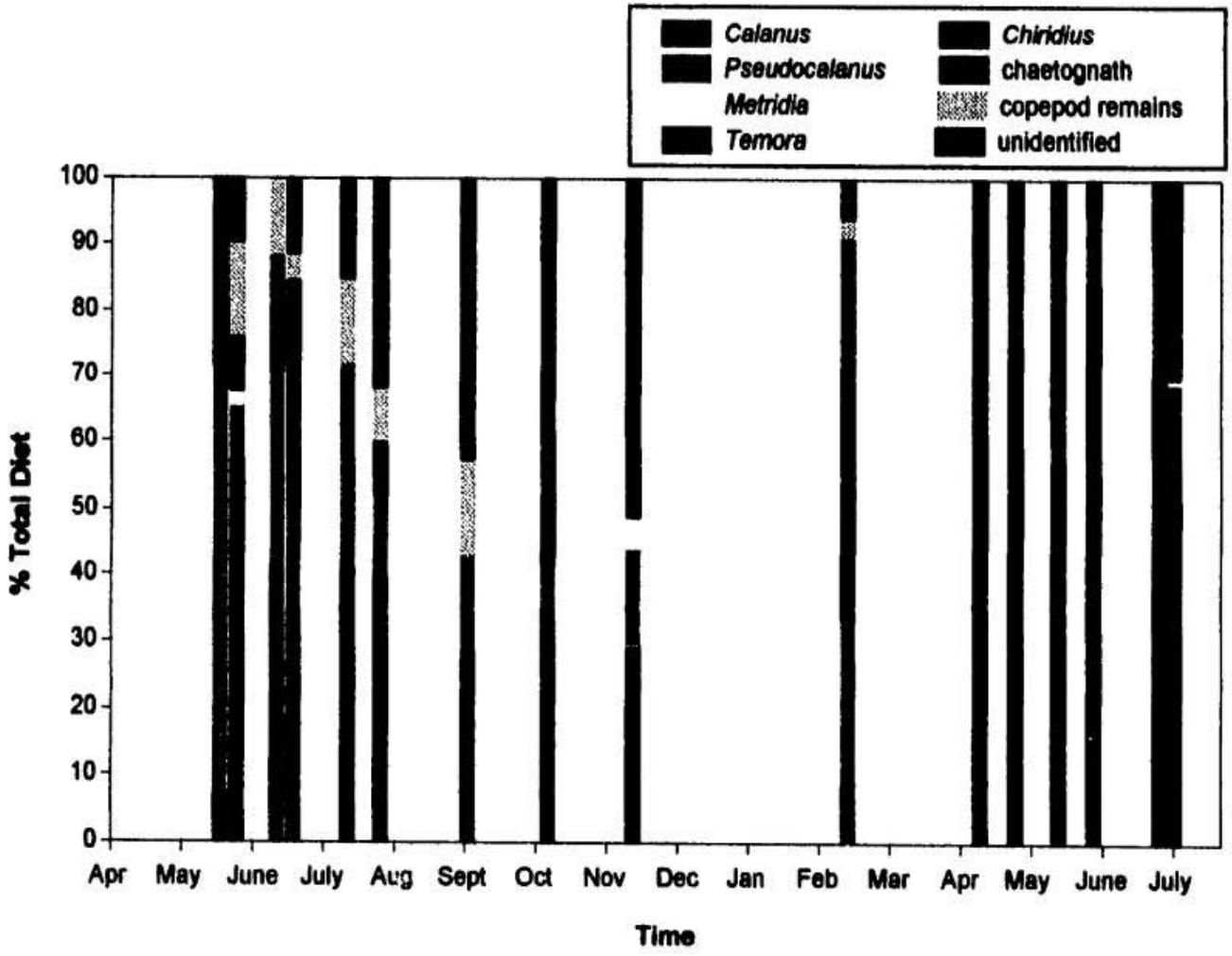

Fig. 3.1 Food composition of *P. elegans* in the BBL of Conception Bay from 1997 to 1998

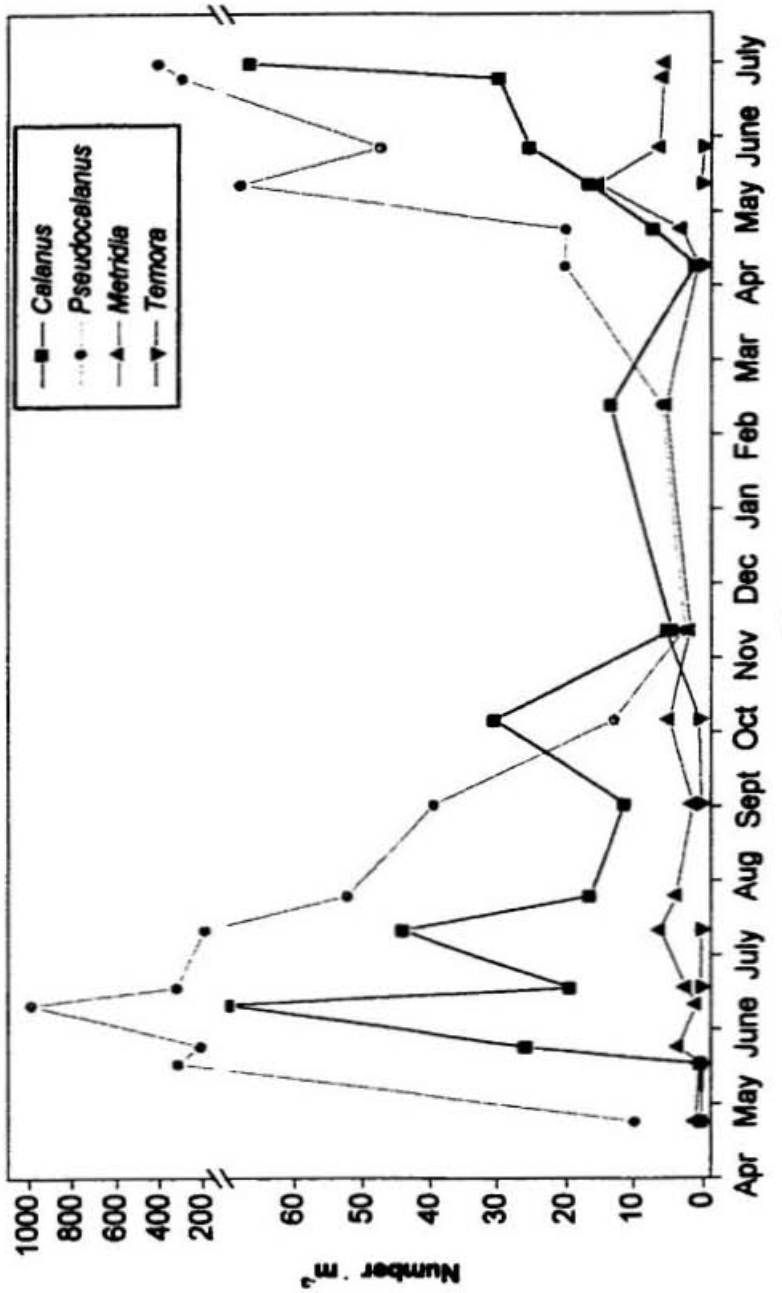

Fig. 3.2 Abundance of copepod species in the BBL from 1997 to 1998

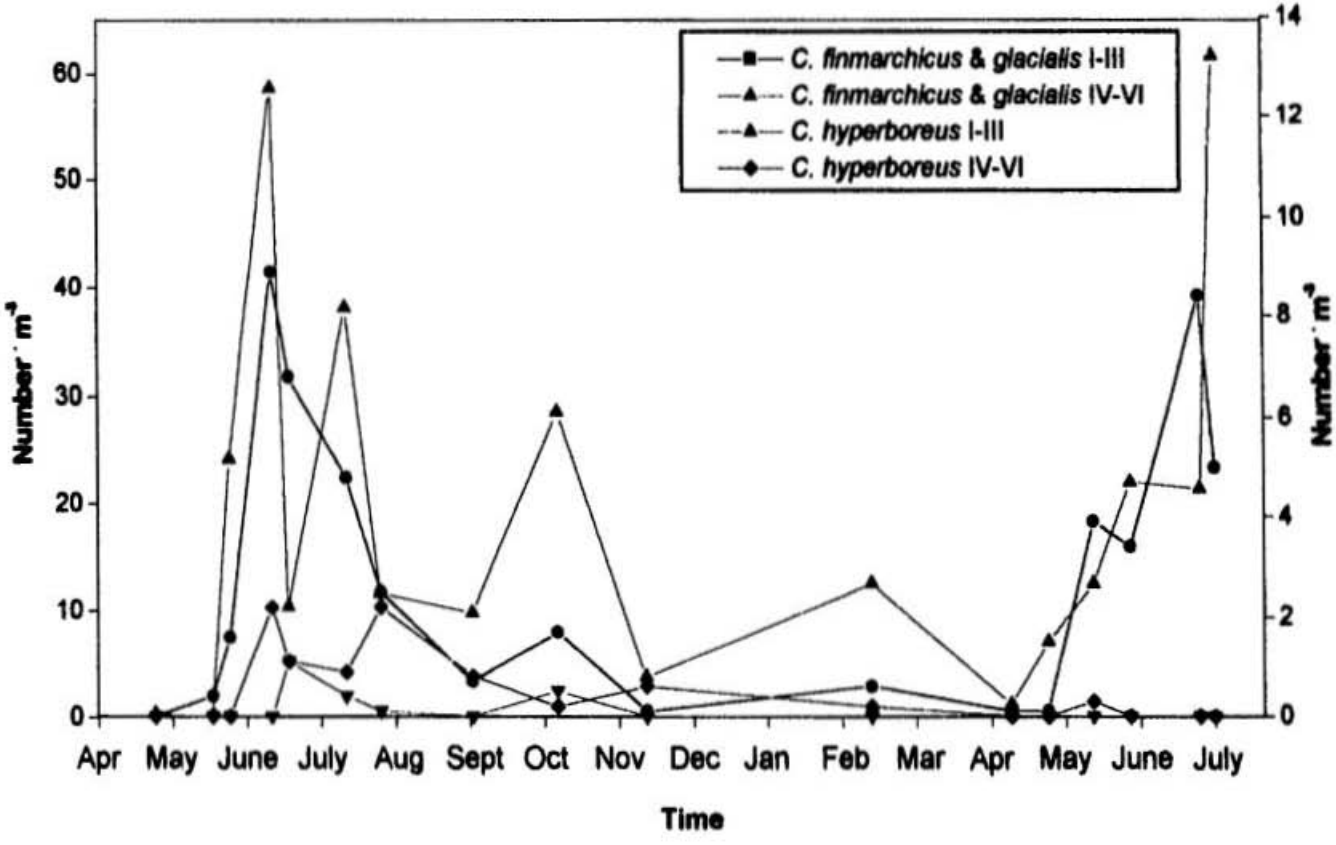

Fig. 3.3. Abundance of *Calanus* spp. in the BBL of Conception Bay from 1997 to 1998

(Left Y axis represents *C. finmarchicus* & *glacialis* IV-VI. Right Y axis represents *C. finmarchicus* & *glacialis* I-III, *C. hyperboreus* I-III and *C. hyperboreus* IV-VI)

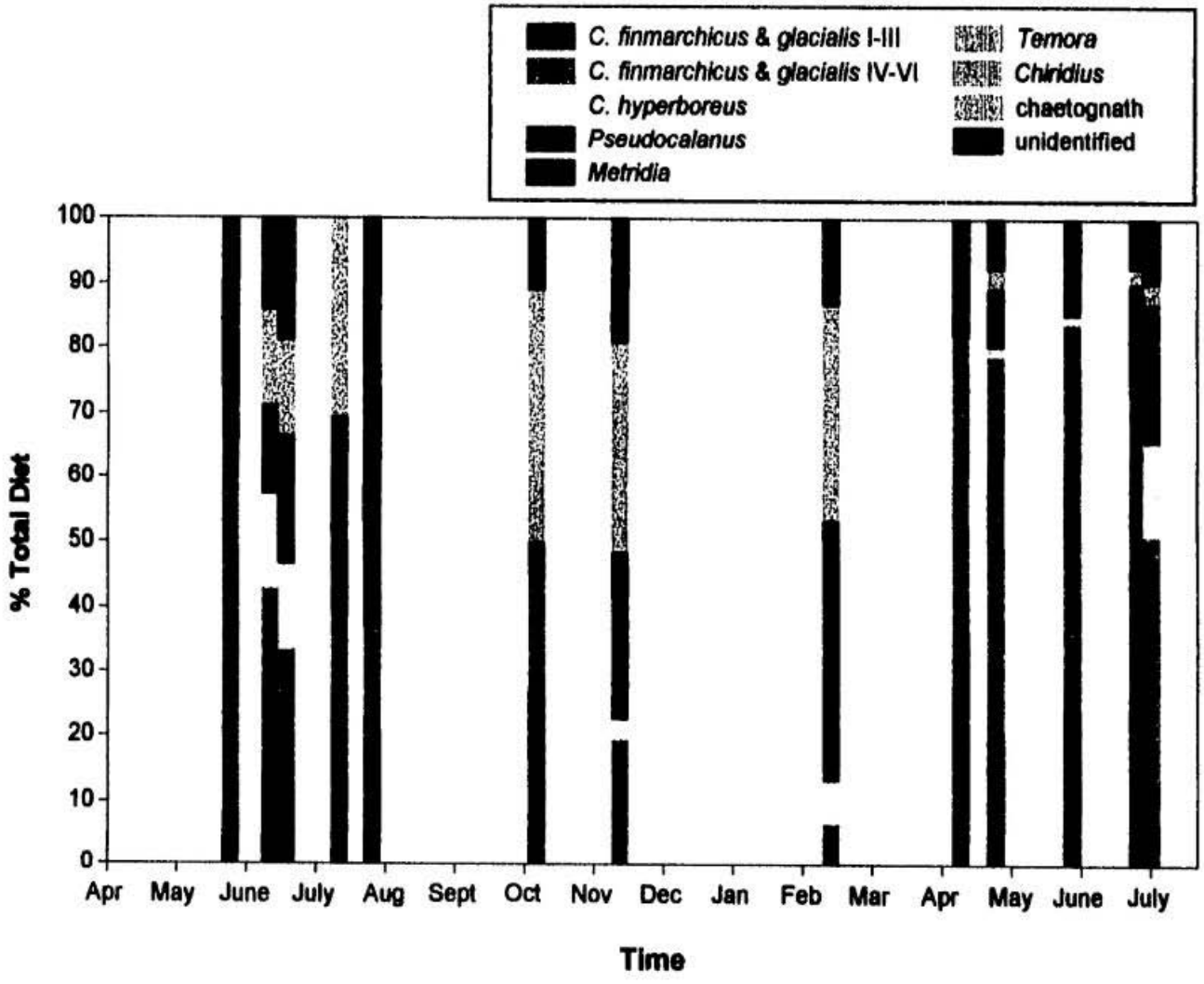

Fig. 3.4 Food composition of small *P. elegans* in the BBL from 1997 to 1998

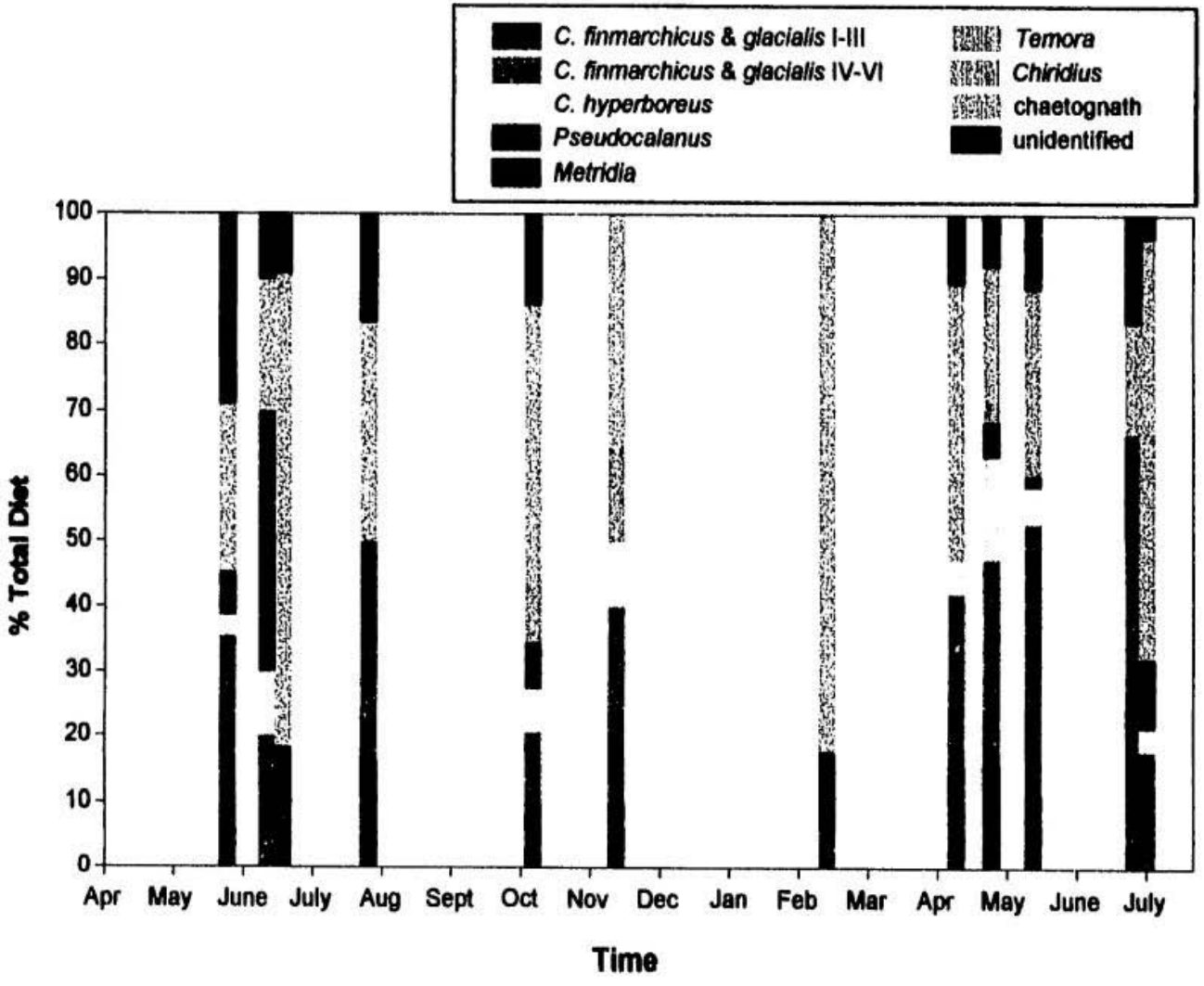

Fig. 3.5 Food composition of large *P. elegans* in the BBL from 1997 to 1998

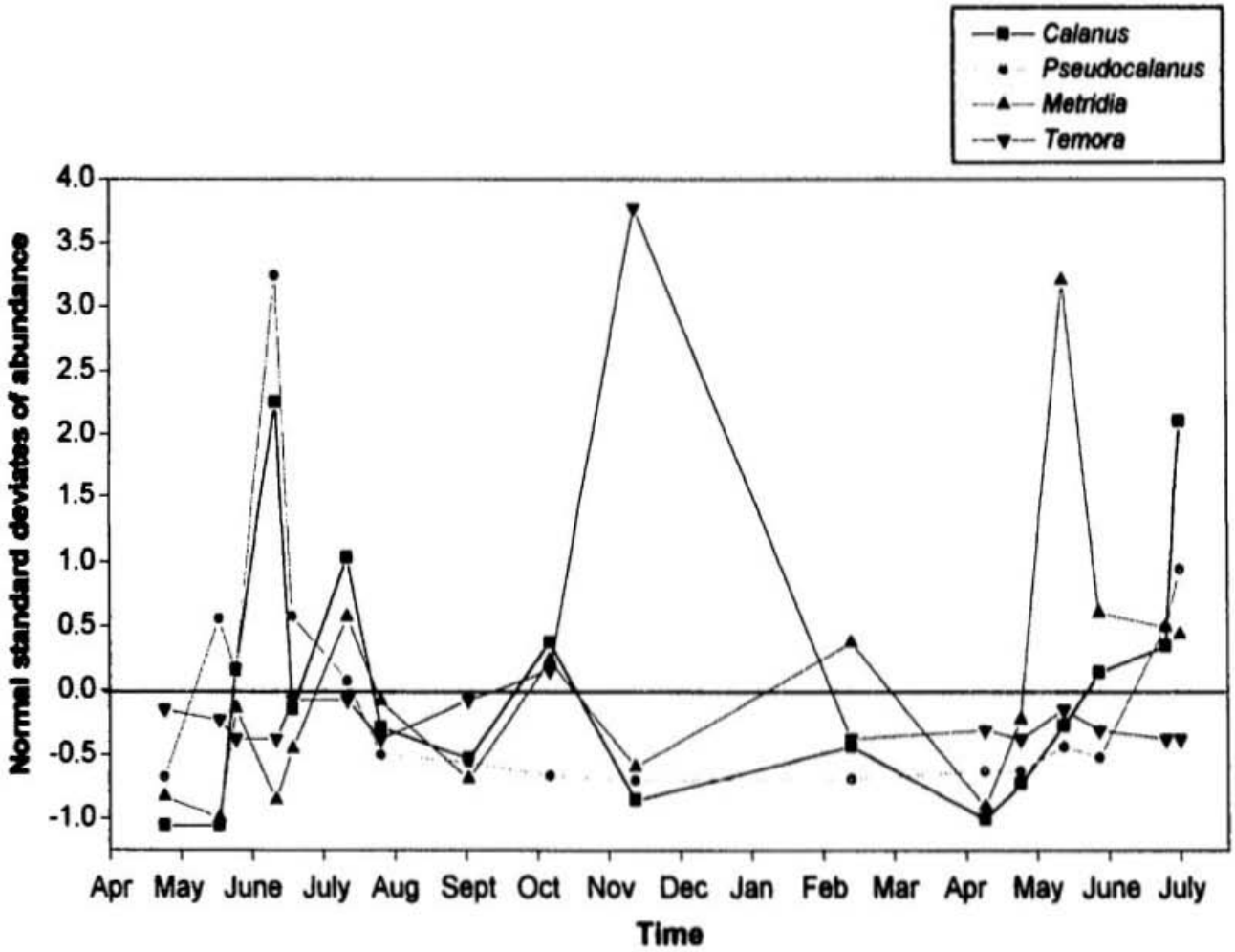

Fig. 3.6 Standard normal deviates of the copepod abundance in the BBL from 1997 to 1998

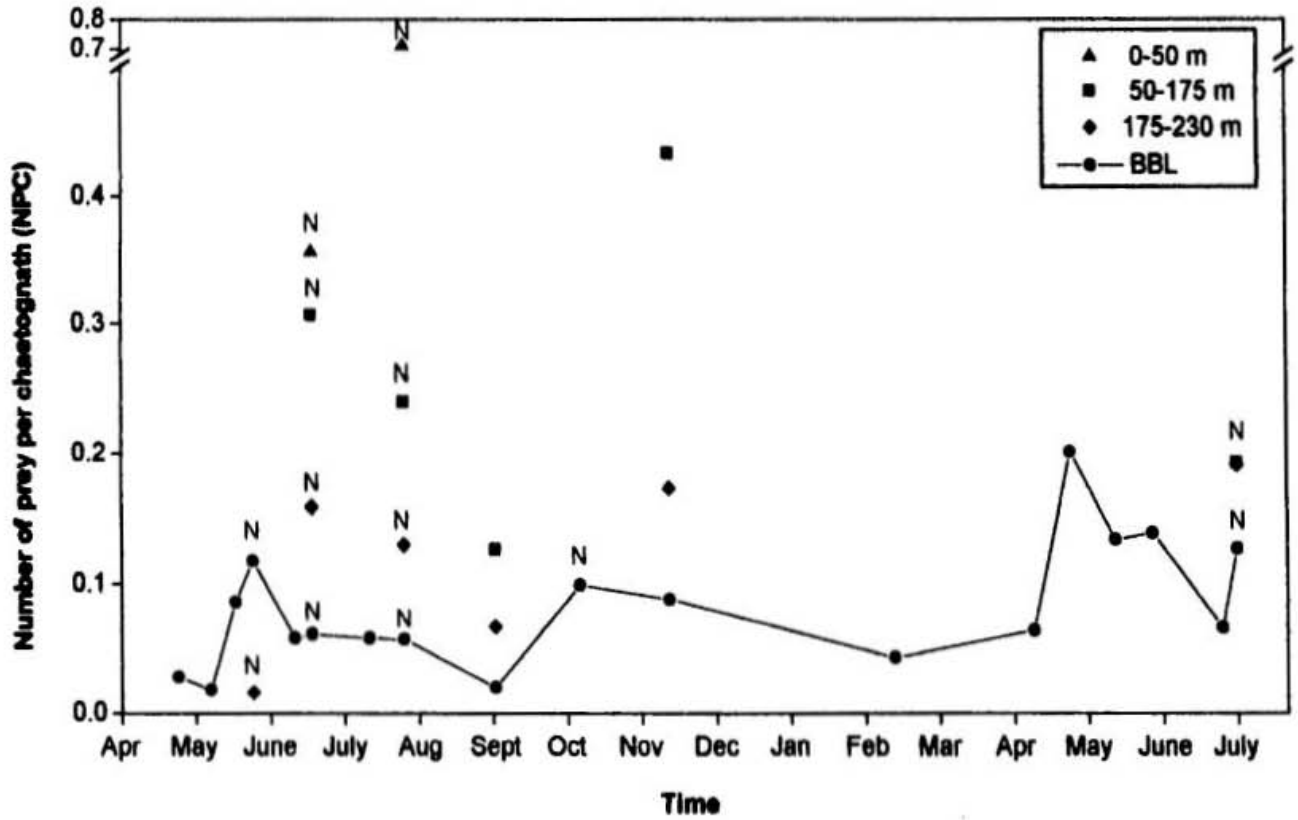

Fig. 3.7 Number of prey per chaetognath (NPC) of *P. elegans* in the BBL and water columns from 1997 to 1998
(N denotes night samples)

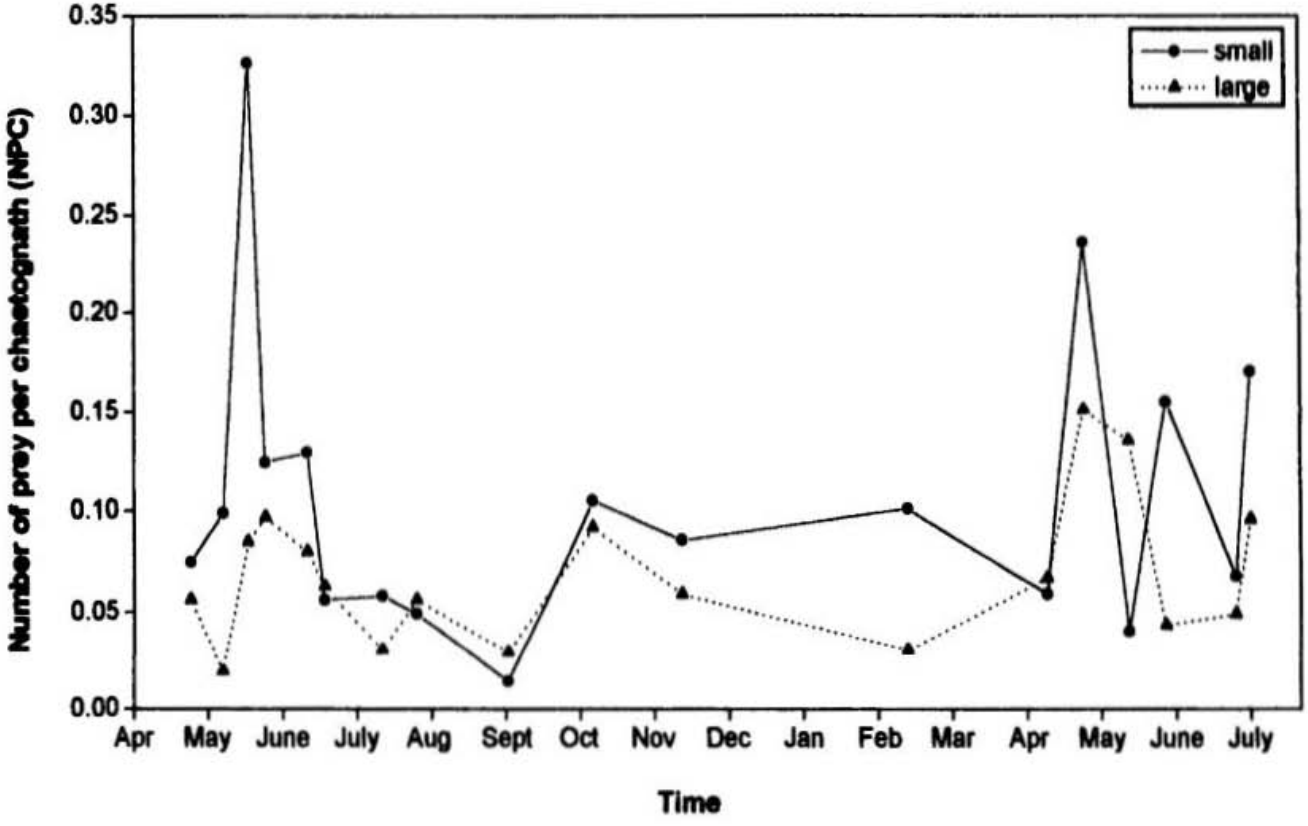

Fig. 3.8 Number of prey per chaetognath (NPC) of small and large *P. elegans* in the BBL from 1997 to 1998

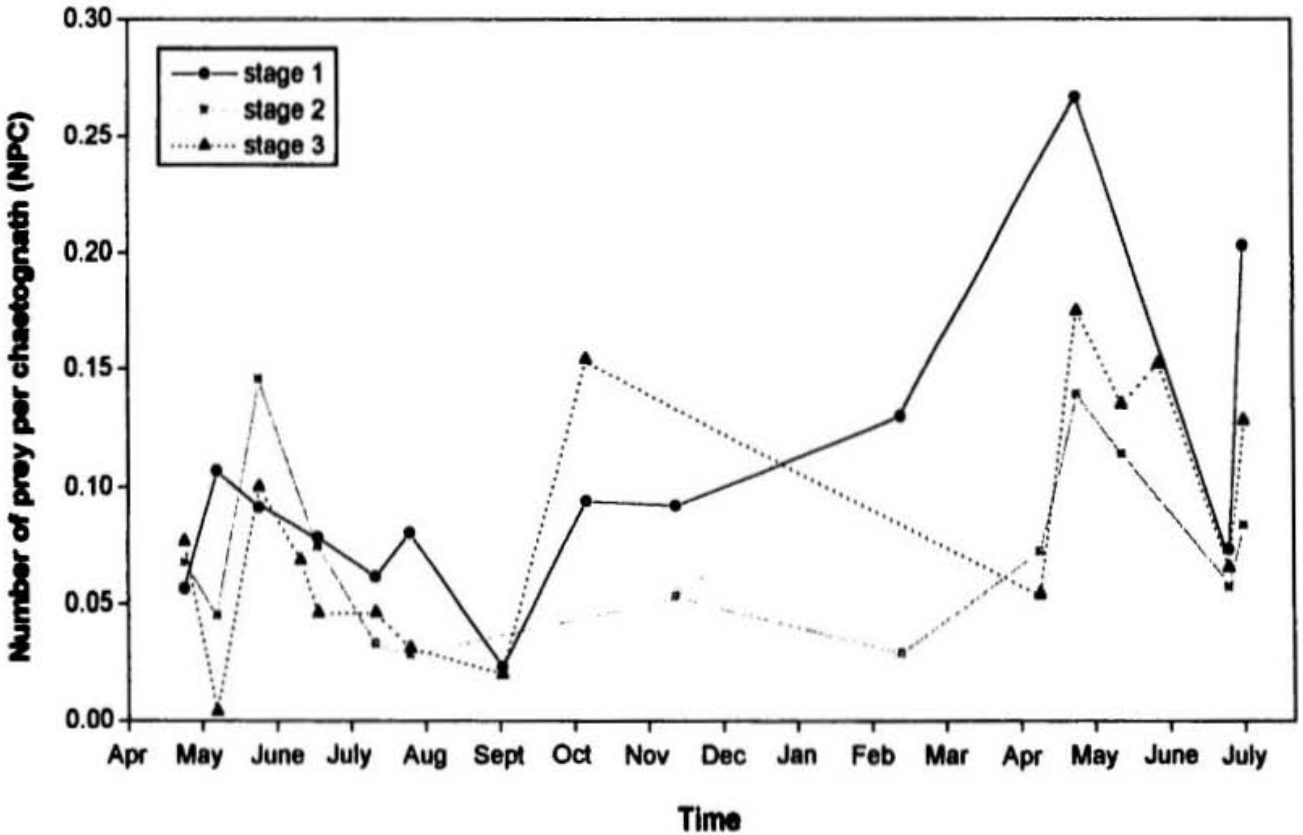

Fig. 3.9 Number of prey per chaetognath (NPC) of *P. elegans* at all maturity stages in the BBL

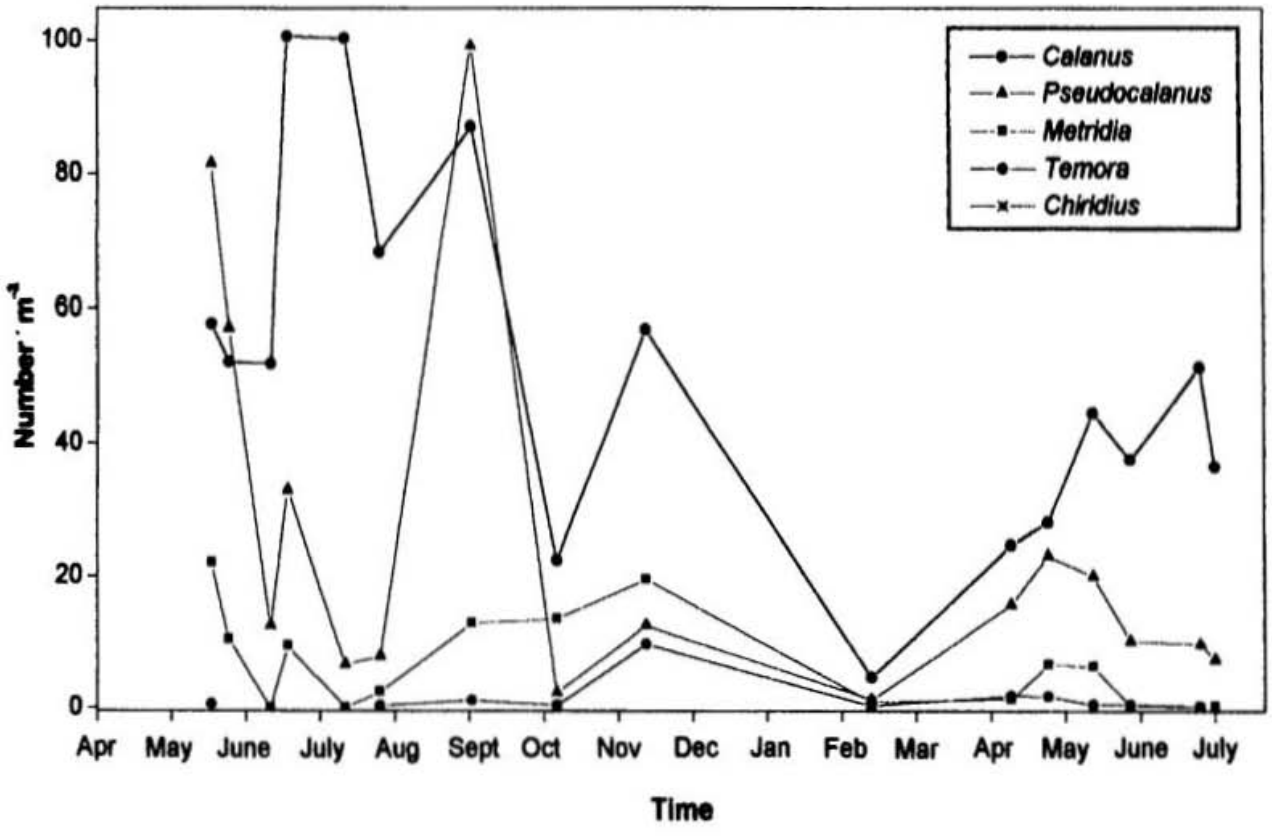

Fig. 3.10 Abundance of copepods in the 50-175 m depth stratum from 1997 to 1998
(The samples were collected with a Tucker trawl net.)

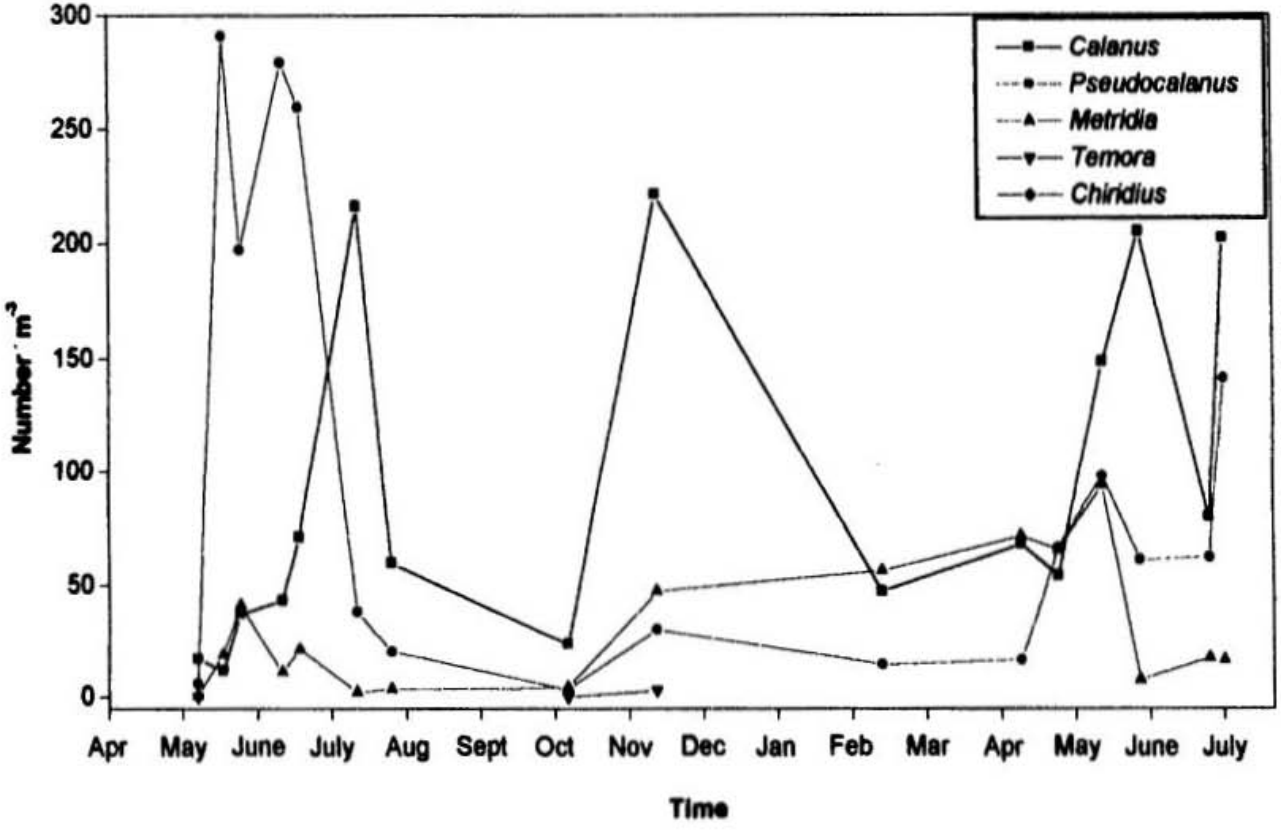

Fig. 3.11 Abundance of copepods in the 175-225 m depth stratum from 1997 to 1998
(The samples were collected with a Tucker trawl net.)

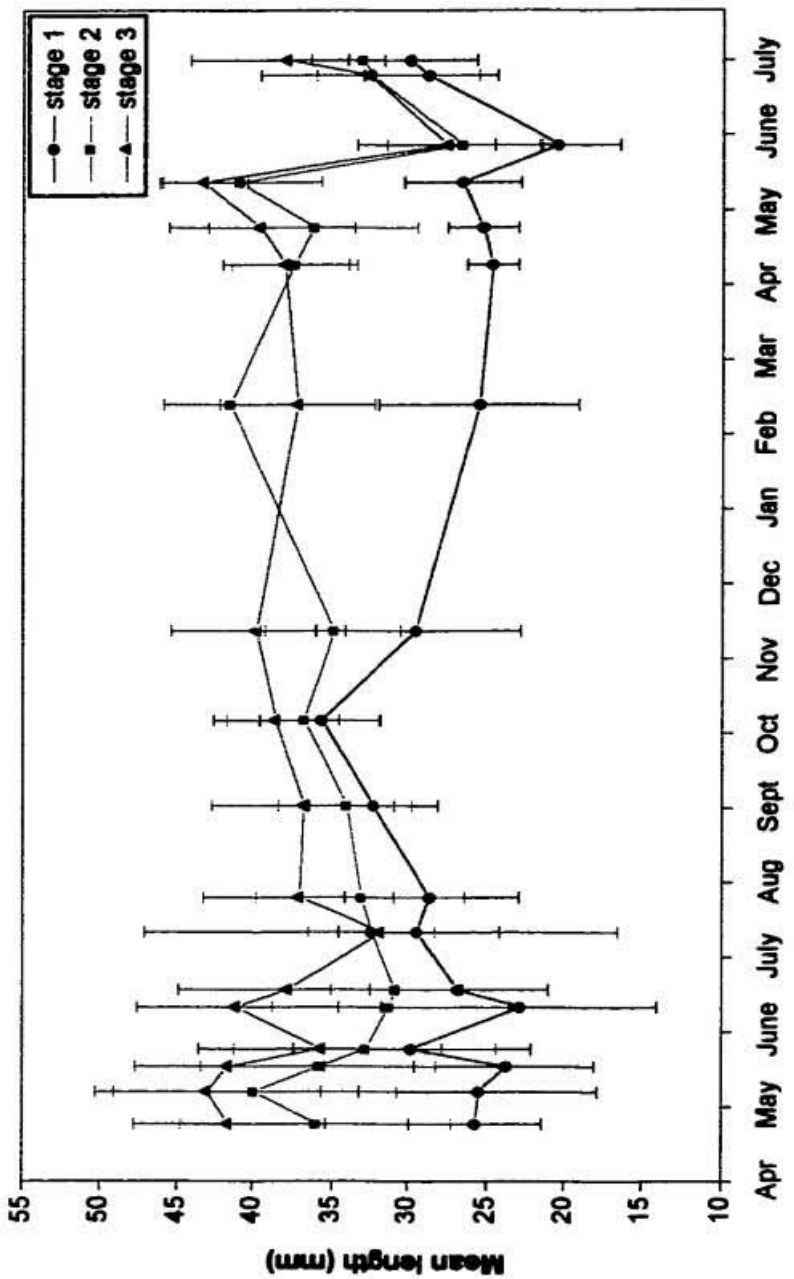

Fig. 3.12 Mean length (± standard deviation) of *P. elegans* in the BBL from 1997 to 1998

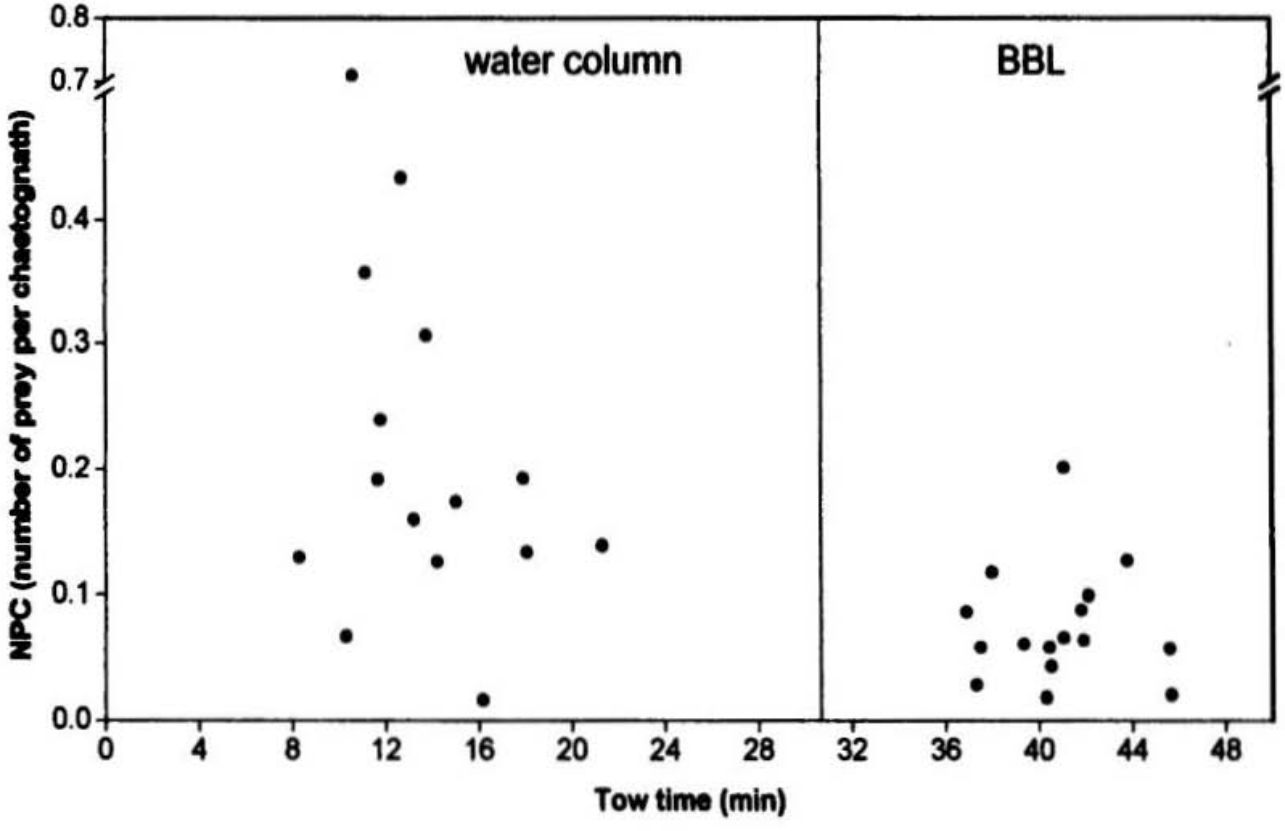

Fig. 3.13 Number of prey per chaetognath (NPC) in relation to tow time
(The water column data are from 0-50 m, 50-175 m and 175-225 m depth strata collected with a Tucker trawl net.)

Chapter 4. Seasonal Variation in the Biochemical Composition of *Parasagitta elegans* from Conception Bay, Newfoundland

4.1 Introduction

4.1.1 Possible causes of variation in the biochemical composition of zooplankton

The biochemical composition of zooplankton is influenced by a large number of ecological factors, which may vary seasonally, one of the most important being food availability. Herbivorous zooplankton are known to respond quickly to increasing rates of primary production. In a study by Jeffries (1979), the lipid levels of the copepods *Acartia clausi* and *Acartia tonsa* respond within 1 month to a pulse in primary production, and their fatty acid chain lengths increase with increasing primary productivity. The planktonic herbivores *Euphausia crystallorophias* and *Calanus hyperboreus* accumulate a large lipid reserve during the summer phytoplankton bloom and then utilize it during the subsequent winter (Littlepage 1964, Lee 1974). Typical herbivorous copepods from the Bering Sea contain a large lipid reserve which is probably an adaptation to an unpredictable and seasonally variable food supply (Ikeda 1972). The copepod *Heterorhabdus austrinus* feeds continuously during the winter in Scotia/Weddell Sea region, whereas *H. farranis* does not feed, resulting in a higher protein content and a lower lipid content *in H. austrinus* than *H. farranis* (Donnelly et al. 1994). The lipid storage of other herbivorous plankton such as euphausiids, *Thysanoessa inermis, T. raschii* and *Meganyctiphanes norvegica* also depends on primary production (Falk-Peterson 1981).

The seasonal variation in the biochemical composition of carnivorous zooplankton may be related to trophodynamics. Båmstedt (1978) determined that the chaetognath *Eukrohnia hamata* in Korsfjorden, Western Norway had the highest lipid and lowest protein level in winter and the opposite in spring. Båmstedt speculated that the changes in the biochemical composition of *E. hamata* throughout the year were related more to trophodynamics than to reproduction, since similar patterns were seen in both small and large specimens. However, Ikeda (1972) found relatively low lipid levels in typical carnivorous species (chaetognaths, pteropods, polychaetes and amphipods) and suggested that they were less tolerant of starvation than were herbivorous species, although food scarcity for these carnivores was less likely in nature, because they depended on other zooplankton which were less variable seasonally than were phytoplankton.

Another factor which may cause seasonal variation in the biochemical composition of zooplankton is the reproductive cycle. According to Littlepage (1964), a 60% increase observed in the lipid level of the predatory *Euchaeta antarctica* was the result of reproduction and development of lipid-rich eggs. Donnelly et al. (1994) reported that the relative water and lipid levels of *Euchaeta antarctica* increased and relative protein and chitin levels decreased from fall to winter, and concluded that these changes were consequences of reproductive demands.

The reproduction of zooplankton is closely related to feeding. Larson (1986) determined that the gonads of hydromedusae represented a substantial fraction of the total carbon content. He speculated that since the size of the gonads of hydromedusae was

directly affected by short-term changes in the availability of food, their biochemical composition might change over brief time periods. Stone (1966) found that *Sagitta enflata* from food-rich neritic waters in the Agulhas current had more eggs per individual than did individuals from an oligotrophic oceanic station. McLaren (1966) pointed out that if newly hatched *P. elegans* were dependent upon newborn copepod nauplii for survival, they could be limited to a brief window of feeding opportunity in early summer. King (1979) also found the reproduction of chaetognaths to be tied to the abundance of small copepods. This was consistent with Welch et al.'s data, which showed that although *P. elegans* in the Canadian Arctic grew year round, young of the year recruitment took place only in June and July, coinciding with the occurrence of copepod nauplii (Welch et al. 1996). Feigenbaum (1982) analyzed *P. elegans* in winter at Vineyard Sound, Massachusetts, and noted that small individuals consumed prey in excess of their requirements, which implied growth during the cold water period, while adults fed at the minimum rate necessary for maintenance. However, Dunbar (1962) found that reproduction of Arctic *P. elegans*, which has a long spawning period, was not closely coupled with food availability.

Temperature may affect the biochemical composition of zooplankton since it affects biological processes such as reproduction, growth rate and metabolic rate. The development rates of eggs and juveniles increase with temperature in *P. elegans* and *S. hispida* (Bone et al. 1991). Growth rates of chaetognaths also increase with temperature (Conway and Williams 1986, Moss 1994) but size at maturity and fecundity

decrease with increasing temperature (Zo 1973).

Spatial factors may account for some of the variation in biochemical composition of zooplankton. There is a consistent increase in the inorganic content of *P. elegans* with increasing latitude. The ash level of *P. elegans* from Southern Baffin Is. (15.6 % - 20.7%) is higher than that of the individuals from the Bering Sea (8.0 %) and from the North Pacific (4.8%) (Omori 1969, Ikeda 1972, Percy & Fife 1981). Mayzard & Martin (1975) found an ash level of 6.7 % in *P. elegans* in Nova Scotia waters. Whether this pattern was due to habitat temperature or other possible physiological factors is unknown (Percy & Fife 1981).

The protein level of pelagic crustaceans and fishes declines as the habitat depth increases (Childress and Nygaard 1974, Stickney and Torres 1989). The depth-related variation in biochemical composition of zooplankton could be due to several causes such as decreasing food availability and temperature with depth. Another possible explanation lies in the visual interaction hypothesis (Thuesen and Childress 1994), which suggests that those visually-orienting animals that live in the deep sea environment, where light is limited, have lower metabolic rates due to a decline in locomotory capabilities. However, the studies of the metabolic potential of various chaetognath species have indicated no overall decline in both oxygen consumption and enzyme activities with increasing depth (Thuesen and Childress 1993).

4.1.2. Objectives of the study

The main purpose of the study in this chapter was to document seasonal variation in the biochemical composition of *Parasagitta elegans* in Conception Bay, Newfoundland from 1997 to 1998. The animals were grouped into small and large size groups (i.e. $\geq <$ 35 mm). The specific questions addressed in this chapter are;

- Does the biochemical composition of *P. elegans* vary seasonally?
- Does the biochemical composition of small and large *P. elegans* differ?
- Does the biochemical composition of *P. elegans* from the water column and the BBL differ?
- Does reproductive state, NPC, diet or food availability affect the biochemical composition of *P. elegans*?

Temperature can be ruled out as a causative factor since it is constant (-1°C) below 50 m throughout the year in Conception Bay, Newfoundland.

4.2 Methods

4.2.1. Sample collection and preparation

Live *P. elegans* were collected from two water column layers (50-175 m and 175-220 m) and the BBL of Conception Bay, Newfoundland, as described in Chapter 2, from April 1997 to June 1998. The animals were left in prey-free seawater overnight to empty their guts and were then sorted by size less than or greater than 35 mm. Each animal was checked under a dissecting microscope and the animals without food and parasites in their guts were picked and rinsed quickly in distilled water, then dabbed quickly on

pre-combusted filter paper to dry them. The animals were frozen at -80 °C and lyophilized for two days.

4.2.2. Chemical analysis

Carbohydrate from the lyophilized tissues was extracted by boiling in a solution of 5 % trichloroacetic acid containing 50 mg silver sulphate (Barnes and Heath 1966), and the concentration of carbohydrate was determined by the phenol-sulphuric acid colorimetric procedure using glucose for a standard (Dubois et al. 1956). Total lipid was determined gravimetrically after chloroform/methanol extraction (Bligh and Dyer 1959). Carbon and nitrogen contents were determined with a Perkin-Elmer CHN analyzer (model 2400) standardized against acetanilide. Total protein was estimated by multiplying nitrogen content values by a factor of 5.8 (Gnaiger and Bitterlich 1984). It should be noted that protein was not directly quantified but was estimated. Ash content was obtained by weighing the dried samples after combusting at 450 °C in a muffle furnace overnight and allowing them to cool in a desiccator. The carbohydrate assay required 20 mg of lyophilized tissue: 10 mg for the lipid assay, 1-5 mg for ash content and 1-2 mg for CHN. Triplicates were made for all assays except for CHN analysis, where duplicates were taken. All values were expressed in terms of % dry weight.

The data were statistically analyzed using the Statistical Analysis System (SAS Institute, Cary, North Carolina). The comparison between two groups of data were analyzed using t-test and the comparison between several groups of data were analyzed using GLM (General Linear Model). Non-parametric statistics were applied for the data

which were not normally distributed. The types and results of the statistical analyses are reported in Appendices 1-15.

4.3 Results

4.3.1 Seasonal variation in the biochemical composition of *P. elegans* in the BBL

Ash, carbohydrate, lipid and protein levels all varied seasonally, but the temporal pattern of variability was different for each constituent. Over the entire time series, none of the mean biochemical levels was significantly different between small and large animals (Appendix 1). However, the levels of all biochemical constituents except carbohydrate were significantly different between small and large animals in at least one of the 3 seasons (Appendix 2). Ash level was significantly higher in smaller animals from spring to summer of 1997. Lipid level was significantly higher in larger animals from fall to winter but protein level was higher in smaller animals from fall to winter. The C/N ratio was significantly higher in larger animals from spring to winter. Therefore, all the data in small and large size groups were treated separately for further statistical analyses.

Mean ash ranged from 8.5 to 18.0 % of dry weight with a mean of 12.0 $\pm$ 2.4 % (Figs. 4.1, 4.2). Ash level increased to a maximum and decreased to a minimum from fall to mid-winter. The mean % ash of small and large animals varied significantly with time (i.e., julian day) (Appendix 3) and varied significantly with season (Appendix 4). The mean % ash of large animals was significantly lower in the spring of 1998 than in the spring of 1997 (Appendix 5).

Mean carbohydrate level ranged from 0.5 to 0.8 % of dry weight with a mean of

0.6 ± 0.1 % (Fig. 4.3, Fig. 4.4). Carbohydrate increased to a maximum from spring to early fall, and decreased to a minimum from fall to winter. The mean % carbohydrate of small animals but not that of large animals, varied significantly with time (Appendix 3). The mean % carbohydrate of small and large animals varied significantly with season (Appendix 4). The mean % carbohydrate of large animals was significantly lower in the spring of 1998 than in spring of 1997 (Appendix 5).

Mean lipid ranged from 8.7 to 15.8 % with a mean of 13.0 ± 1.7 % (Fig. 4.5, Fig. 4.6). Lipid level increased to a maximum from fall to summer, and decreased during fall. The mean % lipid of small animals, but not that of large animals, varied significantly with time and season (Appendix 3, 4). The mean % lipid was not significantly different in the spring of 1997 and 1998 (Appendix 5).

Mean protein ranged from 56.3 to 69.9 % with a mean of 64.2 ± 3.8 % (Fig. 4.7, Fig. 4.8). Protein level increased during fall to a maximum and decreased during spring. The mean % protein of small and large animals varied significantly with time (Appendix 3) and varied significantly with season (Appendix 4). The mean % protein of small and large animals was significantly higher in the spring of 1998 than in spring of 1997 (Appendix 5).

The C/N ratio (w/w) ranged from 3.8 to 4.7 with a mean of 4.3 ± 0.3 (Fig. 4.9, Fig. 4.10). The C/N ratio increased to a maximum from spring to summer, and decreased during fall. The mean C/N ratio of small animals but not that of large animals varied significantly with time (Appendix 3). The mean C/N ratio of small and large animals varied significantly with season (Appendix 4). The mean C/N ratio was significantly lower in the

spring of 1998 for large animals (Appendix 5).

All the biochemical composition values changed from fall to winter. Ash level increased by 50 % and protein increased by 20 %. Carbohydrate decreased by 30 % and lipid decreased by 30 %.

4.3.2 Seasonal variation in the biochemical composition of *P. elegans* in the water column

Sufficient data were gathered from the near bottom depth (175-225 m) to describe the seasonal variability in the biochemical composition of the small animals, but insufficient data were available for large animals.

Over the entire time series, some of the mean biochemical levels were significantly different between small and large animals (Appendix 6). Ash and protein were significantly higher and C/N ratio was lower in small animals in the near bottom depth. Only the C/N ratio was significantly lower in small animals in the mid-depth (50-175 m). Therefore, all the data in small and large size groups were separated for further statistical analyses.

Mean ash of small and large animals from mid-depth and near-bottom waters ranged from 8.4 to 18.3 % of dry weight with a mean of 10.4 ± 2.4 % (Fig. 4.1, Fig. 4.2). Ash level of small animals from near bottom water increased to a maximum from late spring to late summer, and decreased to a minimum from fall to mid-winter. The mean % ash of mid-depth and near bottom waters varied significantly with time (Appendix 7). The mean % ash of near bottom water was not significantly different in the springs of 1997 and

1998 (Appendix 8).

Mean carbohydrate ranged from 0.5 to 0.7 % of dry weight with a mean of 0.6 ± 0.1 % (Fig. 4.3, Fig. 4.4). No well-defined seasonal trend in the carbohydrate content was evident in the animals from the near bottom water column. The mean % carbohydrate of small animals in mid-depths and of large animals in near bottom waters varied significantly with time (Appendix 7). The mean % carbohydrate of small and large animals was not significantly different in the springs of 1997 and 1998 (Appendix 8).

Mean lipid ranged from 9.5 to 15.5 % with a mean of 12.2 ± 1.8 % (Fig. 4.5, Fig. 4.6). Lipid level of small animals in near bottom waters decreased from spring to fall and increased slightly next spring. The mean % lipid of small and large animals varied significantly with time (Appendix 7). The mean % lipid of small animals in near-bottom waters was significantly higher in the spring of 1997 than in spring of 1998 (Appendix 8).

Mean protein ranged from 60.9 to 74.9 % with a mean of 66.1 ± 3.0 % (Fig. 4.7, Fig. 4.8). Protein level of small animals in near-bottom waters increased from spring to winter and decreased during the next spring. The mean % protein of small and large animals varied significantly with time (Appendix 7). The mean % protein of small and large animals was not significantly different in the spring of 1997 and 1998 (Appendix 8).

Mean C/N ratio ranged from 3.6 to 4.5 with a mean of 4.2 ± 0.3 (Fig. 4.9, Fig. 4.10). The C/N ratio decreased from spring to winter and increased during the next spring. The mean C/N ratio of small and large animals in mid-depth and near bottom waters varied significantly with time (Appendix 7). The mean C/N ratio of small and large

animals was significantly higher in the spring of 1997 than in the spring of 1998 (Appendix 8).

4.3.3 Depth variation in the biochemical composition of *P. elegans*

The biochemical variables from mid-depth, near-bottom and BBL waters were compared to test for depth variation. Ash, lipid, protein and C/N ratio of small animals were significantly different as a function of depth (Appendix 9). Ash and C/N ratio of small animals were higher in the BBL. Lipid and protein levels of smaller animals were higher in the shallower depth. Only ash and lipid levels of large animals were significantly higher in the BBL. The depth variations in the biochemical composition of small and large animals were not similar except for protein. Protein levels of small and large animals were higher in the shallower depth.

4.3.4 Relation between the biochemical contents and maturity, feeding and food availability

The data from Chapters 2 and 3 were used to determine whether there was any relationship between biochemical composition and reproductive maturity, NPC, diet and food availability. According to the analysis, the reproductive maturity of *P. elegans* in the BBL varied significantly as a function of season. The small animals were predominantly immature from fall to winter of 1997 (Fig. 4.11), because the frequency of stage 1 of small animals in the BBL was significantly higher from fall to winter (73 $\pm$ 16 %, Appendix 10). The frequency of stage 3 of small animals was not significantly higher in the spring of 1997 and 1998. However, a maximum frequency of stage 3 of small animals occurred in

the spring of 1998 and this may indicate that the small animals matured in the spring of 1998. The large animals were predominantly immature from fall to winter of 1997 and were mature in the spring of 1997 and 1998 (Fig. 4.12). The frequency of stage 1 of large animals was significantly higher from fall to winter and the frequency of stage 3 was significantly higher in the spring of 1997 and 1998 (Appendix 10), suggesting that the animals were spawning from fall to winter. Since major changes occurred in the biochemical composition at the same time, I conclude that the biochemical composition of *P. elegans* primarily reflects the reproductive status of the animals.

However, the interannual variations in the biochemical composition of large animals from the BBL cannot be explained by interannual variation in the maturity status of the animals. Ash and carbohydrate levels of large animals were 8.8 % and 14.3 % higher in the spring of 1997 respectively, while protein level was 5% lower (Appendix 5). There was no significant interannual variation in lipid level. The proportion of stage 1 animals in the BBL was significantly higher in the spring of 1997 by only 2.1 % (Appendix 11). The proportion of stage 2 and 3 animals was not significantly different interannually.

The NPC of *P. elegans* in the BBL did not significantly change as a function of season (Appendix 12) and did not change interannually (Appendix 13). Maximum NPCs in the spring of 1997 and 1998 indicate more frequent feeding in spring. Therefore, the NPC may not explain the seasonal change in the biochemical content levels.

Diet and food availability may have affected biochemical levels. In the spring of 1997 and 1998, the proportion of animals at each maturity stage was similar

(Appendix 10). Despite the fact that there was no interannual difference in the maturity status of the animals, there were interannual differences in the biochemical levels. The diet of *P. elegans* was different in the spring of 1997 and 1998. The consumption of *Calanus* spp., the main food item of *P. elegans*, was significantly higher in the spring of 1998 (Appendix 14). The food availability was not higher in the spring of 1998 because the abundance of *Calanus* spp. in the BBL was not significantly higher in the spring of 1998 (Appendix 15). However, the abundance of *Calanus* spp. and the NPC increased earlier in the spring of 1998 (refer to Fig. 3.3 & Fig. 3.7). This may indicate that the animals were better nourished in the spring of 1998. Protein level of the animals was significantly higher by 5% and the ash (inorganic) and carbohydrate level was significantly lower by 9 % and 14 %, respectively in the spring of 1998. Biochemical content levels may indicate the nutritional status of the animals.

4.4 Discussion

4.4.1. Seasonal biochemical contents of small and large *P. elegans*

In general, there was no consistent size variation in the biochemical composition of *P. elegans*. In this study, animals were divided into small and large size categories since the body size distribution of the population was often divided into two size groups representing different cohorts as shown in Chapter 2. The lack of clear differences in the biochemical levels of small and large animals reflect the fact that animals in each size category matured throughout the year. However, there were differences in the lipid and C/N ratio of small and large animals during late fall and winter, when values for small

animals were lower than those for large animals because the small animals were represented by the new young cohort. According to the body size and stage frequency distribution (Fig. 2.8), cohort 3 emerged during November and matured slowly until the following spring. The lipid and C/N ratio of large animals were higher than those of small animals during late fall and winter because the large animals were represented by cohort 2, which reproduced earlier and was maturing for a second time. Figure 2.8 indicates that cohort 2 spawned during August and October and matured again during winter and the following spring. Furthermore, the rapid increase of lipid level in large animals during late fall and winter may imply that cohort 2 had been maturing rapidly since their somatic growth had been achieved by fall. Slower increase of lipid in small animals during late fall and winter could indicate that the new cohort was achieving somatic growth and the rapid increase of lipid during the next spring could indicate that the new cohort was achieving reproductive maturity.

4.4.2 Seasonal variation in the biochemical composition of *P. elegans* in the BBL

All biochemical components showed changes during fall since the major spawning and introduction of immature animals occurred during that time. Ash (inorganic) increased during fall because the animals were losing organic material while they released eggs. Ash level was low during spring and winter since the animals were maturing. Lipid and carbohydrate levels decreased during fall and increased during spring and winter, suggesting that lipid and carbohydrate are important biochemical constituents for reproduction. Protein level was lower during spring and higher during fall and winter

which may indicate that the protein level was higher in immature animals. According to the maturity stage frequency distribution of *P. elegans*, immature stage 1 and 2 were predominant during fall and winter (Fig. 4.11 & Fig. 4.12). Protein level was higher during this time and lower when mature stage 3 animals were predominant during spring of 1997 and 1998.

Although major changes in the biochemical composition of *P. elegans* were primarily due to reproduction, minor changes may have been caused by changes in the diet. A relative change of 30 % to 50 % in each of the biochemical levels occurred during the reproductive season. The relative change from 5 % to 14 % between the spring of 1997 and 1998 was due to differences in the nutritional status of the animals.

4.4.3 Biochemical contents of *P. elegans* in the water column and BBL

The lipid level was higher and the protein level was lower in animals from the BBL than in those from the water column. This trend may be due to the fact that more mature animals normally lived in the BBL (refer to Fig. 2.7 and Fig. 2.8). Seasonal patterns in the biochemical composition of the animals in the near-bottom water mass and the BBL were similar. Lipid and C/N ratio decreased during fall and winter and increased during spring but ash and protein increased during fall and winter and decreased during spring. Similar trends occurred in the water column and the BBL because mostly mature animals were present during spring and mostly immature animals were present during fall and winter.

4.4.4 Comparison with other studies

Several studies on the biochemical composition of water-column chaetognaths have been published (Table 4.1). In most studies, except that of Donnelly et al. (1994), protein was the highest biochemical constituent of chaetognaths, followed by lipid and ash, with carbohydrate representing the lowest component. The C/N ratios were within a narrow range, from 3.6 to 4.3. The highest C/N ratio ever reported was found in this study. The results from this study are comparable with studies of *P. elegans* in St. Margaret's Bay, Nova Scotia (Mayzaud and Martin 1975) and Baffin Island (Percy and Fife 1981). An exceptionally high amount of ash and low amount of protein were found in *Sagitta gazellae* and *Eukrohnia hamata* from the Weddell and Scotia Seas (Donnelly et al. 1994). The ash content of *S. gazellae* and *E. hamata* ranged from 36.4 to 54.7 % and 20.5 to 45.8 %, respectively. Protein of *S. gazellae*, *S. marri* and *E. hamata* ranged from 15.9 to 39.1 %. The general conclusion from Donnelly's study may be that the organic contents of the chaetognath species in Antarctic seas were lower than those of the chaetognaths from high latitudes in the Northern hemisphere.

Besides this study, there have been two studies which investigated complete seasonal biochemical composition of chaetognaths. Reeve et al. (1970 b) studied the biochemical composition of *Sagitta hispida*, a warm-water species from Biscayne Bay, Florida, over a one year period. Protein level fluctuated widely throughout the year, ranging from 39 to 70 % of dry weight (mean 52.9 %), with highest values in December and January, intermediate values in summer, and lowest values in spring and autumn.

There was much less variability in the lipid, ash and carbohydrate fractions. The biochemical fluctuations had little correlation with fluctuations in seasonal physical factors such as temperature and salinity. Correlations between the seasonal pattern of biochemical composition in *S. hispida* and biological factors such as reproduction and food availability were difficult to make in their study since there were no clear seasonal cycles of reproduction and food availability in warm waters. *S. hispida* breed continuously, and have a life-cycle of weeks in Biscayne Bay, and the copepods which constitute the bulk of its food had similar characteristics.

Reeve et al (1970 b) studied further the relationship between the biochemical composition of *S. hispida* and food availability in the laboratory. The animals were either starved or fed for a week and the changes in the protein/wet weight, protein/dry weight, ash/dry weight and dry weight/wet weight were measured. Starved animals lost dry weight on a wet weight basis. The animals were able to live without food for at least seven days, using body protein as an energy source. The time of starvation was equivalent to 1/4 of a generation. However, protein as a proportion of dry weight remained constant, suggesting that variations of biochemical levels in natural populations were not a function of food availability.

The seasonal variations in the biochemical composition of *Eukrohnia hamata* in Korsfjorden, western Norway were studied by Båmstedt (1978). The animals were divided into four size classes and analyzed for 13 months. Protein was the least variable and lipid the most variable component throughout the year. Protein increased in spring.

Lipid decreased in spring and increased from fall to winter. Ash level increased in spring and decreased from fall to winter. A strong inverse relationship was shown between lipid and ash and a weak inverse relationship was shown between lipid and protein. Båmstedt referred to the quantitative studies of chaetognaths from Korsfjorden by Sands (1977), and pointed out that the decrease in lipid during spring of 1974 coincided with reproduction, since the animals bred from spring to late fall. However, different correlations between size and biochemical composition throughout the year contradicted the argument related to reproduction. According to regression analyses between body size and biochemical levels, protein level had positive correlations with the weight of the animals from summer to winter and negative correlations from spring to summer. Ash had positive correlations with weight from summer to fall and negative correlations from winter to spring. Lipid mostly showed positive correlations throughout the seasons. Negative correlations of lipid with weight during the reproductive season indicate that animals of larger size could have lost lipid from spawning but there was no such seasonal trend of negative correlation of lipid in his study. This contradiction led to the conclusion which related food availability to the variations in biochemical contents of *E. hamata*. The overall increasing lipid proportion during summer-early winter indicated that this was a period with superfluous food, followed by a period from winter to spring with scarcity of food, reflected by the overall decreasing lipid proportion. However, a feeding study would have been necessary to find out whether the animals were food-limited in winter and whether their NPC and diet responded to the food availability.

Båmstedt divided animals into four body size groups at each sampling and regressed biochemical contents against dry weight, but these regressions must have been based on the assumption that *E. hamata* is semelparous (i.e., reproducing once in their life time) and that the maturity of animals depends on their body size. This may not be the case, since my study and others reported multiple occurrence of spawning in other chaetognaths (Reeve 1970b, Koszteyn 1983, Nagasawa 1984, Conway and Williams 1986). Cohort analysis could have been helpful to answer the question of the relationship between seasonal variations of the biochemical contents and reproduction.

4.5. Summary

In Conception Bay, Newfoundland, *P. elegans* fed often and matured when spring phytoplankton bloomed and the abundance of copepods increased (Refer to Figs. 3.6, 3.3). Spawning occurred during fall, and the parent cohort and the new cohort matured over the winter and the next spring. Variation in the biochemical levels of *P. elegans* primarily reflected the pattern of the reproductive cycle. Protein and ash levels increased and lipid decreased at the time of reproduction. Protein and ash levels decreased as the animals matured. Feeding may have caused minor changes in the biochemical composition. Protein level was higher and ash and carbohydrate levels were lower in the spring of 1998 because the animals were better nourished.

Table. 4.1 Biochemical compositions of chaetognaths (% of dry weight)

Species	Protein	Lipid	Carbohydrate	Ash	C/N	Location	Author
Parasagitta elegans	64.2	13.0	0.6	12.0	4.3	Conception Bay,	This study
P. elegans	46.9	8.3	20.5	24.3		Sea of Japan	Zenkevitch (1963)
P. elegans	84.0	6.7	0.7	8.0		Bering Sea	Ikeda, T (1972)
P. elegans	54.2	7.8	1.5	6.7		St. Margaret's Bay, Nova Scotia	Mayzaud and Martin (1975)
P. elegans	56.8-69.8	17.6-23.9	0.03-0.1	15.6-20.7		Baffin Island	Percy and Fife (1981)
Sagitta sp.	69.6	1.9					Krey (1950)
Sagitta sp.	52.5	19.0	11.6	16.9		Sea of Okhotsk	Zenkevitch (1963)
Sagitta sp.			0.3		3.6	Sargasso Sea	Beers (1966)
S. gazellae	15.9-20.7	0.3-6.4	0.3-0.4	36.4-54.7	3.9	Weddell & Scotia Sea	Donnelly et al (1994)
S. hispida	52.9	17.0	3.5	9.3		Biscayne Bay, Miami	Reeve et al (1970)
S. marri	30.8	10.9	0.5	13.5	4.1	Scotia Sea	Donnelly et al (1994)
Eukrohnia hamata	39.1	32.1	1.5	18.3		Korsfjorden, Norway	Båmstedt (1978)
E. hamata	25.6-29.9	4.4-0.5		20.5-45.8	4.1	Weddell & Scotia Sea	Donnelly et al (1994)

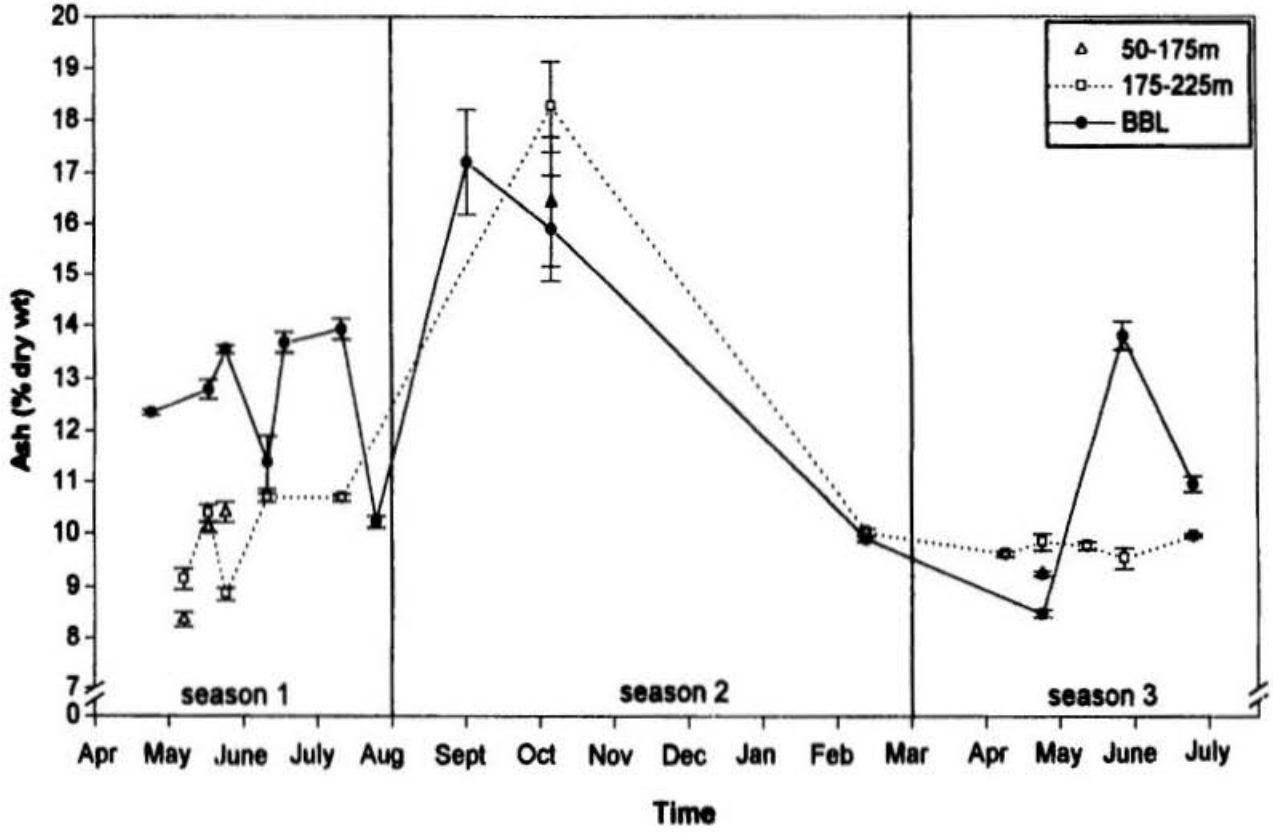

Fig. 4.1 Level of ash in small *P. elegans* in Conception Bay, Newfoundland from 1997 to 1998 (Season 1 indicates spring-summer of 1997. Season 2 indicates fall-winter of 1997. Season 3 indicates spring of 1998. The points denote means and lines denote standard deviations)

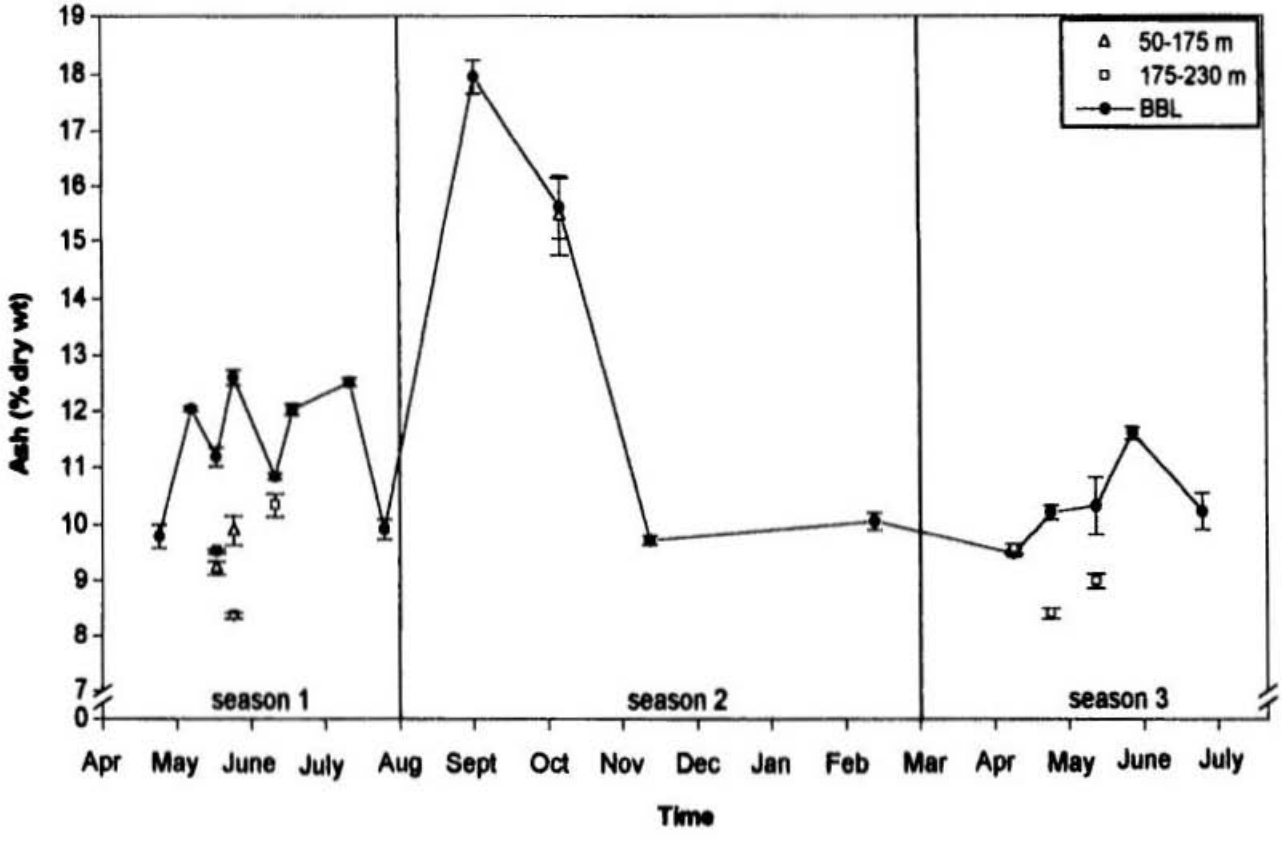

Fig. 4.2 Level of ash in large *P. elegans* in Conception Bay, Newfoundland from 1997 to 1998 (Season 1 indicates spring-summer of 1997. Season 2 indicates fall-winter of 1997. Season 3 indicates spring of 1998. The points denote means and lines denote standard deviations.)

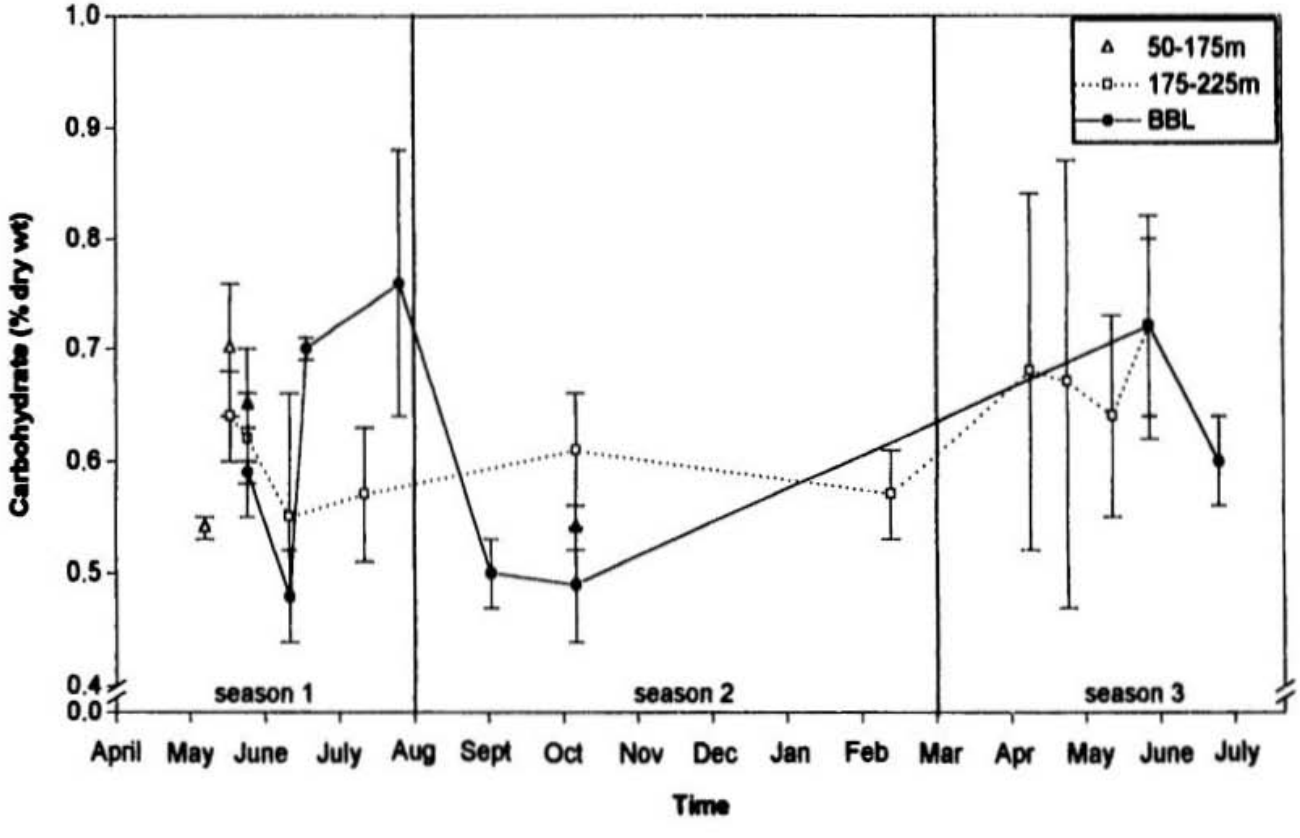

Fig. 4.3 Level of carbohydrate in small *P. elegans* in Conception Bay, Newfoundland from 1997 to 1998 (Season 1 indicates spring-summer of 1997. Season 2 indicates fall-winter of 1997. Season 3 indicates spring of 1998. The points denote means and lines denote standard deviations.)

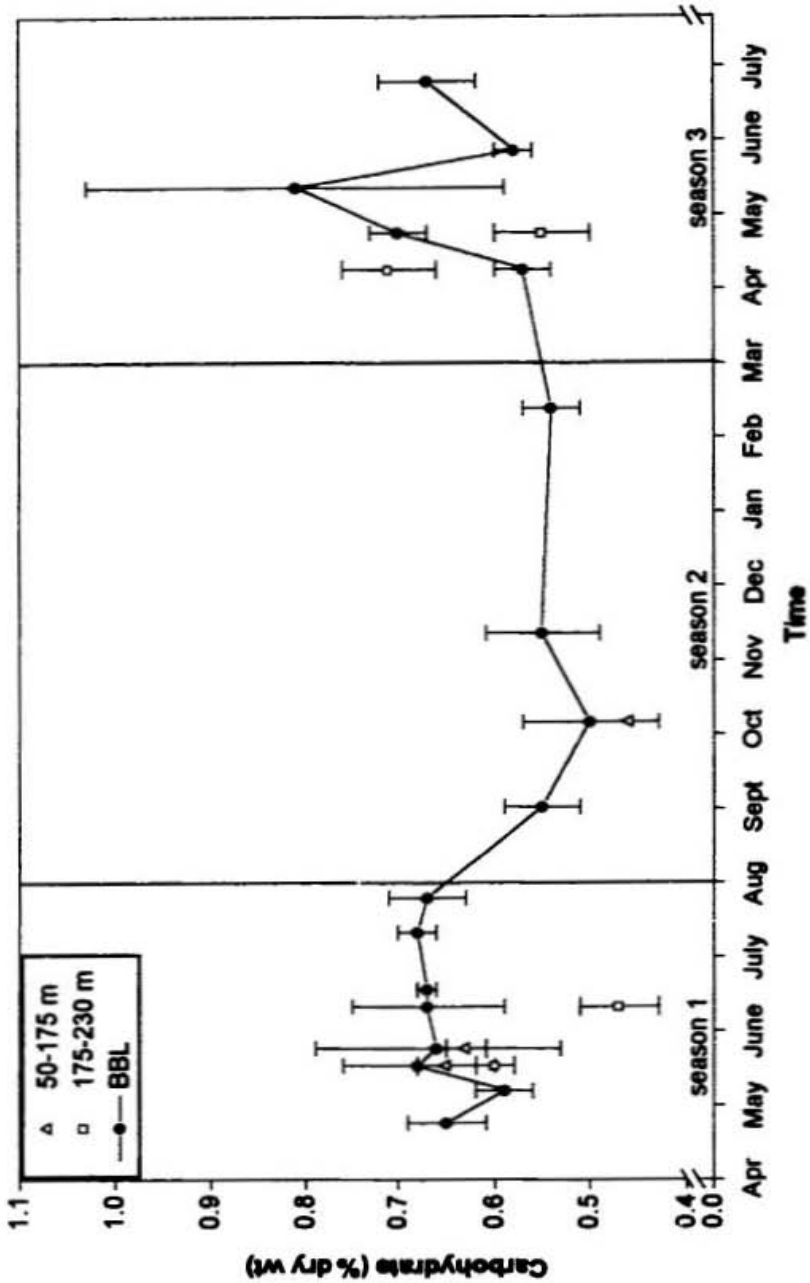

Fig. 4.4 Level of carbohydrate in large *P. elegans* in Conception Bay, Newfoundland from 1997 to 1998 (Season 1 indicates spring-summer of 1997. Season 2 indicates fall-winter of 1997. Season 3 indicates spring of 1998. The points denote means and lines denote standard deviations.)

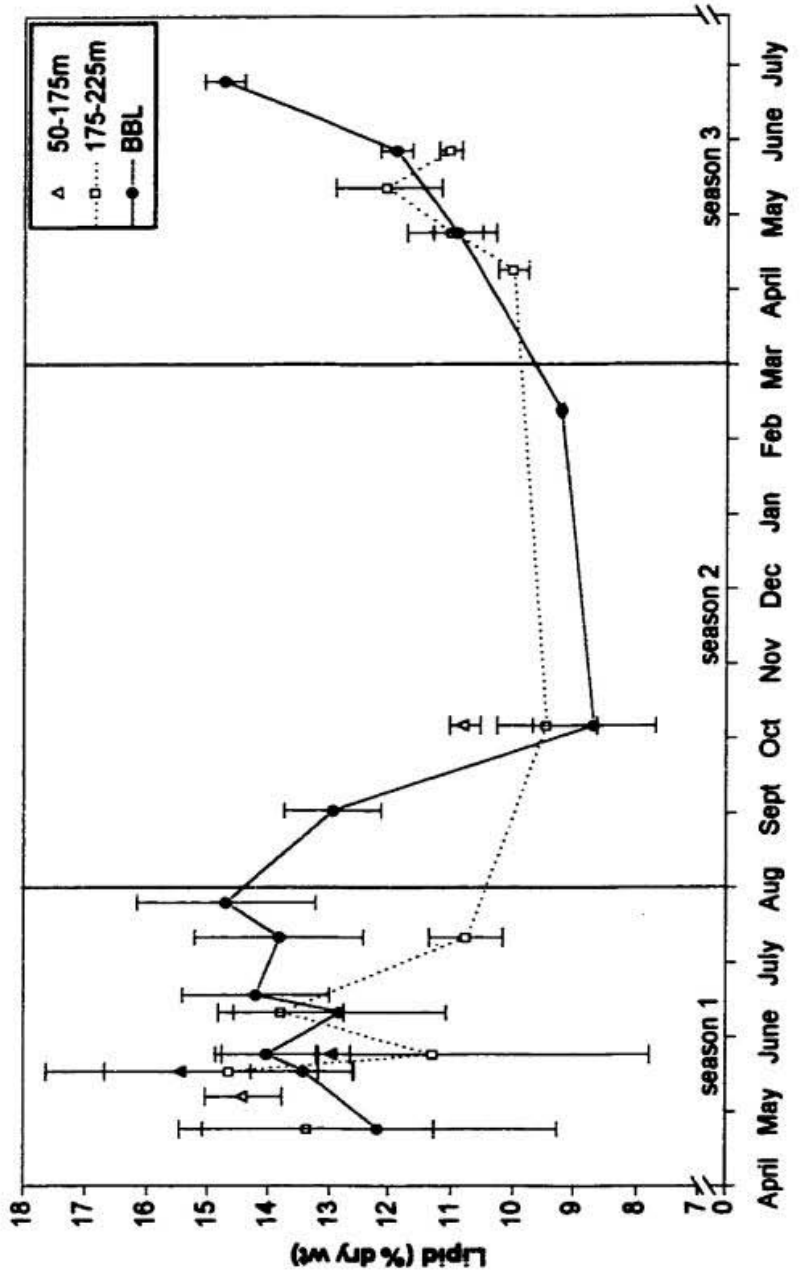

Fig. 4.5 Level of lipid in small *P. elegans* in Conception Bay, Newfoundland from 1997 to 1998 (Season 1 indicates spring-summer of 1997. Season 2 indicates fall-winter of 1997. Season 3 indicates spring of 1998. The points denote means and lines denote standard deviations.)

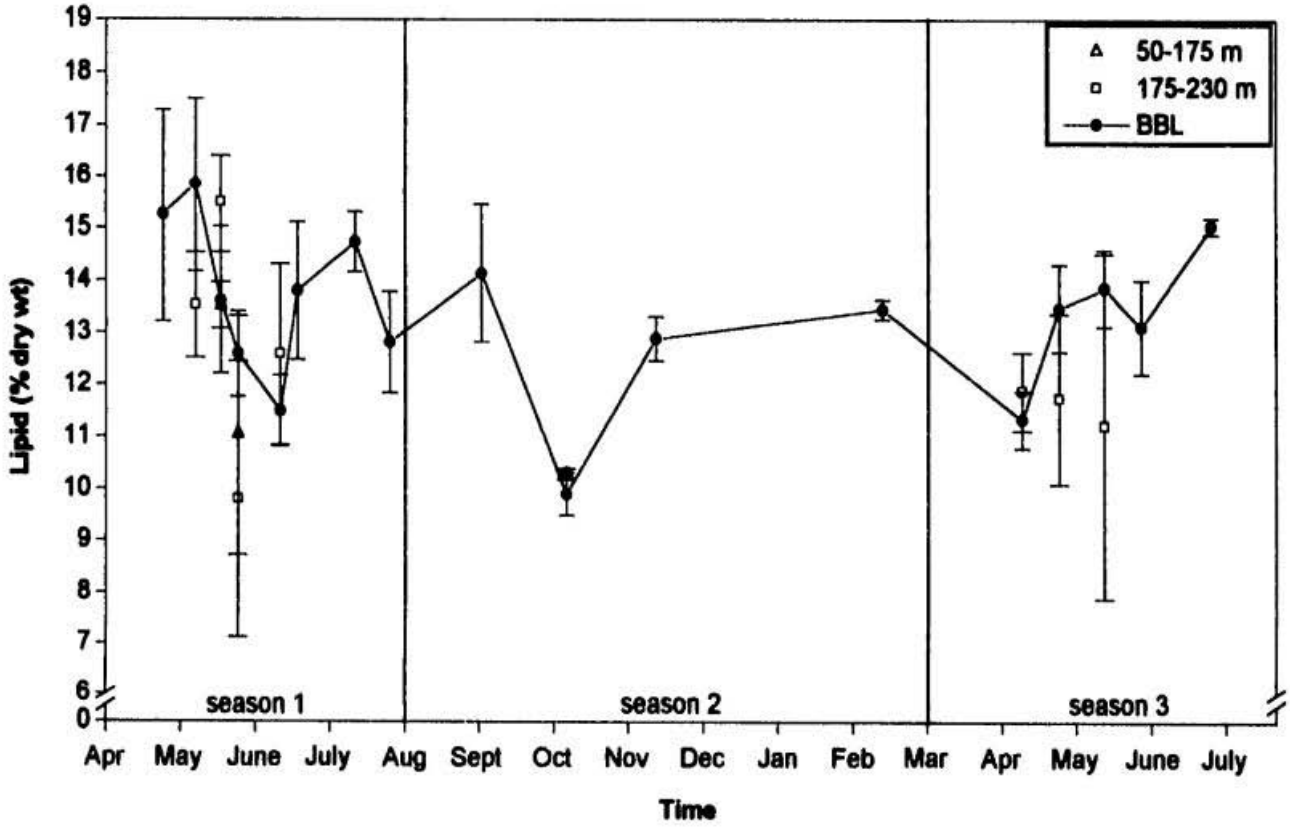

Fig. 4.6 Level of lipid in large *P. elegans* in Conception Bay, Newfoundland from 1997 to 1998 (Season 1 indicates spring-summer of 1997. Season 2 indicates fall-winter of 1997. Season 3 indicates spring of 1998. The points denote means and lines denote standard deviations.)

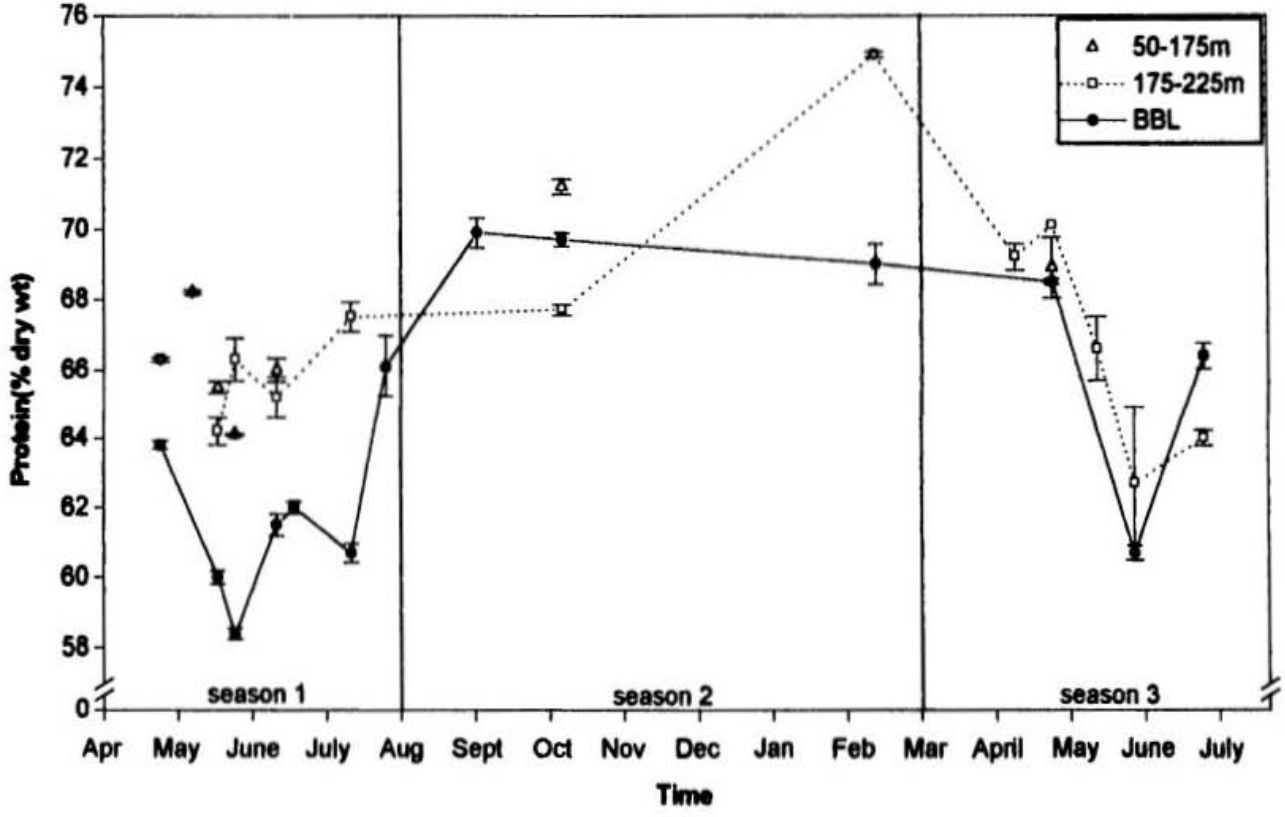

Fig. 4.7 Level of protein in small *P. elegans* in Conception Bay, Newfoundland from 1997 to 1998 (Season 1 indicates spring-summer of 1997. Season 2 indicates fall-winter of 1997. Season 3 indicates spring of 1998. The points denote means and lines denote standard deviations.)

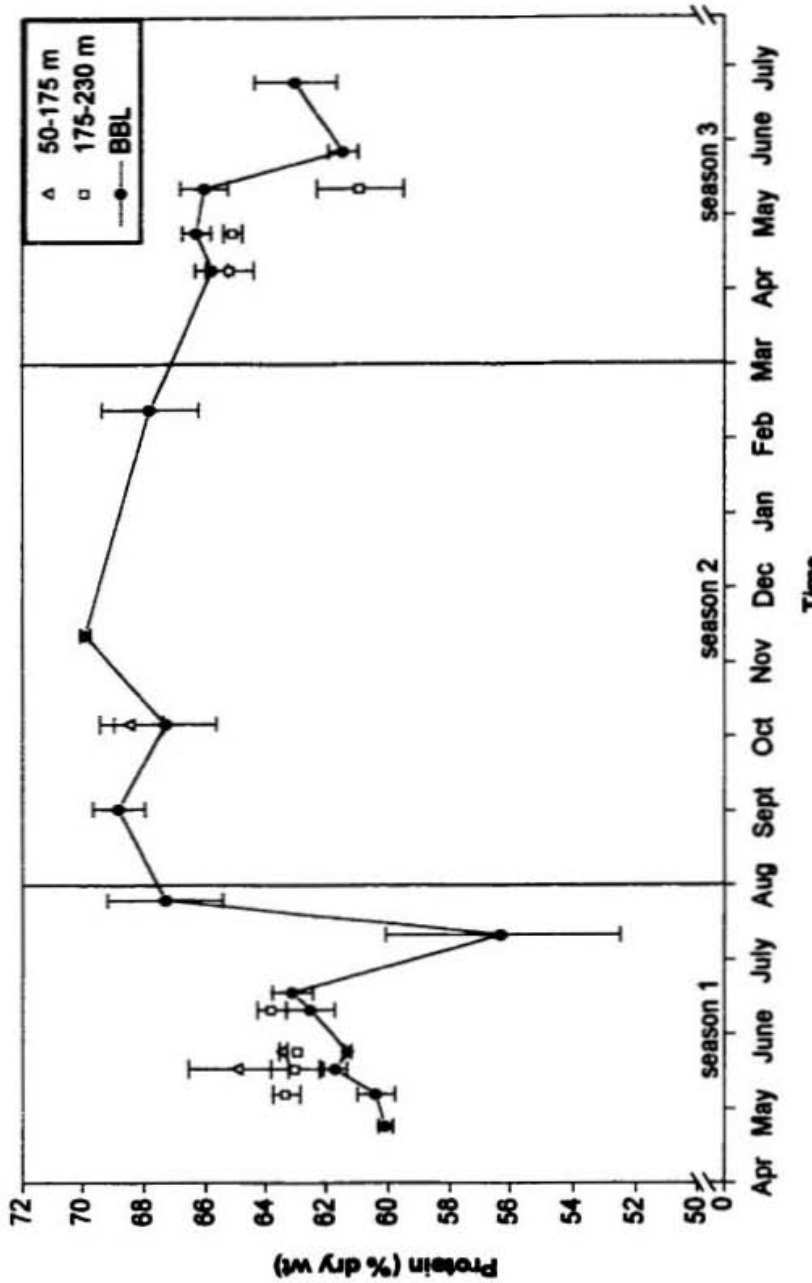

Fig. 4.8 Level of protein in large *P. elegans* in Conception Bay, Newfoundland from 1997 to 1998 (Season 1 indicates spring-summer of 1997. Season 2 indicates fall-winter of 1997. Season 3 indicates spring of 1998. The points denote means and lines denote standard deviations.)

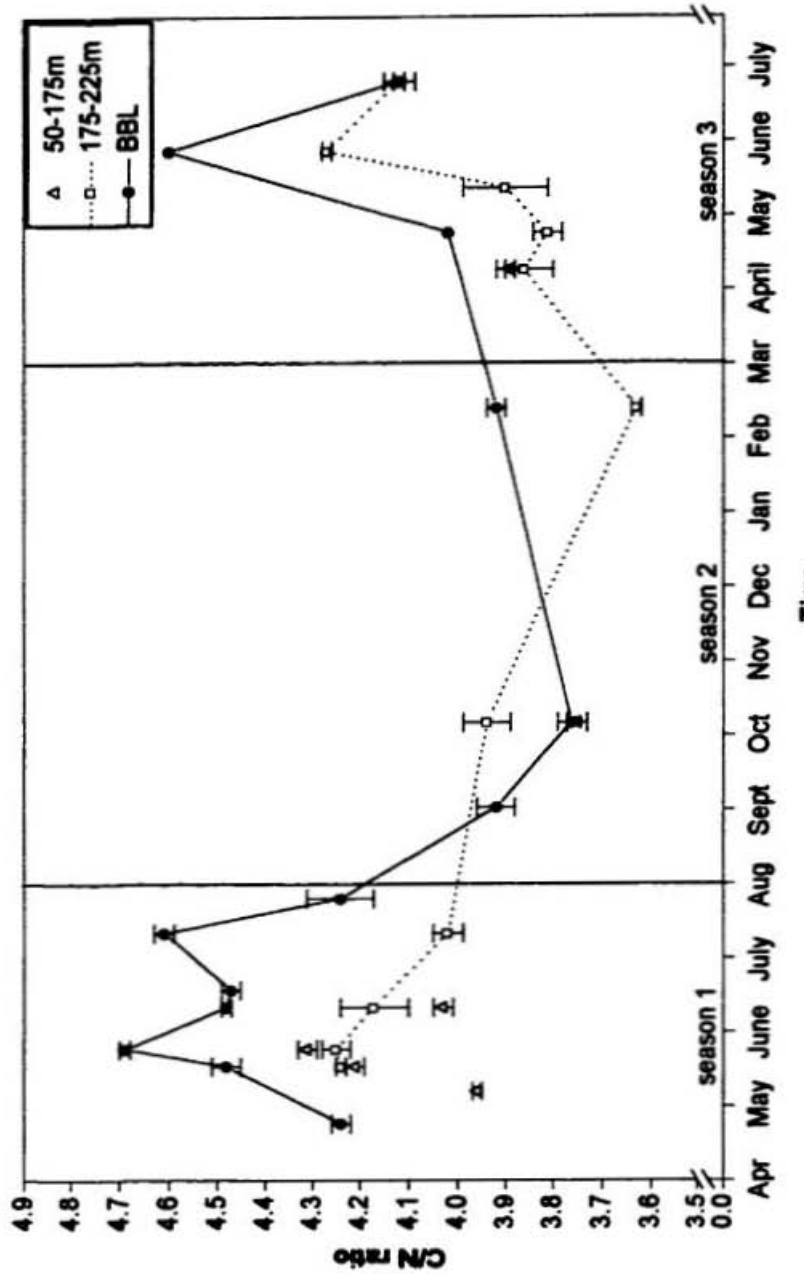

Fig. 4.9 C/N ratio of small *P. elegans* in Conception Bay, Newfoundland from 1997 to 1998 (Season 1 indicates spring-summer of 1997. Season 2 indicates fall-winter of 1997. Season 3 indicates spring of 1998. The points denote means and lines denote standard deviations.)

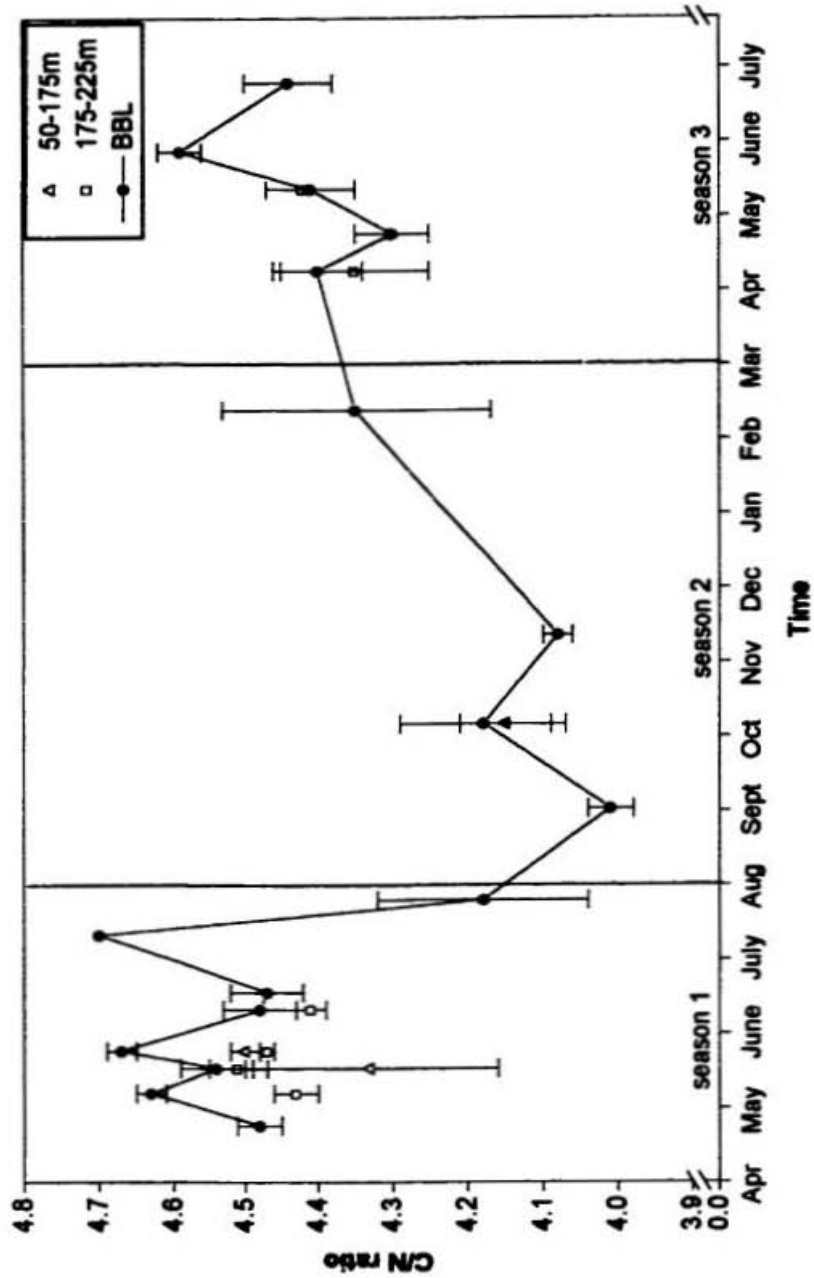

Fig. 4.10 C/N ratio of large *P. elegans* in Conception Bay, Newfoundland from 1997 to 1998 (Season 1 indicates spring -summer of 1997. Season 2 indicates fall-winter of 1997. Season 3 indicates spring of 1998. The points denote means and lines denote standard deviations.)

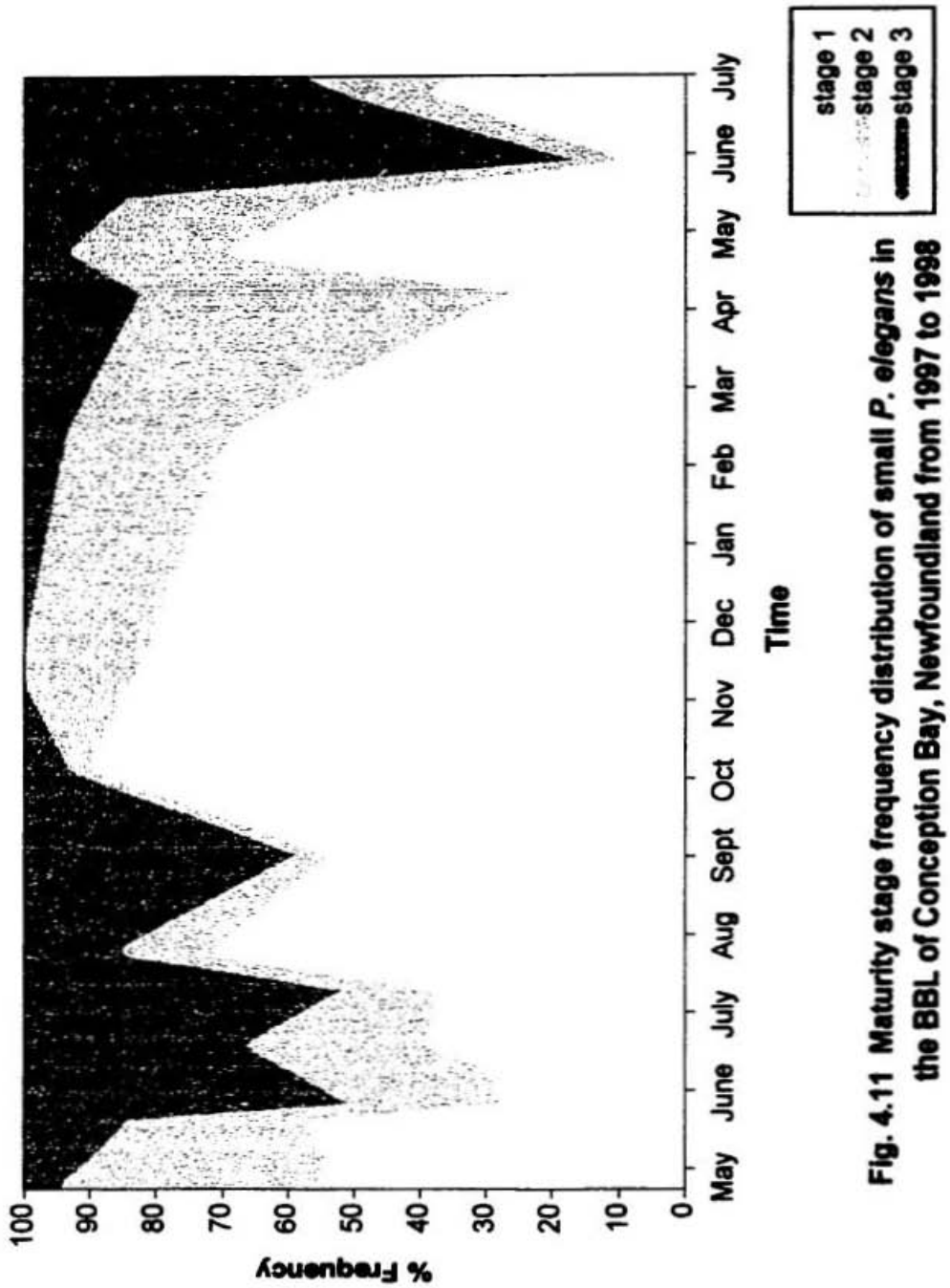

Fig. 4.11 Maturity stage frequency distribution of small *P. elegans* in the BBL of Conception Bay, Newfoundland from 1997 to 1998

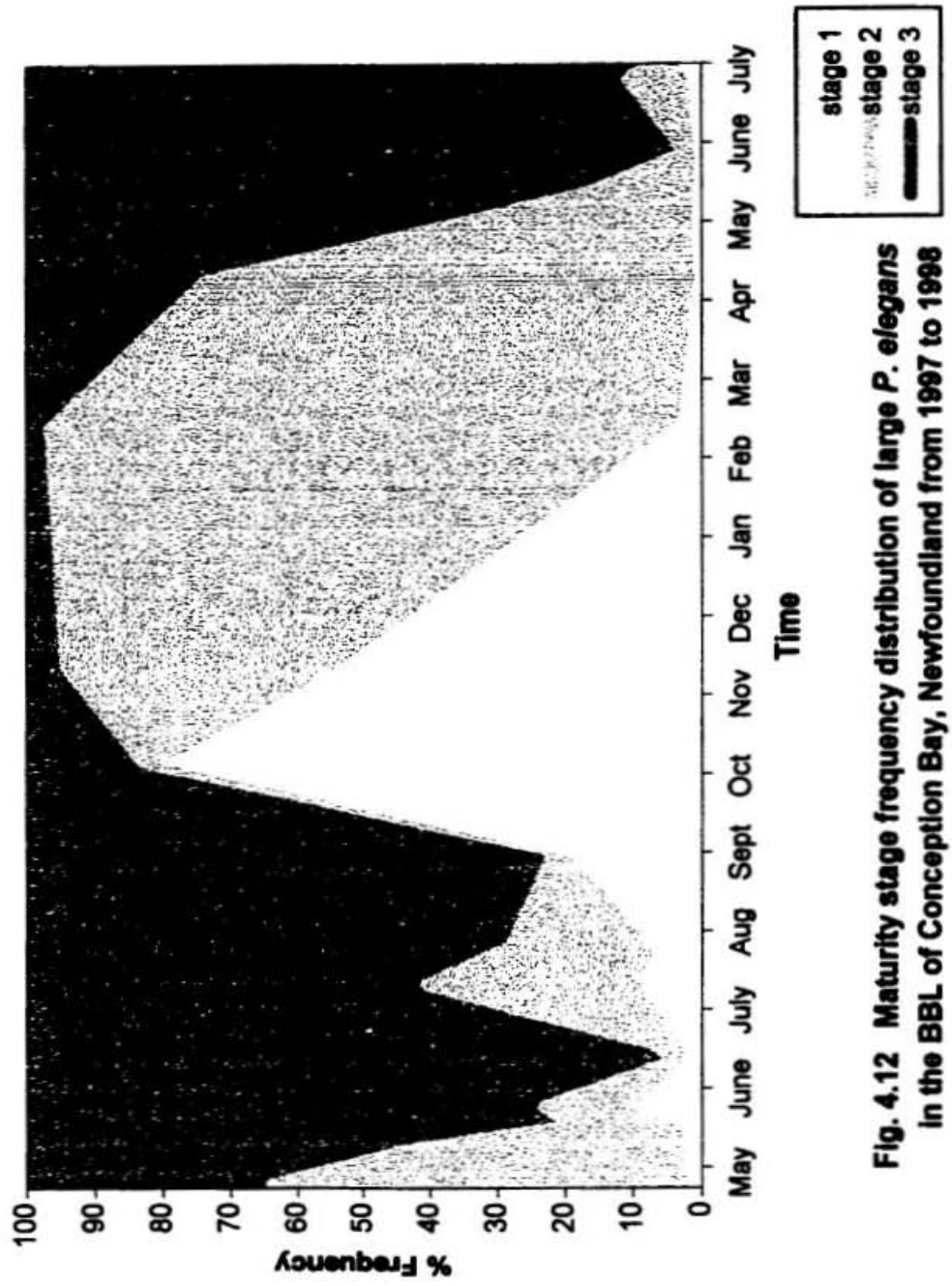

Fig. 4.12 Maturity stage frequency distribution of large *P. elegans* in the BBL of Conception Bay, Newfoundland from 1997 to 1998

General Discussion and Conclusion

Seasonal biochemical composition of *P. elegans* in relation to population dynamics

The study of the population dynamics and feeding of *Parasagitta elegans* was necessary to understand the seasonal variation in biochemical composition, which reflected changes in reproductive and feeding states. Ash level increased after the animals spawned and lost organic material. Lipid and carbohydrate levels increased but protein level decreased after the animals matured. Among all the biochemical components, lipid most clearly reflected the reproductive status of the animals. The changes in biochemical levels should not be interpreted as changes in the actual amount but as changes in the relative proportion of biochemical constituents.

The results from the population dynamics study revealed interesting issues about the vertical distribution and life cycle of *P. elegans*. Residence of large animals in the BBL of Conception Bay suggests that other studies, which did not include chaetognaths in the BBL, underestimated total abundance and biomass. Why are mature animals concentrated in the BBL during day and night? They may be concentrated in the BBL because they are more dense than immature animals or they may enhance copulation by aggregating themselves.

Cohort analysis clearly indicated that *P. elegans* is semelparous. Cohort 2 matured in the spring and summer of 1997 and spawned in the fall then continued to grow and mature until the following spring. The few number of cohorts and long generation time of *P. elegans* in the cold water environment of Conception Bay made the study of population

dynamics relatively easy. However, it should be noted that differentiation among the cohorts was at times subjective. After the Gaussian curve was applied to each group of size modes, the cohorts were numbered subjectively but differentiation among the cohorts was somewhat difficult when the size groups were overlapping during fall and winter.

Seasonal biochemical composition in relation to feeding

To observe the effect of feeding on the biochemical composition of *P. elegans*, other factors such as body size and maturity status must be controlled. Fortunately, the body size and maturity status of animals in the spring of 1997 and 1998 were similar. Higher protein and lower ash levels in the spring of 1998 can be explained by the fact that the proportion of *Calanus* spp. in the diet was significantly higher and the abundance of *Calanus* spp. increased earlier than in 1997. Controlled laboratory experiments will be necessary to test whether biochemical levels depend on the proportion of *Calanus* spp. in the diet.

Herbivorous zooplankton accumulate lipid for energy storage during phytoplankton blooms and utilize it when food is limited, but carnivorous *P. elegans* does not store energy because food is available throughout the entire year. However, this study suggests that *P. elegans* does respond to increasing food availability. *P. elegans* matured in the spring of 1997 and 1998 when it fed most frequently and when the abundance of *Calanus* spp. was high. Understanding the relationship between the population dynamics and trophodynamics of *P. elegans* will enable me to predict the seasonal pattern of reproduction and biochemical levels in the future.

Data from the feeding study should be interpreted with caution because of the confounding effect of cod end defecation, resulting in underestimation of NPC. Depth comparison of NPC was not appropriate since the tow times for the water column and BBL samples differed. Furthermore, the nets with large mesh size (500 μm) excluded small copepods which may have been consumed by *P. elegans*. However, the copepod data were standardized as the standard normal deviates to observe seasonal variations in prey availability.

Therefore, the main hypotheses of the thesis were successfully tested. The biochemical composition of *Parasagitta elegans* in Conception Bay, Newfoundland, changes seasonally and depends on the stage of maturity and feeding state. The BBL is well suited for this study because animals of all maturity stages are present. *P. elegans* in the BBL grows continuously, matures during spring and spawns during fall and winter. Maximum NPCs are observed in the spring and the composition and availability of prey change seasonally. In general, this study indicates a clear seasonal pattern in the biochemical composition of chaetognaths in a cold water environment.

References

Alvarez-Cadena, J. N. 1992. Feeding habitats, gonadic stages and size frequency distribution of *Sagitta setosa* J. Muller to the east of the Isle of Man, North Irish Sea. An. Inst. Cienc. del Mar Limnol. Univ. Nal. Auton. Mexico. 19(2): 215-222

Alvarez-Cadena, J. N. 1993. Feeding of the Chaetognath *Sagitta elegans* Verrill. Estuarine, Coastal and Shelf Science. 36:195-206

Alvariño, A. 1965. Chaetognaths. Oceanography and Marine Biology, Annual Review. 3:115-94

Alvariño, A. 1983. Reproductive Biology of Invertebrates. 2. Spermatogenesis and sperm function. Wiley, London

Angel, M. V. and A. D. Baker. 1982. Vertical distribution of the standing crop of zooplankton and micronekton at three stations in the Northeast Atlantic. Biological Oceanography 2: 1-30

Baier, C. T., J. E. Purcell. 1997. Effects of sampling and preservation on apparent feeding by chaetognaths. Mar. Ecol. Prog. Ser. 146: 37-42

Bailey, T. G., M. J. Youngbluth, G. P. Owen. 1995. Chemical composition and metabolic rates of gelatinous zooplankton from midwater and benthic boundary layer environments off Cape Hatteras, North Carolina, USA. Mar. Ecol. Prog. Ser. 122:121-134

Bajkov, A. D. 1935. How to estimate the daily food consumption of fish under natural conditions. Trans. Am. Fish. Soc. 65:288-289

Båmstedt, U. 1978. Studies on the deep-water pelagic community of Korsfjorden, Western Norway: seasonal variation in weight and biochemical composition of *Chiridius armatus* (Copepoda), *Boreomysis arctica* (Mysidacea), and *Eukrohnia hamata* (Chaetognatha) in relation to their biology. Sarsia 63:145-154

Båmstedt, U. 1981. Water and organic content of boreal macrozooplankton and their significance for the energy content. Sarsia 66:59-66

Barnes, H. and J. R. Heath. 1966. The extraction of glycogen from marine invertebrate tissues. Helgolander wiss. Meeresunters. 13:115-117

Beers, J. R. 1976. Studies on the chemical composition of the major zooplankton groups in the Sargasso Sea off Bermuda. Limnol. Oceanog. 11:520-8

Bligh, E. G. and W. J. Dyer. 1959. A rapid method of total lipid extraction and purification. Can. J. Biochem. Physiol. 37:911-917

Boltovskoy, D. 1975. Some biometrical, ecological, morphological and distributional aspects of Chaetognatha. Hydrobiologia 46:515-34

Bone, Q., H. Kapp and A.C. Pierrot-Bults. 1991. The Biology of Chaetognaths. 173pp. Oxford University Press. Oxford.

Bushing, M. and Feigenbaum, D. and R. C. Maris. 1984. Feeding by an expatriate population of *Sagitta enflata*. Bulletin Marine Science. 34:240-243

Cassie, R. M. 1968. Sample design. *In* Zooplankton sampling. Unesco, Monogra. oceanographic methodology 105-121

Cheney, J. 1985. Spatial and temporal abundance patterns of oceanic chaetognaths in the western North Atlantic I. Hydrographic and seasonal abundance patterns. Deep-Sea Res. 32:1041-59

Childress, J. J. and M. Nygaard. 1974. Chemical composition and buoyancy of midwater crustaceans as function of depth of occurrence off southern California. Mar. Biol. 27:225-38

Conway, D. V. P., and R. Williams. 1986. Seasonal population structure, vertical distribution and migration of the chaetognath *Sagitta elegans* in the Celtic Sea. Mar. Biol. 93:377-87

Dallot, S. 1968. Observations préliminaires sur la reproduction en élevage du chaetognathe planctonique *Sagitta setosa* Müller. Rapports et procèsverbaux des Réunions de la Commission internationale pour l'Exploration scientifique de la Mer Méditerranée. 19:521-3

Darwin, C. 1844. Observations on the structure and propagation of the genus *Sagitta*. Annals and Magazine of Natural History. London. 13:1-6

David, P. M. 1958. The distribution of the Chaetognatha of the Southern Ocean. Discovery Reports 29:199-228

Davis, C. C. 1982. A preliminary quantitative study of the zooplankton from Conception Bay, insular Newfoundland, Canada. Int. Revue. ges. Hydrobiol. 67:713-747

Davis, C. C. 1986. A comparison of the zooplankton in two Newfoundland bays with differing influences from major currents. Int. Revue. ges. Hydrobiol. 71:11-47

Donnelly, J., J. J. Torres, T. L. Hopkins. 1994. Chemical composition of antarctic zooplankton during austral fall and winter. Polar Biol. 14:171-183

Drits, A. V. 1981. Some patterns of feeding of *Sagitta enflata*. Oceanology. 21:624-8

Dubois, M., K. A. Gilles, J. K. Hamilton, P. A. Rebers and F. Smith. 1956. Colorimetric method for determination of sugars and related substances. Analyt. Chem. 28:350-356

Dunbar, M. J. 1962. The life cycle of *Sagitta elegans* in arctic and subarctic seas, and the modifying effects of hydrographic differences in the environment. Can. J. Mar. Ecol. 20:76-91

Falkenhaug, T. 1991. Prey composition and feeding rate of *Sagitta elegans* var. *arctica* (Chaetognatha) in the Barents Sea in early summer. Polar Res. 10(2); 487-506

Falk-Petersen, S. 1981. Ecological investigation on the zooplankton community of Balsfjorden, northern Norway: seasonal changes in body weight and the main biochemical composition of *Thysanoessa inermis* (Kroyer), *T. Raschii* (M. Sars), and *Meganyctiphanes norvegica* (M. Sars) in relation to environmental factors. J. Exp. Mar. Biol. 49:103-120

Feigenbaum, D. 1979. Daily ration and specific daily ration of the chaetognath *Sagitta enflata*. Mar. Biol. 54:75-82

Feigenbaum, D. 1982. Feeding by the chaetognath, *Sagitta elegans*, at low temperatures in Vineyard Sound, Massachusetts. Limnol. Oceanog. 27:699-706

Feigenbaum, D. L. and R. C. Maris. 1984. Feeding in the Chaetognatha. Ann. Rev. of Oceanog. and Mar. Biol. 22:343-92

Furnestin, M. L. 1953. Chaetognaths récoltés en méditerranée par le 'Président Théodore Tissier'. Bulletin de la Station d'Aquiculture et de Pêche de Castiglione, 4:275-317

Gardner, A. C. 1931. The validity of single hauls of the International net in the study of the distribution of the plankton. J. Mar. Biol. Assoc. U.K. 17:449-472

Ghirardelli, E. 1951. Cycli di maturità sessuale nelle gonadi di *Sagitta inflata* Grassi del Golfo di Napoli. Bollettina di Zoologia 18:146-62

Ghirardellli, E. 1968. Some aspects of the biology of chaetognaths. Adv. Mar. Biol. 6:271-375

Gnaiger, E. and G. Bitterlich. 1984. Proximate biochemical composition and caloric content calculated from elemental CHN analysis: a stoichiometric concept. Oecologia 62:289-298

Gorsky, G., S. Dallot, J. Sadou, R. Fenaux, C. Carre and I. Palazzoli. 1988. C and N composition of some northwestern Mediterranean zooplankton and micronekton species J. Exp. Mar. Biol. Ecol. 124:134-144

Hesthagen, I. H. and B. Gjermundsen. 1977. The representativity of sampling the hyperbenthic region by means of Beyer's epibenthic closing net. Meeresforsch 26:1-10

Hoeger, U. 1983. Biochemical composition of ctenophores. J. Exp. Mar. Biol. Ecol. 72:251-261

Hyman, L. H. 1959. The invertebrates: smaller coelomate groups. Vol 5. McGraw-Hill, New York.

Ikeda, T. 1972. Chemical composition and nutrition of zooplankton in the Bering Sea Biological Oceanography of the Northern North Pacific Ocean. Ed. Takenouti et al. Research Institute of North Pacific Fisheries, Faculty of Fisheries, Hokkaido University.

Ikeda, T. and H. R. Skjoldal. 1989. Metabolism and elemental composition of zooplankton from the Barents Sea during early Arctic summer. Mar. Biol. 100:173-183

Jakobsen, T. 1971. On the biology of *Sagitta elegans* Verrill and *Sagitta setosa* J. Müller in inner Oslofjord. Norwegian J. Zool. 19:201-25

Jeffries, H. P. 1979. Biochemical correlates of seasonal change in marine communities Am. Nat. 113(5): 643-658

Kehayias, G., J. Lykakis and N. Fragopoulu. 1996. The diets of the chaetognaths *Sagitta enflata, S. serratodentata atlantica* and *S. bipunctata* at different seasons in Eastern Mediterranean coastal waters. ICES J. Mar. Sci. 53:837-846

Kimmerer, W. J. 1984. Selective predation and its impact on prey of *Sagitta enflata* (Chaetognatha). Mar. Ecol. Prog. Ser. 15:55-62

King, K. R. 1979. The life history and vertical distribution of the chaetognath *Sagitta elegans* in Dabob Bay, Washington. J. Plank. Res. 1:153-67

Koszteyn, J. 1983. Morphological variability and individual development cycle of *Sagitta enflata* (Grassi) 1881 as compared with the shelf-water dynamics of north-west Africa. Oceanologia 16:53-73

Kotori, M. 1972. Vertical distribution of chaetognaths in the northern North Pacific Ocean and Bering Sea. *In* Biological Oceanography of the northern North Pacific Ocean. Ed. Takenouchi A. Y. Idemitsu Shoten.

Kramp, P. L. 1939. The Godthaab Expedition 1928; Chaetognatha. Meddelelsev om Grönland. 80:1-40

Kremer, P., M. F. Canino, R. W. Gilmer. 1986. Metabolism of epipelagic tropical ctenophores. Mar. Biol. 90:403-412

Kuhl, W. 1938. Chaetognatha. *In* Bronn's Klassen und Ordnungen des Tierreichs. Band 4, Vermes, Abteilung 4, Buch 2, Teil

Lalli, C. M. and T. R. Parsons. 1993. Biological Oceanography: An Introduction. Pergamon Press, New York.

Larson, R. J. 1986. Water content, organic content, and carbon and nitrogen composition of medusae from the northeast Pacific. J. Exp. Mar. Biol. Ecol. 99: 107-120

Lee, R. F. 1974. Lipid composition of the copepod *Calanus hyperboreus* from the Arctic Ocean. Changes with depth and season. Mar. Biol. 26:313-318

Littlepage, J.L. 1964. Seasonal variation in lipid content of two antarctic marine crustacea. *In* Biologie Antarctique, Ed. Carrick, R., M. Holdgate and J. Prevost, Paris, Hermann, pp. 463-470

Mahoney, E. M. and R. G. Buggeln. 1983. Seasonal variations in the concentration of *Oikopleura* spp. (Tunicata: Appendicularia) in Conception Bay, Newfoundland. Can. Tech. Rep. Fish. Aquat. Sci.. 1155:1-12

Marazzo, A., C. F. Machado and C. S. R. Nogueira. 1997. Notes on feeding of Chaetognatha in Guanabara Bay, Brazil. J. Plank. Res. 19(7):819-828

Mayzard, P. and J.-L. M. Martin. 1975. Some aspects of the biochemical and mineral composition of marine plankton. J. Exp. Mar. Biol. Ecol. 17:297-311

McLaren, I. A. 1963. Effects of temperature on the growth of zooplankton, and the adaptive value of vertical migration. J. Fish. Res. Bd. Can. 20:685-727

McLaren, I. A. 1966. Adaptive significance of large size and long life of the chaetognath *Sagitta elegans* in the arctic. Ecology 47:852-5

McLaren, I. A. 1969. Population and production ecology of zooplankton in Ogac Lake, a landlocked fjord on Baffin Island. J. Fish. Res. Bd. Can. 26:1485-559

Michael, E. L. 1919. Report on the Chaetognatha of the Albatross expedition to the Phillippines. Bull. U.S. Nat. Mus. 100:235-77

Mironov, G. N. 1960. The food of plankton predators. 2. Food of *Sagitta*. Trudy sevastopol'sskoi Biologicheskoi Stantsii 13:78-88

Moss, M. K. C. 1994. An allometric study of the chaetognath *Sagitta elegans* at Resolute Passage and Bedford Basin. MS thesis. Dalhousie University, Nova Scotia, Canada

Nagasawa, S and R. Marumo. 1972. Feeding of a pelagic chaetognath *Sagitta nagae* Alvariño in Suruga Bay, Central Japan. J. Oceanog. Soc. Jap. 28:181-6

Nagasawa, S. 1984. Laboratory feeding and egg production in the chaetognath *Sagitta crassa* Tokioka. J. Exp. Mar. Biol. Ecol. 76:51-65

Nagasawa, S. 1987. Sperm emission in the chaetognath *Sagitta crassa*. J. Plank. Res. 9:755-9

Ohman, M. D. 1986. Predator-limited population growth of the copepod *Pseudocalanus* sp. J. Plank. Res. 8:673-713

Omori, M. 1969. Weight and chemical composition of some important oceanic zooplankton in the North Pacific Ocean. Mar. Biol. 3:4-10

Øresland, V. 1985. Temporal size and maturity-stage distribution of *Sagitta elegans* and occurrence of other chaetognath species in Gullmarsfjorden, Sweden. Sarsia 70:95-101

Øresland, V. 1987. Feeding of the chaetognaths *Sagitta elegans* and *Sagitta setosa* at different seasons in Gullmarsfjorden. Sweden. Mar. Ecol. Prog. Ser. 39:69-79

Owre, H. B. 1960. Plankton of the Florida Current. Part VI. The Chaetognatha. Bull. Mar. Sci. Gulf. Caribb. 19:255-322

Pearre, S. Jr. 1970. Light responses and feeding behavior of *Sagitta elegans* Verrill. Ph.D. thesis, Dalhousie Univ., Canada

Pearre, S. Jr. 1973. Vertical migration and feeding of *Sagitta elegans* Verrill. Ecology 54:300-14

Pearre S. Jr. 1981. Feeding by Chaetognatha: Energy balance and importance of various components of the diet of *Sagitta elegans*. Mar. Ecol. Prog. Ser. 5:45-54

Pearre, S. Jr. 1982. Feeding by Chaetognatha: Aspects of inter-and intra-specific predation. Mar. Ecol. Prog. Ser. 7:33-45

Pearre, S. Jr. 1991. The Biology of Chaetognaths. Oxford University Press, Oxford

Percy J. A. and F. J. Fife. 1981. The biochemical composition and energy content of arctic marine macrozooplankton Arctic 34(4); 307-313

Rakusa-Suszczewski, S. 1969. The food and feeding habits of chaetognaths in the seas around the British Isles. Pol. Arch. Hydrobiol. 13:213-32

Reeve, M. R. 1970a. Marine food chains. Oliver and Boyd, Edinburgh

Reeve, M. R., J. E. G. Raymont and R. K. B. Raymont. 1970b. Seasonal biochemical composition and energy sources of *Sagitta hispida* Mar. Biol. 6: 357-364

Reeve, M. R., and M. A. Walter. 1972. Conditions of culture, food-size selection and the effects of temperature and salinity on growth rate and generation time in *Sagitta hispida* Conant. J. Exp. Mar. Biol. Ecol. 9:191-200

Reeve, M. R. 1980. Comparative experimental studies on the feeding of chaetognaths and ctenophores. J. Plankton Res. 2(4); 381-393

Russell, F. S. 1932. On the biology of *Sagitta*. The breeding and growth of *Sagitta elegans* Verrill in the Plymouth area. J. Mar. Biol. Assoc. U.K. 18:131-46

Sameoto, D. D. 1971. Life history, ecological production, and an empirical mathematical model of the population of *Sagitta elegans* in St. Margaret's Bay, Nova Scotia. J. Fish. Res. Bd. Can. 29:987-96

Sameoto, D. D. 1973. Annual life cycle and production of the chaetognath *Sagitta elegans* in Bedford Basin, Nova Scotia. J. Fish. Res. Bd. Can. 30:333-44

Sameoto, D. D. 1987. Vertical distribution and ecological significance of chaetognaths in the arctic environment of Baffin Bay. Polar Biol. 7:317-28

Sands, N. J. 1977. Quantitative studies of the chaetognaths from Korsfjorden, Norway. MS thesis, Univ. Washington, Seattle, 102 pp.

Smith, K. L. 1982. Zooplankton of a bathyal benthic boundary layer: *In situ* rates of oxygen consumption and ammonium excretion. Limnol. Oceanog. 27(3): 461-471

Stickney, D. G. and J. J. Torres. 1989. Proximate composition and energy content of mesopelagic fishes from the eastern Gulf of Mexico. Mar. Biol. 103: 13-24

Stone, J. H. 1966. The distribution and fecundity of *Sagitta enflata* Grassi in the Agulhas Current. J. Anim. Physiol. 35:533-41

Strathmann, M. F., and G. L. Shinn. 1987. Reproduction and development of marine invertebrates of the northern Pacific coast. University of Washington Press, Seattle

Sullivan, B.K. 1977. Vertical distribution and feeding of two species of chaetognaths at Weather Station P. Ph.D. thesis, University of Hawaii

Sullivan, B. K. 1980. *In situ* feeding behaviour of *Sagitta elegans* and *Eukrohnia hamata* (Chaetognatha) in relation to the vertical distribution and abundance of prey at Ocean Station 'P'. Liminol. Oceanog. 25:317-326

Szyper, J. P. 1978. Feeding rate of the chaetognath *Sagitta enflata* in nature. Estuar. and Coast. Mar. Sci. 7:567-75

Taggart , C. T. and W. C. Leggett. 1987. Wind-forced hydrodynamics and their interaction with larval fish and plankton abundance: a time series analysis of physical-biological data. Can. J. Fish. Aquat. Sci. 44:438-451

Terazaki, M. and C. B. Miller. 1986. Life history and vertical distribution of pelagic chaetognaths at Ocean Station P in the subarctic Pacific. Deep-Sea Res. 33: 323-337

Terazaki, M. 1993. Deep-sea adaptation of the epipelagic chaetognath *Sagitta elegans* in the Japan Sea. Mar. Ecol. Prog. Ser. 98: 79-88

Thompson, J. 1947. The Chaetognatha of south-eastern Australia. Bull. CSIR. Melbourne. 222:1-43

Thuesen, E.V and Bieri, R. 1987. Tooth structure and buccal pores in the chaetognath *Flaccisagitta hexaptera* and their relation to the capture of fish larvae and copepods. Can. J. Zool. 65:181-7

Thuesen, E. V., S. Nagasawa, R. Bieri and T. Nemoto. 1988. Transvestibular pores of chaetognaths with comments on the function and nomenclature of the vestibular anatomy. Bull. Plank. Soc. Jap. 35:133-141

Thuesen E. V. and J. J. Childress. 1993. Enzymatic activities and metabolic rates of pelagic chaetognaths: lack of depth-related declines. Limnol. Oceanog. 38: 935-948

Thuesen, E. V and J. J. Childress. 1994. Oxygen consumption rates and metabolic enzyme activities of oceanic California medusae in relation to body size and habitat depth. Biol. Bull. 187: 84-98

Tiselius, P. T., and W. T. Peterson. 1986. Life history and population dynamics of the chaetognath *Sagitta elegans* in central Long Island Sound. J. Plank. Res. 8:183-95

Welch, H. E., T. D., Siferd and P. Bruecker. 1996. Population densities, growth, and respiration of the chaetognath *Parasagitta elegans* in the Canadian high Arctic. Can. J. Fish. Aquat. Sci. 53:520-527

Wiebe, P. H. and W. R. Holland. 1968. Plankton patchiness: Effects on repeated net tows. Limnol. Oceanog. 13:315-321

Wimpenny, R. S. 1937. The distribution, breeding and feeding of some important plankton organisms of the south-west North Sea in 1934. I. *Calanus finmarchicus* (Gunn), *Sagitta setosa* (J. Müller), and *Sagitta elegans* (Verrill). Fishery Investigations London, Series 2. 15:1-53

Wimpenny, R. S. 1938. Diurnal variation in the feeding and breeding of zooplankton related to the numerical balance of the zoo-phytoplankton community. Journal du Conseil Permanente International pour l'Exploration de la Mer. 12:323-37

Wishner, K. F. 1980. The biomass of the deep-sea benthopelagic plankton. Deep Sea Res. 27A:203-216

Wishner, K. F. and M. M. Gowing. 1992. The role of deep-sea zooplankton in carbon cycles. Deep-Sea Food Chains and the Global Carbon Cycle. Ed. G. Rowe and V. Pariente. pp. 29-43. Kluwer Academic Publishers

Yen, J. 1983. Effects of prey concentration, prey size, predator life stage, predator starvation, and season on predation rates of the carnivorous copepod *Euchaeta elongata*. Mar. Biol. 75: 69-77

Youngbluth, M. J., P. Kremer, T. G. Bailey and C. A. Jacoby. 1988. Chemical composition, metabolic rates and feeding behavior of the midwater ctenophore *Bathocyroe fosteri*. Mar. Biol. 98:87-94

Zo, Z. 1973. Breeding and growth of the chaetognath *Sagitta elegans* in Bedford Basin. Limnol. Oceanog. 18:750-6

Zouhiri, S. and J. Dauvin. 1996. Diel changes of the Benthic Boundary Layer macrofauna over coarse send sediment in the western English Channel. Oceanologica Acta 19:141-153

Appendix 1. Comparison between the biochemical levels of small and large *P. elegans* in the BBL from April 1997 to June 1998 (t-test)

	Size	P > |t|	N	mean	std
Ash	small	0.1757	39	12.6	2.4
	large		39	11.9	2.4
Carbohydrate	small	0.8804	23	0.61	0.12
	large		29	0.61	0.09
Lipid	small	0.1373	45	12.7	2.2
	large		47	13.3	1.6
Protein	small	0.3463	31	64.3	3.9
	large		34	63.4	3.4
C/N *	small	0.0615			
	large				

Note: All the data are paired at each time point of sampling.
Symbol (*) indicates non-parametric one way analysis.
Biochemical compositions are expressed as % dry weight.

Appendix 2. Comparison between the biochemical levels of small and large *P. elegans* in the BBL within the seasons from April 1997 to June 1998 (t-test)

	Size	season	P > |t|	N	mean	std
Ash	small	1	0.014	21	12.5	1.3
	large	1		21	11.3	1.1
	small	2	0.9041	9	14.3	3.4
	large	2		9	14.5	3.5
	small	3	0.6335	9	11.1	2.3
	large	3		9	10.7	0.7
Carbohydrate	small	1	0.3973	12	0.63	0.13
	large	1		12	0.67	0.06
	small	2	0.278	5	0.5	0.03
	large	2		11	0.53	0.06
	small	3	0.4379	6	0.66	0.09
	large	3		6	0.63	0.06
Lipid	small	1	0.4026	36	12.8	2.3
	large	1		36	13.2	1.7
	small	2	0.0398	9	10.3	2.1
	large	2		9	12.5	1.7
	small	3	0.538	9	12.5	1.7
	large	3		11	13.8	0.9
Protein	small	1	0.9542	16	61.8	2.3
	large	1		18	61.7	3.1
	small	2	0.0127	7	69.4	0.7
	large	2		7	67.6	1.5
	small	3	0.4009	8	64.8	3.5
	large	3		9	63.6	2.3
C/N	small	1	0.0427	16	4.5	0.2
	large	1		16	4.6	0.1
	small	2	0.0018	7	3.9	0.1
	large	2		7	4.1	0.1
	small	3	0.0997	8	4.3	0.3
	large	3		9	4.5	0.1

Note: All the data are paired at each time point.
Season 1: spring-summer 1997, season 2: fall-winter 1997, season 3: spring 1998
Biochemical compositions are expressed as % dry weight.

Appendix 3. Time variation in the biochemical compositions of *P. elegans* in the BBL from April 1997 to June 1998 (GLM)

	Size	P > F	F	N	mean	std
Ash	small	0.0001	89	39	11.1	3
Carbohydrate	small	0.0067	9.8	11	0.6	0.1
Lipid	small	0.0018	11.8	13	13.2	2.1
Protein	small	0.0001	91.1	13	67.2	2.4
C/N	small	0.0001	81.7	14	4	0.2
Ash	large	0.0001	189.5	9	11.5	3
Carbohydrate	large	0.2028	2.3	6	0.6	0.1
Lipid	large	0.0588	4.7	9	11.6	0.9
Protein	large	0.0468	10.1	6	65.5	2.4
C/N	large	0.0972	5.6	6	4.3	0.2

Note: Biochemical compositions are expressed as % dry weight.

Appendix 4. Seasonal variation in the biochemical compositions of *P. elegans* in the BBL from April 1997 to June 1998 (GLM)

	size	season	P > F	F	N	mean (%)	std
Ash	small	1	0.012	5.0	21	12.5	1.3
		2			9	14.3	3.4
		3			9	11.1	2.3
Carbohydrate	small	1	0.0347	4.0	12	0.6	0.1
		2			5	0.5	0.0
		3			6	0.7	0.1
Lipid	small	1	0.0001	12.3	27	13.6	1.7
		2			9	10.3	2.1
		3			9	12.5	1.7
Protein	small	1	0.0001	24.0	16	61.8	2.3
		2			7	69.4	0.7
		3			9	64.8	3.5
C/N	small	1	0.0001	24.2	16	4.5	0.2
		2			7	3.9	0.1
		3			8	4.3	0.3
Ash	large	1	0.0012	7.7	24	11.4	1.1
		2			12	13.3	3.7
		3			15	10.4	0.8
Carbohydrate	large	1	0.0001	32.3	24	0.7	0.1
		2			17	0.5	0.1
		3			15	0.6	0.1
Lipid	large	1	0.1285	2.1	30	13.7	1.7
		2			15	12.7	1.6
		3			17	13.2	1.4
Protein	large	1	0.0001	21.9	18	61.7	3.1
		2			10	68.3	1.7
		3			14	34.4	2.2
C/N	large	1	0.0001	51.4	16	4.6	0.1
		2			9	4.1	0.1
		3			14	4.4	0.1

Note: All the data are not paired at each time point.
Season 1: spring-summer 1997, season 2: fall-winter 1997, season 3: spring 1998
Biochemical compositions are expressed as % dry weight.

Appendix 5. Interannual comparison of the biochemical compositions of *P. elegans* in the BBL (t-test)

	size	year	P > |T|	N	mean (%)	std
Ash	small	1	0.0689	15	12.7	0.9
		2		9	11.1	2.3
Carbohydrate	small	1	0.1776	9	0.6	0.1
		2		6	0.7	0.1
Lipid	small	1	0.2993	18	13.3	1.7
		2		9	12.5	1.7
Protein	small	1	0.0255	12	61.2	1.8
		2		8	64.8	3.5
C/N	small	1	0.0826	12	4.5	0.1
		2		8	4.3	0.3
Ash	large	1	0.0019	18	11.4	1
		2		15	10.4	0.8
Carbohydrate	large	1	0.0239	18	0.7	0.1
		2		15	0.6	0.1
Lipid	large	1	0.2813	21	13.8	1.8
		2		17	13.2	1.4
Protein	large	1	0.0003	13	61.5	1.1
		2		14	64.4	2.2
C/N	large	1	0.0028	12	4.6	0.1
		2		14	4.4	0.1

Note: All data are not paired at each time point of sampling.
Year 1 indicates spring of 1997 and year 2 indicates spring of 1998.
Biochemical compositions are expressed as % dry weight.

Appendix 6. Comparison between the biochemical levels of small and large *P. elegans* in the water column from April 1997 to June 1998 (t-test)

	depth (m)	size	P > |T|	N	mean (%)	std
Ash *	50-175	S	0.8749	14	11.1	3
		L		9	11.5	3
Carbohydrate	50-175	S	0.4323	11	0.6	0.1
		L		6	0.6	0.0
Lipid	50-175	S	0.0901	13	13.2	2.1
		L		9	11.6	1.9
Protein	50-175	S	0.192	13	67.2	2.4
		L		6	65.6	2.4
C/N	50-175	S	0.0028	14	4	0.2
		L		6	4.3	0.2
Ash	175-225	S	0.0048	18	9.9	0.6
		L		18	9.2	0.7
Carbohydrate	175-225	S	0.4061	14	0.6	0.1
		L		12	0.6	0.1
Lipid	175-225	S	0.3643	23	11.7	2.2
		L		24	12.3	2.2
Protein	175-225	S	0.0001	15	66.9	2.1
		L		15	63.7	1.6
C/N	175-225	S	0.0001	14	4	0.2
		L		15	4.4	0.1

Note: All the data from 50-175 m are not paired at each time point of sampling.
All the data from 175-225 m are paired at each time point of sampling.
Size S indicates small and size L indicates large.
(*) indicates non-parametric one way analysis.
Biochemical compositions are expressed as % dry weight.

Appendix 7. Time variation in the biochemical compositions of *P. elegans* in the water column from April 1997 to June 1998 (GLM)

	size	depth (m)	P > F	F	N	mean (%)	std
Ash	S	50-175	0.0001	78.4	14	11.1	3.0
Carbohydrate	S	50-175	0.0067	9.8	11	0.6	0.1
Lipid	S	50-175	0.0018	11.8	13	13.2	2.1
Protein	S	50-175	0.0001	91.1	13	67.2	2.4
C/N	S	50-175	0.0001	81.7	14	4.0	0.2
Ash	L	50-175	0.0001	189.5	9	11.5	3.0
Carbohydrate	L	50-175	0.2028	2.3	6	0.6	0.1
Lipid	L	50-175	0.0588	4.7	9	11.6	0.9
Protein	L	50-175	0.0468	10.1	6	65.5	2.4
C/N	L	50-175	0.0972	5.6	6	4.3	0.2
Ash	S	175-225	0.0001	233.3	34	10.6	2.5
Carbohydrate	S	175-225	0.3326	1.2	37	0.6	0.1
Lipid	S	175-225	0.0017	4.3	35	11.4	2.0
Protein	S	175-225	0.0001	47.2	28	66.9	3.1
C/N	S	175-225	0.0001	39.6	25	4.0	0.2
Ash	L	175-225	0.0001	132.5	18	9.2	0.7
Carbohydrate	L	175-225	0.0007	17.4	12	0.58	0.1
Lipid	L	175-225	0.0263	3.1	27	12.4	2.2
Protein	L	175-225	0.0006	11.4	17	63.7	1.5
C/N	L	175-225	0.0195	4.4	17	4.4	0.1

Note: Size S indicates small and size L indicates large.
Biochemical compositions are expressed as % dry weight.

Appendix 8. Interannual comparison of biochemical composition of *P. elegans* in the 175-225 m water column (t-test)

	size	year	P > |T|	N	mean(%)	std
Ash	S	1	0.8372	11	9.8	0.8
		2		14	9.8	0.2
Carbohydrate	S	1	0.3109	9	0.6	0.1
		2		13	0.6	0.1
Lipid	S	1	0.0065	11	13.3	2.4
		2		17	10.8	1
Protein	S	1	0.2199	9	65.5	1
		2		13	66.5	2.9
C/N	S	1	0.0013	7	4.2	0.1
		2		12	4	0.2
Ash	L	1	0.2304	9	9.4	0.9
		2		9	9	0.5
Carbohydrate	L	1	0.0821	6	0.5	0.1
		2		6	0.6	0.1
Lipid	L	1	0.2367	19	12.7	2.3
		2		8	11.7	1.6
Protein	L	1	0.3117	9	63.3	0.5
		2		8	64.1	2.1
C/N	L	1	0.0041	9	4.5	0
		2		8	4.3	0.1

Note: Year 1 indicates spring of 1997 and year 2 indicates spring of 1998.
Size S indicates small and size L indicates large.
Biochemical compositions are expressed as % dry weight.

Appendix 9. Depth variation in the biochemical composition of *P. elegans* from April 1997 to June 1998 (GLM)

	size	depth	P > F	F	N	mean (%)	std
Ash	S	1	0.0018	6.8	11	10.6	2.6
		2			34	10.6	2.5
		3			39	12.6	2.4
Carbohydrate	S	1	0.8531	0.2	11	0.6	0.1
		2			37	0.6	0.1
		3			23	0.6	0.1
Lipid	S	1	0.0054	5.5	13	13.2	2.1
		2			35	11.4	2
		3			45	12.7	2.2
Protein	S	1	0.0052	5.7	13	67.2	2.4
		2			28	66.9	3.1
		3			31	64.3	3.9
C/N	S	1	0.0001	10.2	14	4	0.2
		2			25	4	0.2
		3			31	4.3	0.3
Ash	L	1	0.0004	8.7	9	11.5	3
		2			18	9.2	0.7
		3			51	11.5	2.2
Carbohydrate	L	1	0.3311	1.1	6	0.6	0
		2			12	0.6	0.1
		3			56	0.6	0.1
Lipid	L	1	0.0114	4.7	9	11.6	1.9
		2			27	12.4	2.2
		3			62	13.3	1.6
Protein	L	1	0.4233	0.9	6	65.6	2.4
		2			17	63.7	1.5
		3			42	64.2	3.6
C/N	L	1	0.6145		6	4.3	0.2
		2			17	4.4	0.1
		3			39	4.4	0.2

Note: Depth 1 indicates 50-175 m, 2 indicates 175-225 m and 3 indicates BBL
Size S indicates small and size L indicates large.
Biochemical compositions are expressed as % dry weight.

Appendix 10. Seasonal variation of maturity stages of *P. elegans* in the BBL (GLM)

stage	season	size	P > F	F	N	mean(%)	std
1	1	S	0.0137	5.79	8	45.1	15.1
	2				4	72.5	16.4
	3				6	36.2	22.1
2	1	S	0.2578	1.49	8	26	10
	2				4	12.8	10.4
	3				6	26	18
3	1	S	0.3271	1.2	8	28.9	18.1
	2				4	14.7	19.5
	3				6	37.8	30
1	1	L	0.0046	7.89	8	3.3	3.3
	2				4	37.4	33.4
	3				6	0.6	0.8
2	1	L	0.6859	0.39	8	25.2	20.2
	2				4	36.3	42.4
	3				6	25.5	28.4
3	1	L	0.0434	3.9	8	71.5	20.1
	2				4	26.4	35.4
	3				6	74	28.1

Note: Stage 1-3 indicate ovary maturity stage.
Season 1 indicates spring-summer of 1997.
Season 2 indicates fall-winter of 1997.
Season 3 indicates spring of 1998.
Size S indicates small size L indicates large.

Appendix 11. Interannual comparison of frequency of maturity stages of *P. elegans* in the BBL (t-test)

stage	year	size	P > |T|	P > F	F	N	mean (%)	std
1	1	small	0.8931	0.1370	5.6	5	40.0	13.4
	2	small				3	36.5	31.7
2	1	small	0.0369	0.7202	1.3	5	29.9	7.3
	2	small				3	14.4	8.8
3	1	small	0.3358	0.1039	6.8	5	30.2	18.5
	2	small				3	49.0	40.4
1*	1	large	0.0164			6	2.3	3.0
	2	large				5	0.2	0.4
2*	1	large	0.9273			6	24.4	23.6
	2	large				5	29.6	29.7
3	1	large	0.9224	0.6344	1.6	6	73.4	23.1
	2	large				5	70.2	29.6

Note: Stage 1-3 indicate ovary maturity stages.
Year 1 indicates spring of 1997 and year 2 indicates spring of 1998.
Symbol (*) indicates non-parametric one way analysis.

Appendix 12. Seasonal variation in the NPC of *P. elegans* from the BBL (GLM)

season	size	P > F	F	N	mean	std
1	S	0.5206	0.68	8	0.11	0.09
2	S			4	0.08	0.04
3	S			6	0.12	0.08
1	L	0.1972	1.81	8	0.06	0.03
2	L			4	0.05	0.03
3	L			6	0.09	0.05

Note: Season 1 indicates spring-summer of 1997.
Season 2 indicates fall-winter of 1997.
Season 3 indicates spring of 1998.
Size S indicates small and size L indicates large.
NPC indicates the number of prey per chaetognath.

Appendix 13. Interannual variation in the NPC of *P. elegans* from the BBL (t-test)

year	size	P > |T|	N	mean	std
1	S	0.7398	6	0.13	0.1
2	S		6	0.12	0.08
1	L	0.3027	6	0.07	0.03
2	L		6	0.09	0.05

Note: Year 1 indicates spring of 1997 and year 2 indicates spring of 1998. NPC indicates the number of prey per chaetognath.

Appendix 14. Interannual comparison of the diet of *P. elegans* in the BBL (t-test)

	year	P > |T|	N	mean (%)	std
***Calanus* spp.**	1	0.0489	4	33.1	21
	2		4	65.9	14.5
Pseudocalanus	1	0.2382	4	29.2	25.1
	2		4	11.6	7.1
chaetognath	1	0.8464	4	15.2	14.8
	2		4	13.4	13.3
unidentified	1	0.4789	4	12.5	11.9
	2		4	8.2	2.4

Note: Year 1 indicates spring of 1997 and year 2 indicates spring of 1998. Food composition is expressed in % composition.

Appendix 15. Interannual variation in the abundance of *Calanus* spp. and copepod from the BBL (t-test)

	year	P > |T|	N	mean	std
***Calanus* spp**	1	0.356	5	-0.04	1.19
***Calanus* spp**	2		5	0.22	0.95
copepod	1	0.198	5	0.72	1.58
copepod	2		5	0	0.77

Note: Year 1 indicates spring of 1997 and year 2 indicates spring or 1998. Abundance is expressed in terms of standard normal deviate.