

POPULATION DYNAMICS AND FEEDING HABITS OF THE
CHAETOGNATHS *SAGITTA ELEGANS* VERRIL AND *SAGITTA*
SETOSA MÜLLER IN MANX WATERS, NORTH IRISH SEA.

' Thesis submitted in accordance with the requirements of
Liverpool University for the degree of Doctor in Philosophy'.

By

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**To the Universidad Nacional
Autónoma de México.**

To the people of México.

To my family

Contents.

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Population dynamics and feeding habits of the chaetognaths
Sagitta elegans Verrill and *Sagitta setosa* Müller in Manx
waters, North Irish Sea

ABSTRACT.

The food and feeding habits were studied of two common chaetognath species in the Irish Sea, *Sagitta elegans* and *S. setosa*. Food analyses were carried out for 21351 specimens. Results include size frequencies and gonadic stages of the animals.

During the two years of sampling (1986-1987), it was found that *S. elegans* overwintered mainly as stage II, with small numbers of stage I and no stage III. Stage III became dominant in the population in March; spawning took place in April and continued until the end of the summer. Animals of this species die after spawning and no mature gonadic stage III were caught by mid-autumn. *S. elegans* has a one-year life cycle in the studied area and animals attained a maximum length of 23 mm. The largest specimens of *S. elegans* showed a typical vertical migration. They were found more or less evenly distributed in the water column at night, but they were scarce near surface by day. Recently hatched organisms showed minimal migratory behaviour. It is proposed that *S. elegans* migrates downwards mainly to avoid predation and also that small sagittas of this species do not migrate, possibly due to inefficient swimming capacity or to the high energy cost.

Sagitta setosa was caught only to the east of the Isle of Man from summer to late winter. Spawning of the species occurred in summer and it overwintered mainly as stage I. The species probably disappeared from the sampled area in March, but analysis of the available data suggests a one year life-cycle for this chaetognath. *S. setosa* dies after spawning, and mature stage III animals were not caught by the end of the winter.

Copepods were the main prey eaten by both species of *sagitta*, but other plankters such as cirriped larvae, appendicularians, dinoflagellates and tintinnids were also readily consumed. Fish eggs and larvae were predated in minimal amounts.

It is possible that low predation on fish fry was due to the relative immobility of the small prey and the high swimming capacity and predation avoidance when the fish larvae had increased in size. *S. elegans* fed on larger species, such as *Pseudocalanus* and *Acartia*, while the main diet of *S. setosa* was made up of smaller items, such as *Oithona* and appendicularia. In spite of these differences in prey consumption, the diet of both *S. elegans* and *S. setosa* overlapped to a great extent.

Predators fed mainly according to prey size, thus only larger sagittas preyed upon food items like *Calanus* and *Temora*, while small specimens up to 5 mm in length fed on items as small as tintinnids and dinoflagellates.

S. elegans and *S. setosa* showed a higher Food Containing Ratio at night from samples collected near the surface, with larger predators having a higher FCR than smaller ones. Most of the predators were usually found with one prey item as food content, however multiple prey was also recorded. The highest number of prey in a single predator was 9 (*Stenosomella*) in small *S. setosa*, but 2 prey per predator was the most common NPC in both species of *Sagitta*. "Cannibalism" was found to occur at times when other food items were scarce (winter), *S. elegans* being the more cannibalistic. The Feeding Rate was higher for *S. setosa* (range from 1.38 to 5.35 prey per day) than for *S. elegans* (range from 0.75 to 3.55 prey per day). Assuming an overall Feeding Rate average of 2 prey per day and an annual maximum abundance of 40 *S. elegans* /m³, the predation impact of the species is minimal. Although *S. setosa* has a higher Feeding Rate, its impact is even less because the species was recorded in the study area only for about six months (September to February) and its abundance was generally lower.

The feeding experiments supported the findings from the field, i.e. the items commonly found in the gut content analyses in natural conditions were readily eaten in laboratory conditions. Results were also consistent regarding *Temora* as the least common copepod species eaten. The experiments also showed an increase in predation rate with increasing prey density, until a critical density was reached and predation became irregular. This critical density was found to be 100 prey items/litre.

1.0.

INTRODUCTION.

The phylum Chaetognatha was characterized by Hyman (1959) as "small bilaterally symmetrical enterocoelus marine animals, of mostly planktonic habits without circulatory or excretory systems". She added that chaetognaths are protandric hermaphrodites, thus the ovaries ripen after the coeloms are filled with sperm. There are controversial conclusions as far as fertilization in chaetognaths is concerned. Hyman (1959) stated that "self-fertilization is apparently the rule in *Sagitta*". However, Alvariño (1965) concluded that "cross- fertilization by copulation is the rule". Reeve and Walter (1972a), who misinterpreted the copulation behaviour in *Sagitta hispida* , observed acts of self-insemination in their specimens. Later, they succeeded in inducing self-insemination by opening the seminal vesicles to release the spermatophores and obtained fertile eggs. They suggested that this reproductive behaviour (self-fertilization) however unusual, could provide a valuable short term survival mechanism for populations temporarily at very low densities. From these results, Reeve and Cosper (1975) reconciled the theories by both Hyman (1959) and Alvariño (1965) mentioned above by saying that " since the morphological characteristics of all planktonic chaetognaths are similar, it may not be speculative to expect that most may be capable of both forms of fertilization". They added that self- fertilization might be expected to occur more frequently in species habitually in lower densities, such as typically oceanic and bathypelagic ones.

A large amount of literature has been published regarding chaetognaths, possibly due to the fact that these animals are only second to copepods in terms of abundance in most zooplankton collections (Feigenbaum and Maris, 1984) or because they are thought to be one of the main predators of the copepod community (Rakusa-Szuscewski, 1969; Reeve, 1970; Szyper, 1978; Pearre, 1980; Canino and Grant, 1985; Øresland, 1987; and many more) as chaetognaths are strictly carnivorous (Alvariño, 1965). Reeve (1970a) estimated a chaetognath biomass of about 30 % of that of the copepods and that this relatively high abundance showed chaetognaths to be an important link between the energy converted from the primary producers into copepod tissue and higher trophic levels.

According to Alvariño (1965) the phylum Chaetognatha comprises about 52 species arranged in seven genera. The genus *Sagitta* is the most successful of the group not only because the great majority of the living species belong to this genus but also because they reach the highest evolutionary level and inhabit the greatest variety of environments and bathymetric levels of the oceans.

Sagitta elegans is a boreal chaetognath with a worldwide distribution in arctic and subarctic waters and usually found in the upper 100 or 150m (Alvariño, 1965). The species is the most abundant in these areas and is capable of withstanding a range of temperatures from - 0.5 °C to 21 °C (Alvariño, 1965).

Sagitta setosa is a more restricted species, usually confined to

neritic waters (Pierce, 1941; Williamson, 1956a; Alvariño, 1965; Jakobsen, 1971; Southward, 1984), and both species are regarded as valuable in characterizing water masses (Russell, 1935, 1939; Williamson, 1956a; Khan and Williamson, 1971; Øresland 1983).

In the Irish Sea, these two species are the dominant chaetognaths, *S. elegans* being the most widespread in the area (Pierce, 1941; Khan, 1970; Lee, 1971). Williamson (1956a) cited that "in May of both 1951 and 1952 *S. elegans* was the dominant species in all areas sampled, although *S. setosa* was probably the more common form in the bays and estuaries of the Welsh, English and Scottish coasts (c.f. Pierce, 1941)". He added that "the results of the four years 1949-1952 together with the results of the eight years of which Pierce (1941) analyzed samples from the Isle of Man region indicate that a change from *elegans* to *setosa* in most of the eastern half of the Irish Sea is a regular occurrence each autumn". Khan (1970), who found similar results, reported a variable overlap in the distribution of both species in the Irish Sea. He mentioned that *S. setosa* was confined in May to Liverpool Bay and adjacent waters and that the species "spread rapidly during June and covered much of the Irish Sea from July to December". He also thought that this was a regular yearly pattern in the distribution of the species.

The main aim of the present work was the study of the food and feeding habits of both *S. elegans* and *S. setosa* in seasonal and 24-hour cycles in relation to changes in population and the predation impact of the chaetognaths on other members of the plankton community.

2.0.

MATERIAL AND METHODS.

2.1

Field work.

Plankton collections in 1986 were obtained at two stations (Fig. 1). Station 1 is approximately 34 m depth and station 2 approximately 120 m. Simultaneous horizontal tows were made at subsurface and near the bottom at station 1, while at station 2 an intermediate sample (about 60 m depth) was taken. The plankton nets used in this study were conical, 1.30 m length and 0.46 m diameter (mesh size 0.335 μ), and with General Oceanics flowmeters attached to the mouth to estimate the amount of water filtered. The nets were tied to a weighted steel warp (weight 250 kg) and towed at 1.5 to 2 knots for 15 min. Sampling was regularly carried out every 3 hours by day and night in cruises of 12 hours each. Unfortunately due to weather conditions and ship availability, day and night samples were often collected on different dates (see Table 1). Although some changes in the species composition and abundance of the plankton were expected, they were treated as if they were collected on a 24 hour cycle. The material obtained was immediately fixed by adding concentrated formaldehyde solution until a final strength of approximately 5 % was obtained. After towing, nets were washed carefully and the washings added to the catches. Temperatures from near bottom and subsurface were obtained by using a Nansen-Petersen water bottle.

In 1987 it was not possible to continue a similar sampling program. Ship time was reduced to an 8 hour day, and day and night samples were only obtained at station 1 (Table 1).

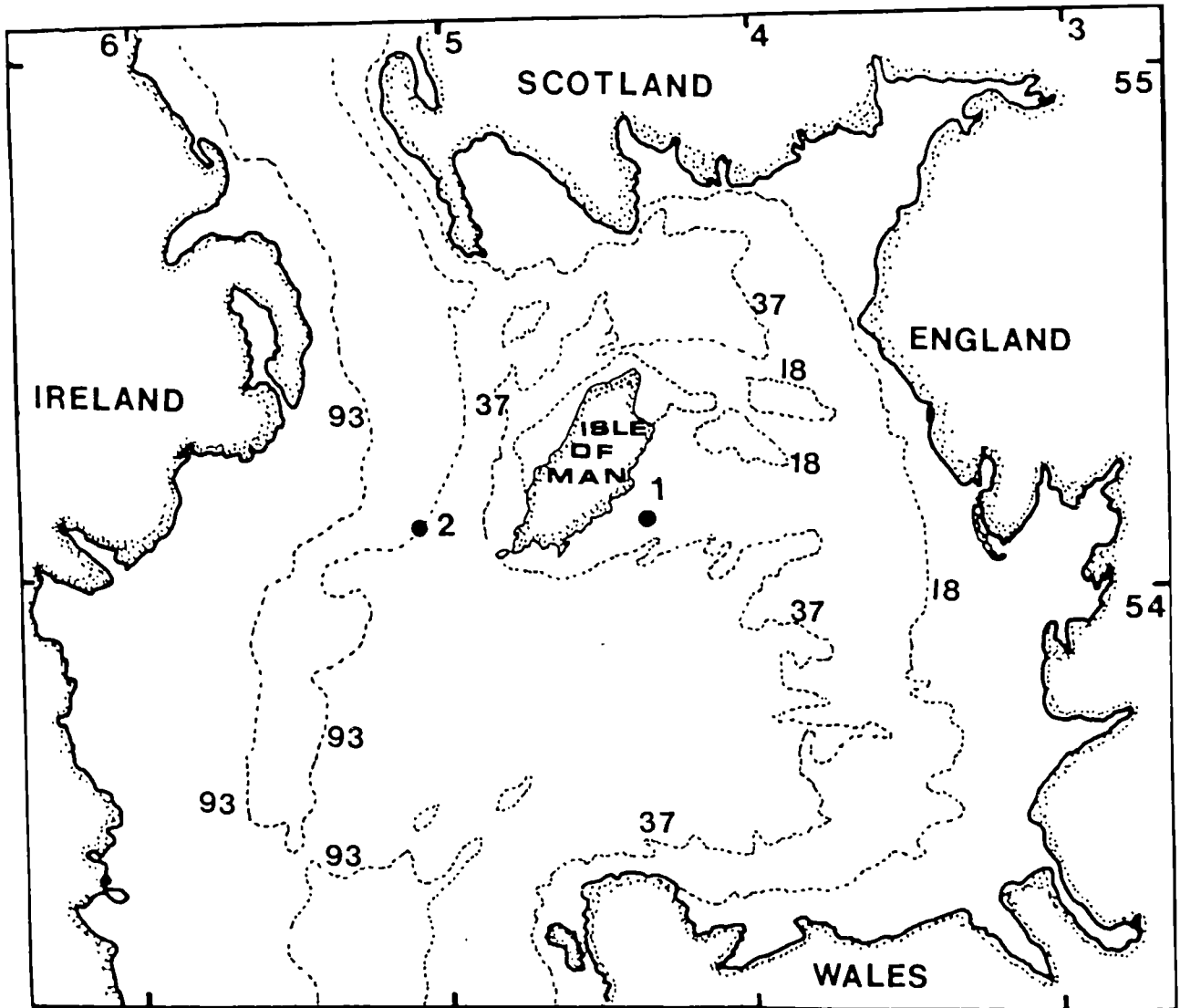


Fig. 1.- Study area with the location of the sampling stations in the Irish Sea. Depth profile in meters.

The time interval between consecutive samples was reduced to two hours. Sampling at station 2 was discontinued as station 1 was considered more important due to the presence of both *S. setosa* and *S. elegans*, thus permitting comparison between the two species.

Station 1	[May 26, 1987
[February 9, 1986	May 26-27, 1987]*
February 20-21, 1986]*	June 10-11, 1987 *
[April 14, 1986	July 16-17, 1987 *
April 24-25, 1986]*	[August 3, 1987
[June 11, 1986	August 4-5, 1987] *
June 15-16, 1986]*	September 17, 1987
[July 29, 1986	[October 21, 1987
July 31- August 1, 1986] *	October 22-23, 1987]*
[September 17, 1986	Station 2
September 23-24, 1986]*	[February 22-23, 1986 *
November, 4 1986	March 17, 1986]
[January 28-29, 1987 *	[May 29, 1986
January 30, 1987]	June 6-7, 1986]*
March 23, 1987	[July 30, 1986
March 23-24, 1987 *	August 4-5, 1986] *
[April 27-1987	[September 16, 1986
April 28-29, 1987]*	September 18-19, 1986] *

Table 1.- Dates of collection of zooplankton samples at station 1 and station 2, in 1986 and 1987. * Night samples. [] Samples analyzed as if collected on a single sampling date.

2.2.

Laboratory work.

2.2.1.

Subsampling.

In the laboratory zooplankton samples were strained with a small piece of cloth net with the same mesh size as used in the tows, and rinsed with seawater to avoid formaldehyde fumes.

Large organisms such as big medusae, euphausiids and juvenile fish, were removed and the remaining organisms transferred to a beaker for obtaining the aliquots. The subsampling method for the estimation of the composition and abundance of the plankton was basically similar to that used by Russell (1931b). Samples were poured into a 2000 cc beaker (height 23.5 cm., diameter 12.8 cm) and seawater was added to produce a volume of 1000 cc. Organisms were then mixed with a circular plastic disc (5.6 cm diameter) on one end of a glass rod. The rod was moved up and down until the distribution of the organisms was as even as possible. Subsamples were taken with a round bottom scoop, with a capacity of 4 cc for small and abundant organisms (e.g. *Pseudocalanus*, *Acartia*) and 10 cc for large animals (e.g. *Sagitta*, *Meganyctiphanes*). Successive dips were made to give a count of at least 300 organisms per sample, as recommended by Omori and Ikeda (1984).

2.3.

Flowmeters.

Plankton samples were taken with a flowmeter (General Oceanic's

type model 2030 with a standard three -blade rotor) attached to the mouth of the net.

Estimation of the volume of water filtered through the nets was calculated by using the formula given by the manufacturing company.

The equation used was :

$$V = \pi r^2 d \quad \text{Where } V = \text{volume of water filtered} \quad (\text{eq. 1})$$

$$\pi = 3.1416$$

$$r^2 = \text{square of radius of mouth of net.}$$

$$\text{and } d = \text{distance}$$

Distance can be calculated by:

$$d = \frac{(R_f - R_i)(26873)}{999999} \quad (\text{eq.2})$$

by developing eq.1

$$V = \frac{(\pi r^2)(26873)(R_f - R_i)}{999999}$$

Then

$$V = \frac{(3.1416)(0.529)(26873)(R_f - R_i)}{999999} \quad (\text{eq.3})$$

$$V = 0.0446606 (R_f - R_i) \quad \text{where}$$

R_i = Initial reading of flowmeter.

R_f = Final reading of flowmeter.

26873 and 999999, constants provided by the company.

The volume of water filtered varied according to the fishing depth and also from tow to tow. Table 2 gives the information related to the performance of the flowmeters.

	Station 1		Station 2		
	Surf.	Bott.	Surf.	Midd.	Bott.
Maximum	120	137	120	178	210
Minimum	85	118	85	140	16
Mean	111.2	129.5	109.5	160.5	181.5
Std. Dev.	8.5	5.7	6.7	10.4	10.2
No. of observations	38	50	40	30	30

Table 2.- Volume of water (m³) filtered through the nets at different depths at station 1 and station 2, as calculated from the flowmeters.

Occasionally, readings were exceptionally low, usually because malfunction of the flowmeters (the inside mechanism of the flowmeters requires to be filled with tap water, and because they are not waterproof, leaking is common). In these cases, the mean values of the water filtered, as listed in table 2, were used for density calculations (org./m³)

2.4.

Population analysis in *Sagitta* spp.

Between 50 and 100 (unless stated otherwise) specimens of *Sagitta elegans* and *S. setosa*, were randomly drawn from the samples, measured (0.2 mm maximum accuracy), and gonadic stage and food content recorded. Measurements were made from the tip of the head to the end of the tail, without including the tail fin. Maturity stages using the gonads in *Sagitta* were grouped as follows: Stage I (young) with ovaries absent or just visible; stage II (immature) with small ova in ovaries and stage III (mature) with large ova in ovaries (Russell, 1932; McLaren, 1969; Sameoto, 1973; Zo, 1973). Species identification was made by body wall transparency and shape and position of the vesiculae seminales (Fraser, 1957), but all this is difficult when the length of the chaetognaths is 6 mm or less.

2.5.

Feeding analysis.

Specimens of *Sagitta* containing food were placed in a small tray, gut contents removed and analyzed with a dissection microscope or when higher magnification was required, with a non-stereo microscope, 400X, 600X.

Sagitta elegans is known to feed actively in the densely packed net can when sampling (Pearre, 1974). Thus, some extra feeding may have occurred before fixing the samples with formaldehyde. For this reason only those food items found in the posterior 1/3 of the gut and with some evidence of digestion were recorded.

However when the food items found were small organisms (e.g. dinoflagellates or tintinnids), they were recorded regardless of the position in the gut. The assumption was that such small organisms would not be retained by the net with a mesh size as described above, and consequently the catch of these prey is likely to have occurred in natural conditions.

Identification of the food items was not always possible, even for those with hard skeletons (e.g. crustaceans). This was mainly due to digestion, and structures like swimming feet or antennae were often not recognizable. In many cases, however, identification was possible by using the cutting blades of the copepod mandibles (Sullivan, 1975). This allowed the identification of most of the food items, as copepods are by far the most important prey of *Sagitta* (see also Rakusa-Suszczewski, 1969; Pearre, 1973, 1974; Feigenbaum and Maris, 1984; Øresland, 1987).

2.6.

Gut content analysis.

Digestion of food in *S. elegans* and *S. setosa* is mainly carried out at the rear end of the gut (Feigenbaum, 1982). By dissecting this part of the gut, it is possible to determine the quality and number of prey eaten. In assessing the impact of predation by these species the following data were recorded:

FRC= Food Containing Ratio = $\frac{\text{Number of predators with prey}}{\text{Total number of predators analyzed}}$

NPC = (mean) Number of Prey per Chaetognath (multiple prey).

FR= Feeding Rate, in number of prey eaten per day, where

$$FR = \frac{NPC (24)}{DT} \quad \text{and } DT = \text{Digestion time, in hours.}$$

Bajkov (1935), developed this formula to determine the feeding rate in fish. Since then this formula has been used in a similar way for determining the feeding rate in several species of *Sagitta* (Feigenbaum, 1979, 1982; Nagasawa and Marumo, 1972; Canino, 1981; Szyper, 1978).

Digestion time has been defined as the time between ingestion of prey and its defecation (Feigenbaum and Maris, 1984), and it is temperature dependant, being shorter with higher temperature (Pearre, 1981, Mironov, 1960). Nature and number of prey eaten have also a direct influence, with a general trend of higher digestion time for prey with hard skeletons (e.g. crustaceans), as compared with those without (e.g. appendicularians). Digestion time also increases with increasing number of prey eaten (Canino, 1981). Digestion time in several species of *Sagitta* has been investigated. Khulman (1977), found that in *S. elegans* the digestion time was 147 minutes at 15 °C, while Feigenbaum (1982) found a digestion time for the same species of 614 minutes at 0 °C. Pearre (1981), developed the following equation for the relationship between digestion time and temperature for this chaetognath: (See also Table 3). Digestion Time = $DT = 10.24 e^{-0.095 t}$

Temp. °C	DT (Hours)	Temp. °C	DT (Hours)
0	10.2	11	3.6
1	9.4	12	3.3
2	8.5	13	2.3
3	7.7	14	2.7
4	7.0	15	2.5
5	6.4	16	2.2
6	5.8	17	2.3
7	5.3	18	1.8
8	4.8	19	1.7
9	4.4	20	1.5
10	3.9		

Table 3.- Regression of digestion time as a function of temperature for *S. elegans*. Data calculated using the formula given by Pearre (1981).

$$\text{Digestion time DT} = 10.24 e^{-0.095t}$$

Mironov (1960), estimated a digestion time of 2 hours at 11.5 °C and 1.5 hours at 15 °C for *S. setosa*. By extrapolation he arrived at an estimate of 1 hour at 20 °C. Both Pearre's equation and Mironov's estimates are used for calculating the feeding rates of *S. elegans* and *S. setosa* in this work.

Temp. °C	DT (Hours)	Temp. °C	DT (Hours)
0	3.3	11	2.0
1	3.2	12	1.9
2	3.1	13	1.8
3	3.0	14	1.7
4	2.8	15	1.6
5	2.7	16	1.5
6	2.6	17	1.3
7	2.5	18	1.2
8	2.4	19	1.1
9	2.3	20	1.0
10	2.2		

Table 4.-Regression of digestion time as a function of temperature, for *S. setosa*. Data calculated from the estimates given by Mironov (1960).

$$\text{Digestion Time } DT = 3.34 e^{-0.117t}$$

2.7.

Feeding experiments in *S. elegans*.

Specimens of *S. elegans* were obtained by making short tows at the pier in the Port Erin Bay. Tows were made horizontally near the surface at night, and repeated two or three times for increasing the possibility of catching enough animals. The resulting plankton was then diluted in a 10 litre plastic bucket, brought to the laboratory and diluted again to a volume of 100 litres in a glass aquarium (stock tank) measuring 66X40X40 cm.

The Sagittas were kept in this stock tank for 24 hours, together with the rest of the plankton and those which survived were sorted and placed in another aquarium (rearing system). The rearing system was similar to the one mentioned by Rice and Williamson (1970). It consisted of 15 cm. diameter and 16 cm. long perspex cylinders, suspended on an aquarium with continuous running water. The tops of the cylinders were above of the water level and the lower ends were covered with a 140 μ mesh cloth net. Both the rearing system and the stock tank were filled with seawater previously filtered with a wool filter polymer cartridge which would retain particles of about 0.5 μ (H. Omar, pers. comm). The rate of the water flow was such that the rearing system exchanged its contents 1 to 2 times per day. The stock tank was periodically emptied and replenished with fresh plankton.

The experiments were carried out at 10 $^{\circ}$ C in a constant temperature room. The temperature was controlled by a cooling system operated by a thermostat (± 1 $^{\circ}$ C). The room was illuminated by a neon tube lamp, for 12 hours a day.

After the chaetognaths were isolated in the perspex cylinders, food was provided. Experiments were planned to obtain knowledge about prey selectivity (Table 27) and feeding rate with changes in prey concentration. (org./litre) (table 28). All the experiments were carried out for 24 hours. The food supplied to the Sagittas was collected from the stock tank, poured in small Petri dishes and identified and counted with the aid of a low power microscope.

At the end of the 24 hours and before termination of the experiments by fixing the samples, observations were made by counting those food items which were alive. This was because, as reported by Feigenbaum and Reeve (1977), *Sagittas* feed on active prey. Consequently those prey found dead at the end of the experiment without any sign of digestion were reported as "unavailable food items" (see table 28). In all cases it was assumed that the feeding rate of the *Sagittas* was not affected as the number of food items unavailable for this reason was always negligible.

2.8.

Identification of the food items.

Food items were mainly identified with the aid of the following literature: For copepods, Giesbrecht (1892); Rose (1933); for dinoflagellates, Dodge (1982); other plankters; Tregouboff and Rose (1957) and Newell and Newell (1972). For the identification of the heavily digested material, permanent slides were made of the cutting blades of the mandibles of the following copepods: *Calanus spp.* (copepodite II, IV and adult), *Pseudocalanus* (copepodite III and adult), *Temora* (Copepodite II and adult), *Centropages* (copepodite III and adult), *Acartia* (copepodite III and adult) and *Oithona* (adult). These species represent only about 30% of the planktonic copepod species reported from this area by Lee (1971). However, they are the most numerically important in the area, and as will be shown, they are the most important food items both in *S. elegans* and *S. setosa*.

2.9.

Statistical analysis.

Statistical analyses of the samples were made by running the Statistical Package for the Social Sciences eXtended (SPSSX) program in an IBM computer mainframe system. Histograms were made in an Apricot X₁ computer with a SC₃ (Super Calc 3) spread sheet program and modified in an Apple MacIntosh Plus.

2.10.

Errors in Methods and comments.

2.11.

Sampling.

Due to the fact that nets were permanently open, midwater and near bottom samples were inevitably contaminated to a certain extent by organisms from the upper levels, e.g. midwater samples contaminated by organisms from surface. However this source of error was minimized by the relatively long towing times at the required depth, thus the great majority of the organisms caught came from the desired depth.

In normal weather conditions the 250 kg. weight gave a very constant wire angle of 5 to 8 degrees, but in rough weather it was greater and more variable, ranging from 10 to 15 degrees. In such rough conditions the subsurface tows were taken from 10 to 15 m depth, to avoid the net surfacing, and the deepest samples were taken 10 to 15m above the bottom to ensure that the net did not go into the

sediment. The differences in sampling depth between rough and calm weather are not great and the samples are not considered separately.

At certain times of the year the R/V "CUMA" was out of action, and due to this, samples from September 1987, were collected on board of the R/V "SULA". Sampling was made 5 miles off Port St. Mary, and the following events may have affected the results:

1) Samples were obtained only at 10 a.m. and 12 noon.

2) Tows were made from the stern of the boat (instead of from the beam as in "CUMA"). It could be observed that the nets were just behind the propeller and while some organisms were directed into the net at the surface, others may have avoided it. Also most planktonic animals showed serious damage, and measurements and gonadic stage determination in chaetognaths was difficult to achieve. Samples from these tows were extremely low in abundance.

3) The weight for making the "near bottom" tows was not heavy enough (as indicated by the wide angle on the wire), and tows from this depth were at best collected at midwater (ca. 15 m). This may have resulted in large chaetognaths not being sampled, as they are known to migrate to deeper strata during the day (see discussion).

2.12.

Subsampling.

Subsampling methods have greatly improved (see Omori and Ikeda, 1984), and various devices have been developed for this purpose.

Among the most used are Motoda splitters, Folsom splitter and Stempel pipette. However, obtaining a representative aliquot in kind and abundance from the whole sample can be sometimes difficult to achieve (see Lee, 1971 for discussion). The method followed in this study is similar to that used by Russell (1931b), Worthington (1931) and Lee (1971).

2.13.

Food Containing Ratio.

Observations made on the time for the prey to reach the anal area of the gut in *S. elegans* was estimated to be between 10 and 15 minutes (similar results were found by Khulman, 1977). Because sampling continued for 15 minutes, some of the food in the posterior third of the gut might have been ingested in the net can, where the prey is very concentrated, and this might have produced an overestimation of feeding in both species of *Sagitta*.

3.0.

Results.

3.1.

Temperature.

Variation of temperature at station 1, 1986-1987 and station 2, 1986, is shown in Figure 2. It can be observed that the lowest values were recorded in late winter and spring. Highest temperatures were found at the end of summer and beginning of autumn. After autumn temperatures dropped again and the cycle started again.

It should be noted that the temperatures shown are averages from those recorded from near bottom and surface. Possibly because of this, slightly lower temperatures were recorded at station 2. The reason for averaging the temperature was because it is the best way to assess the digestion time for the chaetognaths (digestion time is inversely related to temperature, i.e. the higher the temperature the shorter the digestion time, see chapter 4 for the results on feeding and references). Although this may give a slightly different picture for this parameter in an annual cycle, it was observed that differences were in fact ≈ 1 °C for both depths and only at station 2 in summer a 3 °C difference was recorded. The actual temperatures for station 1 and station 2 at both depths during 1986 and 1987 can be found in Graziano (1988, Ph. D. thesis in progress) (his stations 6 and 1 respectively).

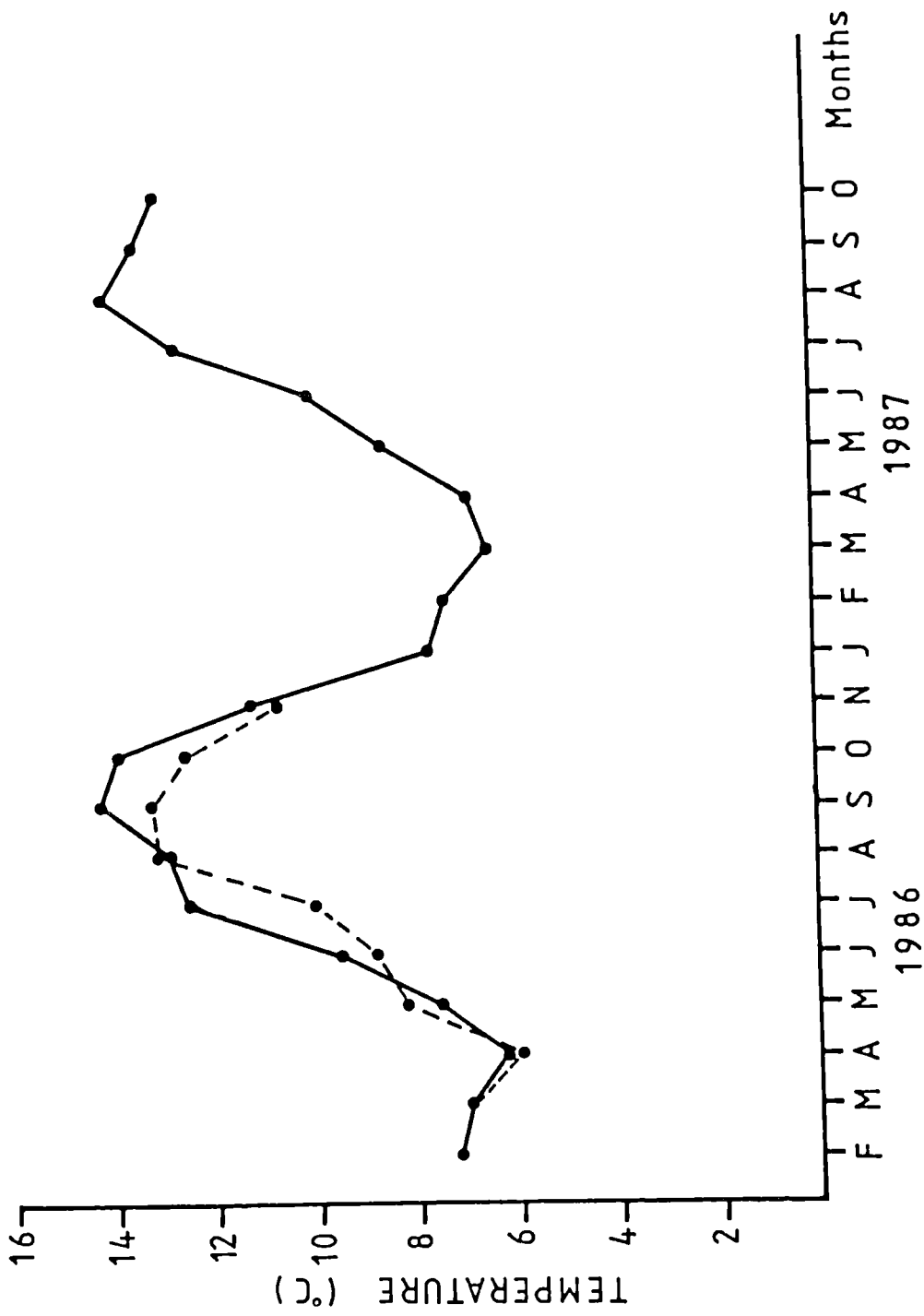


Fig. 2. Annual variation of the temperature °C (average) at station 1 (—) in 1986-1987 and station 2 (----) in 1986.

3.2.

Populations.

3.2.1.

Sagitta elegans.

3.2.1.1

Growth

Size frequency histograms and percentages of gonadic stages for *S. elegans* for station 1 in 1986 and 1987 and station 2 in 1986 are presented in figures 3c through 23c and 24. The size of the chaetognaths collected in 1986 at station 1 ranged from 1.2mm in April to 21.0mm in February. After the main spawning in April, the mean size of the *S. elegans* population decreased as the summer season approached. This decrement in mean size was observed until late summer. The population started to increase again in mean size in autumn, in such a way that in May of the following year the largest specimens were caught. At station 1, from February to April, 1986, due to relatively larger proportions in the catches of nearly newly hatched animals, the mean size of the population decreased drastically from 12.65 mm to 3.02mm. However, from April to June an increment in size of 5.51mm was recorded. This increment was the highest observed throughout the whole year. In June-July the mean size decreased again (1.24mm). Samples were not obtained in August and October this year, but increments in mean size were observed both from July to September (1.79mm) and from September to November (4.56mm). Growth for *S. elegans* was rather low from late autumn (November, 1986) to spring (March, 1987).

The mean size increased 0.57 mm between November and January and 0.41mm between November and March. In April 1987, spawning occurred, as was recorded the year before, and the cycle was completed.

Similar fluctuations in mean size and growth were observed in both 1986 and 1987, and station 2 (sampled only in 1986), showed essentially the same pattern as station 1.

3.2.1.2.

Gonad stages. Station 1, 1986

In February 1986, most sagittas were found to be in stage II. However, maturation had started, as was revealed by a low percentage of stage III individuals. Stage I made a slight contribution to the population in this month (Fig. 3c). The few stage I animals present had a rather high mean size (9.6mm, range 8.0mm to 14.2mm). They were very probably the survivors of the late spawners from the preceding year. Samples were not obtained in March this year (see however results for station 2 same year and results for station 1 in 1987 below). In April the onset of the spawning was clearly shown as the composition of the population had changed and stage I with a mean size of 2.6mm accounted for 98% of the collection (Fig. 4c). Once spawning started, it was more or less continuous until September. At that time stage III had practically disappeared and stage I made up 98.6% of the population and had significantly increased in mean size to 9.47mm (Fig. 7c). Stage I dominated the population from

April until November when it declined dramatically (Fig. 8c), This decline was probably due to maturation to stage II which became the main component of the population at that time of the year.

S. elegans overwintered mainly as stage II. Although stage II was recorded throughout the whole sampling period, maximum contributions were found in February and November. In April the numbers of stage II decreased sharply, but spawning had started, resulting in an increment in stage I (Fig. 4c). Although no samples were obtained in March 1986 at station 1, it was very likely that stage III sagittas were the most abundant, as they were at station 2 at that time and also in March 1987 at station 1. Stage III was recorded from February until September (Figs. 3c to 7c) and probably had a peak in March, but for the rest of the period they contributed only low numbers of specimens. No samples were obtained in October, and by November, stage III had disappeared from the population (Figs. 8c and 9).

3.2.1.3.

Gonad stages. Station 1, 1987.

In 1987, sampling was carried out more consistently, and plankton collections were obtained nearly every month from January to November except in February. The general trend of the population followed that described for 1986 (Figs.10c to 18c), however some small changes were detected. Samples from January 1987 contained a higher proportion of stage III (Fig. 10c) than those from February 1986, while stage I contributed with only 0.3%. Stage III was

abundant in March (Fig. 11c) and accounted for 98.6% of the animals; the remaining 1.4% were in stage II. No stage I was found in this month. In April spawning had occurred and Stage I, with a mean size of 3.4mm, became the most abundant (Fig. 12c). As in the previous year stage I was the main contributor throughout all the sampling period, except in May-June (Figs. 13c and 14c) where stage II was the main component. Stage II made a higher contribution during the whole period than the year before, but it was not collected in the tows in September (Fig. 17b), when a general decrease in abundance was observed in the whole population. However, sampling in this month was carried out in rather unusual conditions (see Material and Methods above). In October stage II had increased markedly in number (Fig. 18c), and by November it was the dominant stage, as was also found the year before. Observations of the results for the gonadic stages in November are included in figure 19.

3.2.1.4.

Gonad stages. Station 2, 1986.

Sampling at station 2 was carried out only in 1986 (Table 1). Results generally agree with those found at station 1, therefore stages I to III were recorded in February-March (Fig. 20c). The onset of maturation was evident at this time as an increase of stage III and a concomitant decrease in abundance of stage II. Only at this time individuals at this gonadic stage (III) were caught in high numbers. After that period they were recorded in various degrees

of abundance until September (Fig. 23c) when they practically disappeared. Stage I abundance was as described for station 1 from May to September (Figs. 21c to 23c, and 24). No samples were obtained in December both years at both stations. However, night tows at the Pier of Port Erin Bay carried out on the 26th of December 1987, showed that stage II was the most abundant, a small contribution of stage I was observed and stage III was not recorded. This may well also be applicable to the preceding year, and Pierce (1941), also found similar percentages of the respective stages in this area in December.

It is generally accepted that *S. elegans* dies after spawning (Kramp, 1917; Russell, 1932a; Alvariño, 1965). This work confirmed those findings and very low quantities of "spent" organisms (large, empty and flaccid ovaries, detached seminal vesicles) (King, 1979), were recorded for the whole study period. Spent individuals were not considered in the quantification of the *S. elegans* populations.

3.2.1.5.

Abundance.

Sagitta elegans was recorded on every sampling date and was usually the most abundant chaetognath in the study area for both years. The abundance of the animals (org/m³) at the depths sampled is presented in tables 9 to 26.

There were great fluctuations in abundance from month to month (Fig. 25a,b), with high numbers in June–July and November for station 1, 1986. In 1987 at the same station peaks of maximum abundance occurred in January and July. Major collections of this species at station 2, 1986, were recorded in July and September. Important recruitment of young stages is evident in April with the onset of breeding (both years). There was an increase in the numbers of stage I animals at this time, these having a mean size of 2.6mm and 3.4 mm at station 1 in 1986 and 1987 respectively, and 5.0mm at station 2 in 1986. The mean size allows us to differentiate two types of stages I in the population, i.e. those individuals with higher mean size found in January were thought to be the progeny from the late spawners of the preceding year; on the other hand stage I of smaller size recorded in April were most probably the progeny of the March spawners. Although an increment in numbers of stage I was recorded in April, the abundance of *S. elegans* in this month was actually not very high. This could be due to substantial mortalities of the young chaetognaths or to escapement of small animals through the net or both.

3.2.2.

Sagitta setosa.

3.2.2.1.

Abundance and Growth.

S. setosa was found from late summer to late winter at station 1. However, it was abundant only in September 1986 and October–

November 1987. Due to this seasonality and also because other factors such as currents and sampling method could have influenced the size frequencies of the populations, the assesment of growth and abundance for this species is difficult (see discussion below).

In September 1986, the mean size of the population was 8.59mm and increased to 10.49mm by November same year, and increased further to 11.50mm in January 1987 (Figs. 27c to 30c). In October 1987, the species was collected again and at that time the mean size of the population was 8.85mm and decreased to 7.81mm next month (reelevant statistics for the populations, e.g., Standard deviation, are included in the legends for the corresponding figures).

Vertical migration. See discussion.

3.2.2.2.

Size frequencies and gonadic stages.

Due to the seasonal occurrence of the species, the changes in the composition of the size frequencies and gonadic stages of the *S. setosa* population are difficult to interpret. This chaetognath was only found in sufficiently large numbers to the east of the Isle of Man (station1), from late summer to late winter (see Tables, 9,13,14,15,21). Although some small numbers were also collected in February 1986 at station 2, they are not included in the analysis of the results or discussion due to their scarcity. These records are however included in Table 23.

Size frequency histograms are shown in Figures 26c to 30c and 31-32, including the percentages of gonadic stages. Animals of this species with a maximum length of 14.80mm and minimum of 5.80mm were first recorded in the samples collected in February 1986. At that time stage I dominated the population contributing 83%, the remaining 17% were animals in stage II and no stage III individuals were recorded (Fig. 26c). The species disappeared from the area in the following months and was not recorded until September when spawning had already started as evidenced by the presence of the three maturity stages (Fig.27c). In this month stage I (38%) had a minimum size of 4.40mm (mean size stage I was 6.63mm), suggesting that spawning had probably begun the month before (see discussion below). 33% of the population was in stage II and 28 % was in stage III, so there was no clear dominance of any stage in this month. No samples were collected in October that year. November was characterized by the dominance of stage I (75%), which had also increased in mean size (9.85mm), while stage III had practically disappeared (ca. 2%), indicating that breeding had nearly been concluded (Fig.28c). *S. setosa* overwintered mainly as gonadic stage I individuals. In January 1987, stage I had increased its dominance to 87% and also increased in mean size (11.25mm). Stage II contributed with the remaining 13% and no stage III animals were recorded (Fig. 29c). As in the preceding year *S. setosa* disappeared from the area in the following months. Although samples were obtained in September 1987, animals of this species were not caught. However, samples in that month were obtained only 5 miles

off Port St. Mary and the species was probably present further east (see Material and Methods above). In October the population mainly consisted of stages I and II (40% and 59%, respectively). The mean size of stage I (6.70mm) indicated that spawning had started several weeks ago, while the scarcity of stage III individuals (1%) indicated that breeding was nearly completed (Fig. 30c). In November stage I was more dominant (94%) and the mean size had increased (7.60mm). The remaining 6% consisted of stage II and no stage III animals were recorded in the population (Figs. 31 and 32).

Largest specimens were collected in winter samples in both years, i.e. February 1986 (14.80mm) and January 1987 (16.80mm), while small specimens with minimum length less than 5mm were frequently caught in the summer and autumn.

4.0.

Vertical Migration.

Although the sampling was not primarily designed to assess the vertical distribution of the sagittas (see Material and Methods), a general view of this well known biological phenomenon is presented for *S. elegans*. Data for station 2, 1986 and station 1, 1987 (figure 33a, b) were chosen for explaining the diel vertical migration in this species. These data were more suitable for this purpose as day and night samples were collected closer together and also intervals from one sample to the next were shorter than at station 1 in 1986 (see table 1). As for *Sagitta setosa*, only some comments are

presented as this species was abundantly present only at station 1, and although found from summer to late winter they were usually abundant only in late summer and autumn. Also, according to some authors (see discussion), this species keeps a higher position in the water column than *S. elegans*, and the method followed in this study could lead to a misinterpretation of the vertical migration pattern.

4.1.

Sagitta elegans.

4.1.1.

Station 1, 1987

In January at station 1, when stage II dominated the population and stage III was also recorded, the population showed clearly a migratory pattern, i.e. the highest numbers of specimens were found near the bottom by day, while at night the highest numbers were caught near the surface (fig. 33a). During daytime, however, substantial catches were also obtained near the surface, and at night they were fairly evenly distributed at both sampling depths, with only slightly lower numbers near the bottom (fig. 33a). In March, spawners (stage III) were the main component of the catches and migration was rather more marked than in January. By day sagittas were very scarce near the surface and abundant near the bottom. At night time, however, they were found more abundantly near the surface although a significant number were also collected near the bottom.

This suggested that, as in the preceding month, sagittas were distributed more or less evenly in the water column at night. In April with the occurrence of spawning and high numbers of newly hatched stage I sagitta (mean size 3.4mm), the vertical migration was restricted. The small sagittas migrated downward to a lesser extent than the populations in the previous months, and animals were found more abundantly near the surface both by day and by night. In May a higher abundance of stage II was recorded and the population had recovered the migration pattern as described for January. In June and July only night samples were obtained and both of them showed a similar higher abundance near the surface, but with moderate numbers also present near the bottom. August was characterized by abundant catches near the surface both by day and night, as found for April, and again the population was made up mainly of small sagittas (mean size 4.95mm). September is not included due to the way the sampling was carried out (see Material and Methods). In October, chaetognaths were found nearly evenly distributed by day, while at night they were more abundant near the surface.

4.1.2.

Station 2 , 1986.

At station 2 in February only night samples were collected. It can be observed that similar quantities of animals were caught from near surface and midwater, while near bottom animals were scarce. In March samples were obtained only in the daytime, and the graphical representation (Fig. 33b) shows that sagitta stage III,

which was the main component of the population, was mainly abundant in the midwater tows, with practically no specimens at the surface and low quantities of individuals near the bottom. In June during daytime animals were found mainly near bottom, but midwater samples had also an important number of specimens. At night the animals were fairly evenly distributed at the three depths sampled. In July by day most of the animals were in midwater but also an important number of animals were caught near the bottom. At night highest numbers were obtained near the surface and midwater. In September during daytime no sagittas were collected and most of the animals were found near the bottom. At night most sagittas were found in the samples from near the surface.

5.0.

Discussion.

5.1.

Sagitta elegans.

In the Irish sea *Sagitta elegans* decreases in mean size from late spring to summer probably due to mortalities of the spawners and recruitment of young stages. Large specimens in stage III have been reported to die after spawning by Kramp (1917), Russell (1932a) and Alvariño (1965). Some workers however have reported "spent" organisms, i.e. animals with large, empty, flaccid ovaries and detached seminal vesicles, (King, 1979). These animals usually will sink rapidly to the bottom or will be predated by carnivorous copepods like *Centropages* (pers. obs., see also Jakobsen, 1971). In this study mortalities could be detected by looking at the number of animals caught. In June 1986 at station 1 the percentage of stage III was 9.6%, while in July it was only 1.5%. At the same station in 1987, these figures were 10.9 % and 0.8% respectively. No comparisons are offered for station 2 as no samples were collected in June. However, in July a high proportion of stage III were caught (19.11%), and consequently mean size had not decreased as for the population at station 1. This may be due to the differences in temperature, which although small, may have a direct influence on the gonad development. Rakusa-Suszczewski (1967), found that a *S. elegans* population may vary in length frequency and gonad development even in neighbouring stations with minor differences in temperature and salinity. Jakobsen (1971), suggested that small differences in temperature could promote distinct gonad

development in *Sagitta* due to the extent of the period they exerted their influence. McLaren (1963), found *S. elegans* development from egg to mature stages to be temperature dependant, i.e. the lower the temperature the longer it takes to reach maturity. This obviously has a direct influence on the number of generations produced annually. In boreal areas, higher latitudes usually have colder waters and Alvarino (1965) pointed out that the number of generations varies with latitude. Russell (1932a), reported four or probably five broods per year in the Plymouth area. His results were however criticised by Jakobsen (1971), explaining that Russell was very probably not sampling the same population during his collections. On the other hand, Dunbar (1941, 1952, 1962), working at the North Pole found one generation every two years, with alternating groups spawning every other year. This prolongation of the growth period was also observed in the other zooplanktonic groups collected simultaneously with the sagittas by Grainger (1962, 1965; see also Cairns, 1967). However, most authors reported a single breeding annually, which usually starts in spring and extends until the end of summer or beginning of autumn (Pierce, 1941; Dunbar, 1962, Sherman and Shaner, 1968, McLaren, 1969, O'Brien, 1976; Tande, 1983, Øresland, 1985). Some others have also found evidence of a second breeding starting in the late summer or autumn (Clarke *et al*, 1943; Sameoto, 1973; Zo, 1973, King, 1979). However they also acknowledged that this second breeding was far less successful and that it can vary from year to year depending on the food resources (cf. Clarke, *et al*, 1943). Wimpeny (1937), working in the North Sea, suggested three

possible broods, but he also mentioned that his data were insufficient to draw conclusions. Results from this work confirm those of Pierce (1941), i.e. only one *Sagitta elegans* generation is produced annually in the Irish sea.

A pattern can then be drawn from the life cycle of this species. Quoting Tande (1983): " The general trend emerging from comparisons between the various investigations appears to be that the number of generations of *S. elegans* produced yearly increases and the length of the life cycle decreases with increasing distance from the North Pole".

Temperature has a similar effect on the size reached by the animals. Dunbar (1962), collected animals up to about 44mm length at Ugava Bay and Frobisher Bay (from his figures 5 and 6), but size of specimens caught at Lake Ogac, where temperatures reached 8 °C in summer, were considerably smaller and maximum sizes were attained at about 20mm length (from his fig. 7). Other authors working at lower latitudes, reported also smaller sizes for this animal (e.g. Zo, 1973; King, 1979; Øresland, 1985). The maximum length for *S. elegans* in the present study was 23mm, but usually animals this size were rather scarce, and smaller animals were frequently caught. Pierce (1941) obtained similar results for the population of this species in Port Erin Bay (from his fig. 1).

Growth rate is also influenced by temperature. Reeve (1970), reported that the growth rate *S. hispida* in laboratory conditions

was directly proportional to temperature and level of feeding. In this work it was observed that the growth rate was low from November 1986 to March 1987 at station 1. At this time of the year three conditions were thought to influence in this low growth rate :

1) Temperature, which had already started to decrease in November and reached lowest values in February-March of the following year (Fig. 2).

2) Zooplankton was at its lowest abundance, and accordingly less food was available for the chaetognaths. Attention is however drawn to the discussion on feeding, as it seems that animals can meet their metabolic requirements even at low prey density, and other factors than prey availability affect the feeding behaviour of the sagittas in natural conditions (e.g. Pearre, 1973; Sullivan, 1980; Øresland, 1985).

3) *Sagitta elegans* population had overwintered mainly as stage II individuals, and these animals were dominant at that period. As suggested by several of the authors mentioned before, energy is mainly channelled to gonadic development, rather than somatic tissues (e.g. King, 1979; Øresland, 1985).

In summer this situation is reversed, i.e. gonad development was minimum, growth rate was high and temperature and plankton abundance were also high.

Seasonal fluctuations in abundance of the *S. elegans* population in this study agreed to a great extent with the results recorded by

Russell, (1933b), Pierce (1941), Clarke *et al* (1943), Sherman and Shaner (1968), O'Brien (1976), King (1979), Tande (1983), and Tiselius and Petersen (1985). They all recorded this species as being most abundant in the summer. Russell (1933b) reported also a secondary high abundance in February 1930 and November 1932. Pierce (1941) found a similar secondary high abundance at Port Erin Bay in November 1937. This all suggests that *S. elegans* thrives in summer when food is abundant. At the end of summer and beginning of autumn, the *S. elegans* population decreased numerically (see Fig. 25). This pattern was observed in September 1986 and from August through October 1987. Similar results were obtained by Pierce (1941). High numbers of animals could also be expected in April with the onset of the main spawning. However, at that time the population consisted mainly of small young sagittas and they probably escaped through the net. Kotori (1976), observed that *S. elegans* hatched at about 1.2 mm length and specimens up to 4mm had a diameter of only about 200 μ . Russell (1933b) was also aware of this problem and acknowledged that specimens up to 8mm length could be missing in his plankton collections. As the mesh size of the plankton nets used in this work was 330 μ m, small young specimens might have been lost from the samples, which would lead to underestimates of the real abundance of the small chaetognaths and of the population abundance as a whole. However the possibility of high mortalities of small animals, as suggested by King (1979), can not be discarded.

Gonad stage determination of the animals is subjective, and depends to a certain extent of the observer. This is particularly

applicable when trying to determine if a specimen belongs to stage I or stage II. This could have affected the gonadic development proportions, specially for those specimens from late summer-autumm when the stage I specimens were larger and the abundance of both stages (I and II) was high. King (1979) noted that sagittas can show intermediate stages between those mentioned above and this lead him to subdivide stage I into two stages. These discrepancies in gonad staging in chaetognaths might also have influenced the results of other authors specially those for the *S. setosa* populations (e.g. Øresland 1983)

There are several theories dealing with the vertical migration of planktonic chaetognaths. Different authors have tried to explain why or (better) what is the benefit gained by the organisms by changing their position in the water column. However no review of the extensive literature dealing with this biological phenomenon is attempted, some of the hypotheses are put forward, with some of the authors proposing them. The theories are mainly in the following groups:

- 1) Searching for a light optimum (Russell, 1927, 1931,).
- 2) Gaining in potential breeding (McIaren, 1963).
- 3) Beneficial substances (Clarke, *et al.*, 1943; Lee, 1971).
- 4) Food searching (Jakobsen, 1971).

5) Avoiding predation by visual hunters (Pearre, 1973).

Russell (1927, 1931), working in the area of Plymouth, observed that the size of the chaetognaths had a striking relation with their vertical distribution, i.e. the larger the organisms the deeper they would be found. He also reported that small sagittas could endure a higher and wider range of light intensities, quoting him: " The younger stages of *S. elegans* appear to withstand higher intensities of light in the daytime than do the older stages and they migrate first to the surface at dusk. The older stages leave the surface first at dawn". He concluded that sensitivity to light increased with increasing age, and that chaetognaths migrated in the daytime to deeper waters following a light optimum. McLaren (1963), proposed that chaetognaths would gain in potential breeding capacity by retarding growth at lower temperatures. Thus vertical migration would allow efficient feeding in the upper strata where more suitable and abundant food could be found, while migration downwards would allow a slower development which would permit channeling more energy to gonad development. On the other hand, Jakobsen (1971), working on samples collected by day, found that feeding could be slightly higher near the bottom. He suggested that food availability was the main reason for migrating to deeper strata. Clarke, *et al* (1943), in explaining the tendency for *S. elegans* to occur in shallow waters on Georges Bank, suggested the existence of some chemical element derived from the bottom or the presence of some food organisms dependent on the bottom which

were not present in deeper waters. Lee (1971), proposed that planktonic organisms react to gradients of nutrient values at least to the same degree as to thermoclines and haloclines, and suggested that: "gradients of taste may be as important as gradients of density in influencing the behaviour of planktonic organisms".

More recent theories about the reasons for the vertical migration of the animals, relate position changes in the water column to the avoidance of predation. Hutchinson (1967), in his Treatise of Limnology, commented that: "illumination is certainly the main variable to be considered" (in the vertical movement of the animals), although he also accepted that avoiding predation could at least play a role. Pearre (1973), proposed that "the state of satiation of the animal influences its depth control mechanism" and concluded that "*S. elegans* left surface during daytime primarily to avoid predation by visual hunters". In this work it was found that small sagittas in stage I undertook very short migrations during daytime (in fact at anytime of the day for those nearly newly hatched), as they were nearly all caught in the tows made near the surface. Stage II and Stage III were caught in deeper strata. This would corroborate Russell's theory of increasing sensitivity to light with increasing age. As for the theory of gaining in potential breeding (Maclaren, 1963), this would imply the existence of substantial differences in temperature between surface waters and near bottom, but the main area sampled (station 1) is characterized by well mixed waters, and important temperature differences were not observed. Regarding the presence of beneficial substances from

the bottom (Clarke, *et al*, 1943), or gradients of taste (Lee, 1971), no clear evidence has been given. Pearre's theory (1973), however sounds interesting. It would explain migration downward after satiation (feeding). When quiescent, chaetognaths are nearly invisible, but this situation changes when they move with their characteristic darting movements (as when hunting). Visibility is increased when they have undigested prey in their gut. As will be shown in the next chapter and references therein, copepods made up the main prey items for chaetognaths, and they can be seen through the body walls of the sagittas even after fixation when animals become more opaque. Copepods are rich in oils as a reserve material (Corkett and McLaren, 1978; Marshall and Orr, 1955), which has a larger digestion time. In this study 10% to 25% of the gut content of the sagittas with prey contained a certain amount of oil in their digestive tract. After the body of the copepods has been compacted, telescoped or even defecated, traces of oil could still be discerned (see also Øresland, 1978). This oil tracing is also applicable to other crustaceans like cirripede larvae, which can sometimes be heavily preyed upon. Appendicularians can also be sometimes important prey (see results on feeding and also Feigenbaum and Maris, 1984). Although appendicularians are considered to be fragile organisms, their faecal pellets resist digestion (Shelbourne, 1962; Feigenbaum and Maris, 1984) and can be easily detected as dark brown spots in the gut. Zaret (1972) found higher predation pressure on one of the two forms of *Ceriodaphnia cornuta*, the form with the bigger eyespot. He concluded that this large-eyed

cladoceran was more readily eaten by *Melaniris chagres*, (Pisces:Atherinidae) due to its higher visibility. Zaret and Kerfoot (1975), also found that predators would prey more heavily on easily detectable prey as compared with larger ones, i.e. these predators (*Melaniris chagresi*) were feeding according to visibility selection, rather than body-size selection. Also, chaetognaths with a more advanced gonadic stage (stages II and III) are more easily visually detectable, as ova have a different refractive index. In this respect it seems that very frequently the gonads of many invertebrates have oils or oil derivatives as main chemical components (see Giese and Pearse, 1974). This could be also a complementary explanation for stronger migrations to deeper strata by day with increasing mean size (and consequently gonad development). All these factors would make the sagittas more visible and more vulnerable to an attack by a predator. Pearre's theory, however, does not explain why newly or recently hatched sagittas do not undertake significant migrations. According to Reeve and Cosper (1975), newly hatched sagittas do not feed (and accordingly they are less visible), and they only start feeding two or three days after hatching. Pearre, in his results found very few small sagittas at night near the surface and none by day, and he interpreted this as evidence for vertical migration. His figure 4 showed his results in this respect, and it can be observed that all his small specimens in stage I were found above 20 m depth (actually \approx 18 m). Although this distance could be regarded as substantial for such a small animals, from the point of view of avoiding predation through invisibility, it may not be of great advantage, particularly because July was the time of his

collections, a month when high light intensities were recorded (twice as high as those recorded in December). One simple explanation is that small sagittas do not migrate and high mortalities occur. McLaren (1963), reported that, although mortalities of young animals were high in surface waters due to predation, they maintained their position in the upper strata because of appropriate food and the higher temperature. He also pointed out that the small organisms were less efficient in obtaining their food and less resistant to food shortages, thus a constant supply of food was necessary. This should be regarded not only in terms of abundance but also the prey needs to be of the right size for the predator to handle it. He stated " surface waters are almost universally warmer which would allow faster growth and although predation was high, any retarding effect due to low temperature will entail proportionally higher mortalities". He concluded that " Under these conditions a rapid development could be selected for". Apparently this fast growth by small sagittas is indeed very important and evidence is provided by the fact that they have a greater Specific Daily Ration than larger specimens (SDR is defined as the weight of food consumed daily per unit / weight of chaetognath) (Feigenbaum, 1979). Reeve (1970), working with *Sagitta hispida* also found that growth was directly influenced by both temperature and level of feeding. Another possible explanation could be found by looking at the metabolic expenditure for the smaller migration of the small animals. Bone *et al* (1987), found that *S. elegans* has neutral buoyancy, and therefore migration downwards is not the product of passive sinking but an active

mechanism with cost of energy. McLaren (1963), stated : " the small size of the surface-dwelling species means that a given extent of migration would be proportionally more energy consuming". Unfortunately there are not any measurements of energy expenditure for vertical migration in these animals, but if small sagittas are less efficient swimmers, as inferred by the differential swimming rates (Pearre, 1973), then the metabolic energy expenditure involved in large migrations could be too costly for small sagittas. This also would imply a slower growth, because more energy would be utilized in migrating, with the consequent higher mortalities mentioned above.

Although Pearre's theory does seem to give a reasonable explanation for the vertical migration of the larger specimens, it does not explain the absence of large migrations of the newly or recently hatched sagittas.

The abundant supply of suitable food and high temperatures have been suggested as reasons why small animals do not migrate to deep waters. The high metabolic cost of swimming is another possible reason. However, nothing can be concluded in this respect and more studies will be necessary for clarifying the different behaviour of small sagittas.

5.2.

Sagitta setosa

Results obtained in this study agree with those from Russell (1932,

his plate II), Pierce (1941, his fig. 2), Jakobsen (1971, his Figs. 14-15) and O'Brien (1976, his fig. 3). All these authors found that *S. setosa* overwintered mainly as stage I, which was also found in this work. Khan (1970), however, found that stage II was dominant in the winter. Øresland (1983) found stage I from summer until autumn from 1975 to 1977 and they were only abundant for a short time in the middle of that period (his figures 5, 6 and 7). In that study he recorded stage I as late as October 1975 and recorded it again in January 1976. In 1976 stage I was collected until November but it was not recorded at the beginning of the next year. In 1977, it was collected until December. At no time was stage I found to be dominant in late autumn-winter, and his results showed that the population at this time mainly consisted of stage II. The different results obtained by Øresland (1983) and Khan (1970) on the one hand and this study and those of other authors (e.g. Pierce, 1941) on the other, could possibly be explained by discrepancies from author to author concerning the staging of the animals. This is supported by the fact that Øresland (1983), found stage II even smaller than 5mm length. The minimum length for stage II found in this work was 5.80mm in September 1986. Minimum size for this stage recorded by Russell (1932b) and Pierce (1941) was about 7mm, while Jakobsen (1971) reported stage I as small as ca. 5mm.

There are also controversial findings concerning the number of broods produced yearly by this species. Russell (1933), suggested five or six generations per year in the English channel, but his

results were analyzed by Jakobsen (1971), who pointed out that Russell's findings were difficult to interpret due to possible import of other *S. setosa* populations. Pierce (1941), mentioned two possible breeding periods in the outer Mersey channels, one starting in April which would extend until June, the second spawning in August. However, during the period from April through August he found only small numbers of stage I (April), and these animals had already a minimum size of about 8mm (his fig. 2). In his results no stage I was recorded in the following months, i.e. from May through August, so although gonadic stage III animals were present in April, it seems to be that spawning actually did not occur until September, when small stage I were found. Øresland (1983), also recorded stage III from April-May but no evidence of spawning was found. *S. setosa* is an allochthonous species in the Kattegat, and the species is transported to that area as a mixture of adults and juveniles, i.e. no eggs were found. Because of this, Øresland, (1983) defined spawning as the presence of small stage I, less than 3mm length. He found a life span of one year in that area and pointed out that: " the appearance of stage III individuals is not an appropriate definition of breeding period since such individuals were also found at a time (April-May) when no breeding is evident". Khan and Williamson (1970) working in the Irish Sea, found low abundances for this species in April-May at all stations, and high abundance in August-September mainly at stations 5, 6 and 7 (their fig. 2). They pointed out : " *Sagitta setosa* has a prolonged breeding period with one peak in spring and another in late summer-autumm". Khan (1970), found animals less than 5mm in

March and April (his fig. 3), and 2mm specimens in August. However, no animals this size were found in spring by Russell (1932b) in the Plymouth area and neither did Pierce (1941) in the Irish Sea. Several authors have acknowledged the difficulty of identifying *sagitta* specimens of less than about 6mm (e.g. Williamson, 1956a). This is of particular importance because *S. setosa* and *S. elegans* overlap in their distribution in the sampled area. *S. elegans* spawning, however, is well established as occurring in spring (Russell, 1932a; Pierce, 1941; Jakobsen, 1971; Zo, 1973; O'Brien, 1976; King, 1979; Tande, 1983; Øresland, 1983; this work), which is not the case for *S. setosa*, and the records of such small animals by Khan (1970) could well have been misidentifications.

Establishing the number of broods for *S. setosa* in this work is difficult to achieve because the species disappeared from the sampling area in spring-summer. However, if we combine the results obtained by Pierce (1941), with those obtained here, it could be possible that *S. setosa* has only one brood annually.

This, however would imply the acceptance of the following assumptions, which are nonetheless not difficult to believe:

- 1) As suggested by Øresland (1983), the presence of stage III does not imply breeding.
- 2) The small numbers of stage I animals larger than 7mm length recorded by Pierce (1941) are not the result of breeding at that

time. The large minimum size of the animals suggests instead that they are the progeny from the spawners of the preceding year.

3) The conditions in Liverpool Bay and neighbouring sea areas (e.g. temperature and food availability), are similar to those found in the sampled area. Consequently the population found near the Isle of Man, which spreads from about June until December from the west coast of England into this area (see Williamson, 1952, 1956a; Khan and Williamson, 1970), undergoes similar changes.

Expanding on assumption 2, it is worth noticing that spawners in stage III can be found as late as November. *Sagitta elegans* hatches at about 1.2 mm length (Kotori, 1975), and although the hatching size of *S. setosa* is not known this species is smaller than the former and a similar or smaller hatching size would be expected. In the present work, stage I *S. setosa* were observed to increase in length by 1.38mm between November 1986 and January 1987. No figures are available for February–April, but the average temperature in these months would be similar to that in November–January and a similar growth increment may be assumed. A specimen hatched in November would then reach a length of ca. 8mm in April and would provide an explanation of the specimens found by Pierce (1941) at that time.

If the 3 assumptions presented above are accepted, then the following theoretical picture of the life cycle of *S. setosa* can be constructed.

S. setosa breeds from about July-August to November, all the three stages are present throughout that period, stage I having a minimum length of less than 5mm. The species overwinters from December to February mainly as stage I, with maturation to stage II of part of the population mainly in the latter month. No stage III are present at this time of the year. In April-May stage II becomes more abundant and the mean size increases. This stage is dominant at that time and part of the population (stage II) matures to stage III. This maturation to stage III extend until June-July. However, no stage I would be present in spring or early summer or if recorded (as in April), the relatively large minimum length of the specimens would identify them as originating from the brood of the preceding year. This situation, with no stage I specimens of less than 5mm, would extend until June-July. In July-August breeding starts again and the life cycle is completed. Although this scheme seems reasonable, the number of generations of *S. setosa* produced annually in the eastern Irish Sea should be regarded as not yet determined, and a more consistent sampling program is required to give definitive results.

Few observations on the position of *S. setosa* in the water column were made in this work. It occurred only in the autumn samples, and the sampling was restricted to two depths. Most authors have found that this species dwells in upper waters. Russell (1931), found higher numbers of small specimens near the surface, but he also pointed out that large *S. setosa* were usually found higher in the water column than *S. elegans*. Jakobsen (1971), however, found no

correlation between size of individuals and vertical distribution. He stated " *S. setosa* in the Oslofjord is rather strictly confined to the upper waters". Kramp (1915) (cited in Øresland, 1983), reported that *S. setosa* was a well marked surface species. The results of the present work add little to these earlier observations.

6.0.

Results (feeding).

6.1.

Food items.

Analysis of the gut content was carried out for 21,351 specimens; 17225 for *Sagitta elegans* and 4026 for *S. setosa*. The results are presented in figures 3a to 23a for station 1, 1986-1987 and station 2, 1986 for *S. elegans*; figures 26a to 30a show in a similar way the results for *S. setosa* both years at station 1.

Sagittas mainly preyed upon copepods, with *Pseudocalanus* usually as the dominant food item. Other copepods, such as *Oithona*, *Acartia*, *Centropages*, *Temora* and *Calanus*, were also consumed in large numbers although never to the same extent as *Pseudocalanus*. Other plankters, like Cirripedia larvae and tintinnids or dinoflagellates, were abundantly recorded in the digestive tract of the chaetognaths at the times when those animals were abundant in the field (e.g. Cirripeds) or when the size of the sagittas was such that they could only handle the smaller prey available such as dinoflagellates or tintinnids.

Appendicularians also contributed consistently to the diet of both species, and it were particularly important for *S. setosa*. Fish eggs and larvae (*Clupea harengus* mainly) were found in much lower percentages in the stomachs of the predators.

6.2.

Gut Content analysis.

Sagitta elegans.

In February 1986, at station 1, copepods made up to 83 % of the

plankton samples (table 9). The main component of *S. elegans* prey also consisted of copepods (76%) with *Pseudocalanus* contributing 40 %. Other important prey were *Oithona* (10.4%) and *Sagitta* (10.0 %). In April important changes in the plankton were observed and *Temora*, *Pseudocalanus*, and cirriped larvae were dominant. However, changes in the population of sagittas were also recorded (i. e. spawning has occurred) and small sagittas which made up the main bulk of the population did not feed substantially on the most abundant species at that time of the year. Instead they preyed upon small organisms as tintinnids (21.3%), nauplii (15.6%) and *Dinophysis* (7.1%). The large amount of OMNI (Organic Material Not Identifiable) was probably due to ingestion of small soft-bodied animals, which by effect of digestion were not possible to recognize (see discussion).

Temora (30 %), *Acartia* (25%), *Pseudocalanus*(22%), *Calanus* (10%) and *Centropages* (5.5%) dominated the plankton samples taken in June, and this was to a certain degree mirrored in the gut content of the sagittas. *Pseudocalanus* had recovered its importance as prey (39%) followed by *Centropages* (28%) and *Acartia* (7.4%). Nauplii (7.7 %) were mainly found in the smallest predators.

In July *Acartia* (36.6%) was most abundant in the field and this was reflected in the stomach content of the sagittas ; 15 % of the animals with food content contained this copepod, but it was second to *Pseudocalanus* which was again the main contributor to the diet although second in abundance in the field (26.7%). Although, nauplii (10.7%), *Oithona* (10.4%) and appendicularians (7.0%) also contributed substantially to the diet of the predators, these

organisms were not as abundant in the field as expected (see discussion). *Acartia* increased in abundance in September (69%) and increased also its percentage as food of the sagittas (30%), *Pseudocalanus* continued to be the principal prey (40%), while *Oithona*, Appendicularia, nauplii and *Centropages* (in that order of importance) were also found in the stomachs of the chaetognaths. At this time spawning of herring has occurred but the contribution to both the plankton samples (0.8%) and gut content (0.7%) was very low.

In November the same pattern as for September was observed. *Acartia* decreased in abundance in the field (51%) and in the gut content (25%). *Pseudocalanus* maintained its position as main food and increased in abundance in the samples (17%). Herring, however, decreased numerically in the field but increased as prey to 1.8 % in the diet.

In 1987, same station, a generally similar pattern in plankton and sagitta's prey composition was observed. However, there were some minor variations. Field samples from March were abundant in cirripeds (36 %) and this was mirrored in the gut content of the animals where they were the main component (68%). *Pseudocalanus* was the second most abundant both as prey (21%) in the plankton samples (20%). The other main difference for this year was found in June when *Temora* was found abundantly in the samples (43%) and this species was second in frequency in the gut content (23%).

At station 2, 1986 some differences in the food composition and in

the plankters were observed. Firstly, in February-March higher proportions of appendicularians and *Calanus* were found both in the field (35% and 9.6%) and in the gut content (13.6 and 11.8% respectively) than for station 1. Polychaetes were abundant in this area (13%) and had also a certain degree of importance in the diet.

S. elegans as prey also appeared at this time (3.6%). Zooplankton samples from May-June were dominated by *Calanus*, *Temora*, Cladocera and *Pseudocalanus* and in the stomach content the main species found were *Temora* and *Pseudocalanus*, followed by nauplii, *Calanus*, Appendicularia and *Centropages*. Cladocerans made up only 1.7% of the recorded prey. The plankton composition and abundance of July-August and September were also mirrored in the stomach content of the animals.

6.3.

Sagitta setosa.

Relating the kind and abundance of the zooplankton with the gut content of this species is more difficult than for *S. elegans*. This was possibly due to the fact that *S. setosa* fed on smaller particles and these organisms were not always representatively caught by the net. A more detailed explanation will be offered in the discussion, in this paragraph only observations of the main food items are presented.

S. setosa was first caught in February 1986 (for this species only results for station 1, are included, because as mentioned before, this species was very rarely caught both in numbers and frequency

at station 2). At that time *Oithona* (28.6%), *Pseudocalanus* (22%) and appendicularians (15.4%) were the main food items eaten. *Sagitta* contributed with 1.8% and food items as small as Lamellibranchia and *Coscinodiscus* were recorded, although in the lowest percentages (Fig. 26a).

In September of the same year this species was feeding mainly on appendicularians (29%), 3 species of copepods, namely *Acartia* (23%), *Pseudocalanus* (20%) and *Oithona* (10%) (see Fig. 27a). November showed a similar pattern for the gut content analysis, with the inclusion of *Dynophysis* contributing 6% of prey eaten (Fig. 28a). In January 1987, when the species was collected again, the main food found was in order of importance : Appendicularia (41%), Nauplii (12%), *Pseudocalanus* (9.6%) and *Oithona* (7.4%). Herring was also preyed upon more heavily than found before (6%) and *Coscinodiscus* was recorded again in the lowest percentages (Fig. 29a)

S. setosa was collected until October, and appendicularians and the tintinnid *Stenosomella* contributed to its food in similarly high percentages (27.7% and 24.3% respectively). *Pseudocalanus*, *Oithona* and *Acartia* were the other important prey in the diet (Fig. 30a).

6.4.

Feeding in relation to depth and time of day.

Figures 3b to 23b provide the information of the Food Containing Ratio (FCR) in percentages, regarding the feeding of *Sagitta elegans* at station 1 in 1986-1987 and station 2 in 1986. No figure is provided for for September 1987, due to the way the sampling was

carried out (see Material and Methods above). Graphs 26b to 30b show similarly the same results for *Sagitta setosa*. It can be observed that with few exceptions *S. elegans* fed more heavily at the surface in darkness. On the other hand *S. setosa* did not show a regular pattern, i. e. the species was feeding similarly at both depths and regardless of the time of the day. Further information for the FCR (food Containing Ratio) mean NPC (Number of Prey per Chaetognath) and Feeding Rate (FR) is presented in tables 5 to 8 for the different gonadic stages of both species of *Sagitta*.

6.4.1.

Sagitta elegans

In February 1986, at station 1, the curve for the feeding rate was similar for both depths, with slightly higher percentages near the bottom (Fig. 3b). This situation was reversed in April when spawning had occurred. Small sagittas which made the main bulk of the population fed at all times near the surface (Fig. 4b). Samples from June (fig. 5b) show that feeding was similar at surface and bottom during daytime. However, this figure also shows higher feeding activity at the surface at night, with a peak at 04 hrs. The lowest FCR was recorded from the samples collected at 06 hrs (Fig. 5b). In July a similar pattern was observed as in the month before with only small changes. The highest predation rate was recorded at 03 hrs., and three periods of low food consumption were detected; these were at 09 hrs., at 12 noon and at 06 hrs next day (Fig. 6b). Sagittas in September fed in very low percentages at both depths during daytime, a dramatic increase was recorded at 21 hrs.,

and this high predation increased even further at 24 hrs. at the surface and decreased at the bottom. At 03 hrs., feeding frequency decreased at both depths and by 06 hrs. a similar low predation was recorded as the day before (fig. 7b). Samples from November were obtained only by day. Specimens were not collected at the surface, and at the bottom the FCR was more or less steady at about 30%.

In January 1987, the animals fed in similar percentages at both depths, and the FCR increased at night. In March, due to the strong vertical migration behaviour of the adult sagittas, which dominated in the population, specimens were not caught at the surface during the daytime. By day feeding was low near the bottom and increased dramatically at night at both depths. From April onwards the feeding behaviour of the animals essentially did not change. Thus, within certain limits, the results observed followed the same pattern as described for 1986, same station.

In February-March at station 2, samples were obtained mainly at night in February (see Table 1); the samples taken by day in March are not included for the food containing ratio of the species. *S. elegans* at this station shows similar results to those described for station 1, although some minor variations were observed, mainly related to the fact that this station is much deeper than station 1. Animals were often abundant at samples taken in midwater tows, particularly by day (see Tables 23 to 26), and this was reflected in the feeding frequency of the animals. At night, however, when predation was heavier, near surface and midwater strata had more

specimens with food in the stomach than those from samples near the bottom.

6.4.2.

Sagitta setosa.

This species is known to dwell less deeply in the water column than *S. elegans* (see discussion for vertical migration, above). This behaviour was somehow mirrored in the feeding activity of the species. However in February 1987, the curve for the FCR shows that feeding near the bottom was slightly heavier than at the surface. *Sagitta setosa* also showed an increase in feeding activity at night, as found for *S. elegans*.

6.5.

Seasonal feeding .

Regardless the higher prey availability at certain periods, as evidenced by the zooplankton abundance (org/m³), *S. setosa* and *S. elegans* did not show a regular pattern. i. e. they did not necessarily predate more heavily when there was more food available, and the results in this respect will be considered in the discussion.

6.6.

Comparison of the FCR for *S. elegans* and *S. setosa*.

From Figures 3b to 23b and 26b to 30b, it can be observed that in general a higher predation was recorded for *S. elegans*. This species oftenly reached FCR values above 50 %. On the other hand *S. setosa* frequently had values below that figure, the exception being

for specimens collected in October 1987, when a FCR of about 60% was recorded.

6.7.

Food Containing Ratio, Multiple Prey and Feeding Rate.

Results concerning the Food Containing Ratio (FCR), for the three gonadic developmental stages, Mean Number of Prey per Chaetognath (NPC) and Feeding Rate (FR) for the samples as a whole, are provided in Tables 5 to 8 for both species in 1986-1987 at station 1 and 1986 for station 2.

The following general pattern for the chaetognaths studied can be observed :

- 1) Although sometimes smaller specimens (mean size) had similar or (rarely) higher values, usually the larger specimens had higher FCRs.
- 2) The FCR was always higher at night than during the day.
- 3) Regarding the depth, the FCR did not follow a regular pattern, i.e. at times it was higher near the surface and in other occasions it was similar or higher from samples collected near bottom. This is also applicable to station 2; however it was observed that specimens from midwater samples frequently had a higher FCR than specimens from the other two depths.
- 4) The FCR was usually lower than the NPC, and this is only logical, as NPC includes multiple prey. When the FCR and NPC had the same

Month	Gonad stage	%	Mean size	FCR Day	FCR Night	FCR Surf.	FCR Bott.	FCR (per stage)	FCR (sample)	Mean NPC	FR
FEB.	I	34.0	9.62	0.156	0.167	0.137	0.184	0.161			
	II	61.0	11.92	0.203	0.260	0.214	0.229	0.226	0.227	0.270	1.231
	III	5.0	14.80	*	*	*	*	0.294			
APR.	I	98.0	2.60	0.362	0.668	0.570	0.460	0.515	0.515	0.540	2.236
	II	0.1	*	*	*	*	*	*			
	III	1.9	15.90	*	*	*	*	*			
JUN.	I	69.0	6.33	0.168	0.350	0.266	0.231	0.254	0.346	0.404	2.023
	II	21.5	10.01	0.156	0.391	0.287	0.304	0.284			
	III	9.4	13.80	*	0.517	0.562	0.428	0.502			
JUL.	I	91.0	7.95	0.169	0.341	0.242	0.235	0.246	0.313	0.354	2.144
	II	7.5	9.94	*	0.446	0.388	0.308	0.380			
	III	1.5	11.60	*	*	*	*	*			
SEP.	I	98.6	9.47	0.099	0.331	0.251	0.204	0.221	0.221	0.278	
	II	1.0	*	*	*	*	*	*			
	III	0.3	*	*	*	*	*	*			
NOV.	I	11.0	11.11	0.302	**	*	0.302	0.302	0.311	0.311	2.504
	II	89.0	13.84	0.32	**	*	0.32	0.32			
	III	0	*	*	**	*	*	*			

Table 5.-Gonadic stages, Food Containing Ratio (FCR), Mean Number of Prey per Cheetognath (NPC) and Feeding Rate (FR) in *S. elegans* at station 1 in 1986. * Not enough data or no sagittas collected. ** No samples obtained.

Month	Gonad stage	X	Mean size	FCR Day	FCR Night	FCR Surf.	FCR Bell.	FCR (Per stage)	FCR (Sample)	Mean NPC	FR.
JAN.	I	0.3	10.6	*	*	*	*	*	0.138	0.150	0.751
	II	71.0	13.84	0.116	0.180	0.153	0.137	0.146			
	III	28.6	15.96	0.087	0.170	0.141	0.123	0.130			
MAR.	I	0	*	*	*	*	*	*	0.320	0.382	1.581
	II	1.3	12.12	*	*	*	*	*			
	III	98.6	15.10	0.051	0.506	0.469	0.257	0.32			
APR.	I	88.0	3.44	0.175	0.293	0.293	0.176	0.234	0.234	0.237	1.100
	II	3.0	9.67	*	*	*	*	*			
	III	9.0	16.75	*	*	*	*	*			
MAY	I	22.7	5.99	0.117	0.300	0.228	*	0.215	0.309	0.376	2.073
	II	49.5	10.71	0.053	0.400	0.354	0.372	0.304			
	III	27.8	15.08	0.088	0.572	0.563	0.415	0.409			
JUN.	I	33.7	5.95	**	0.353	0.378	0.328	0.353	0.475	0.535	
	II	55.5	9.992	**	0.591	0.668	0.534	0.597			
	III	10.8	13.52	**	*	*	*	*			
JUL.	I	83.3	4.36	**	0.319	0.354	0.285	0.319	0.377	0.454	
	II	15.6	9.08	**	0.436	0.498	0.375	0.436			
	III	1.1	12.93	**	*	*	*	*			
AUG.	I	97.4	4.90	0.082	0.262	0.143	0.156	0.160	0.160	0.173	1.536
	II	2.6	8.96	*	*	*	*	*			
	III	0	*	*	*	*	*	*			
SEP.	I	100	9.20	0.99	**	0.062	0.136	0.099	0.099	0.099	
	II	0	0	*	**	*	*	*			
	III	0	0	*	**	*	*	*			
OCT.	I	62.3	10.34	0.224	0.448	0.345	0.327	0.336	0.367	0.400	3.551
	II	37.7	12.95	0.239	0.559	0.412	0.386	0.399			
	III	0	0	*	*	*	*	*			

Table 6.-Gonadic stages, Food Containing Ratio (FCR), Mean Number of Prey per Chaetognath (NPC) and Feeding Rate (FR) in *S. elegans* at station 1 in 1987. * Not enough data or no sagittas collected ** No samples obtained.

Month	Gonad stage	\bar{x}	Mean size	FCR Day	FCR Night	FCR Surf.	FCR Midd.	FCR Bott.	FCR (Per stage)	FCR (Sample)	Mean NPC	FR
	I	7	10.13	*	*	*	*	*	*			
FEB.-	II	72	12.6	0.272	0.298	0.266	0.342	0.238	0.283	0.329	0.374	1.548
MAR.	III	21	14.75	0.375	*	*	0.353	0.398	0.375			
	I	59.8	5.06	0.328	0.350	0.263	0.358	0.345	0.333			
MAY-	II	35.3	12.41	0.432	0.572	0.580	0.552	0.410	0.509	0.421	0.437	2.410
JUN.	III	4.9	18.30	*	*	*	*	*	*			
	I	52.4	6.24	0.159	0.205	0.200	0.189	0.140	0.179			
JUL.-	II	28.4	12.08	0.155	0.301	*	0.215	0.141	0.203	0.251	0.304	2.226
AUG.	III	19.2	17.07	0.171	0.452	0.705	0.277	0.263	0.373			
	I	88.2	12.22	0.107	0.175	0.141	0.131	0.072	0.127			
SEP.	II	11.4	14.86	*	*	*	*	*	*	0.127	0.133	1.389
	III	0.4	*	*	*	*	*	*	*			

Table 7.-Gonadic stages, Food Containing Ratio (FCR), Mean Number of Prey per Chaetognath (NPC) and Feeding Rate (FR) in *S. elegans* at station 2 in 1986. * Not enough data or no sagittas collected ** No samples obtained.

Month	Gonad stage	%	Mean Size	FCR Day	FCR Night	FCR Surf.	FCR Bolt.	FCR (Per stage)	FCR (Sample)	Mean NPC	Feeding rate.
FEB. (1986)	I	82.8	10.23	0.175	0.213	0.202	0.186	0.194	0.216	0.229	2.181
	II	17.2	12.41	0.188	0.244	0.199	0.246	0.219			
	III	0	0	0	0	0	0	0			
SEP. (1986)	I	40.3	7.28	0.038	0.262	0.131	0.094	0.131	0.213	0.222	3.152
	II	31.4	8.96	0.057	0.477	0.243	0.211	0.247			
	III	28.3	11.09	0.157	414	0.277	0.198	0.261			
NOV. (1986)	I	36	9.33	*	*	*	*	0.246			
	II	64	11.63	*	*	*	*	0.165	0.205	0.205	2.549
	III	0	0	*	*	*	*	0			
JAN. (1987)	I	33.5	10.38	0.66	0.181	0.067	0.159	0.118	0.135	0.138	1.380
	II	66.5	11.75	0.98	0.206	0.14	0.164	0.152			
	III	0	0	*	*	*	*	0			
OCT. (1987)	I	42.4	6.70	0.162	0.419	0.310	0.272	0.291	0.286	0.379	5.350
	II	57.6	10.26	0.134	0.432	0.286	0.279	0.282			
	III	0.1	12.42	*	*	*	*	*			

Table 8. -Gonadic stages, Food Containing Ratio (FCR), Mean Number of Prey per Chaetognath (NPC) and Feeding Rate (FR) in *S. setacea* at station 1 in 1986-1987. * Not enough data or no sagittas collected ** No samples obtained.

value, this is indicative that no predators were found with more than one prey at a time.

Most of the animals were found with only one prey specimen in their gut, but specimens with two prey items were recorded fairly frequently, and predators with more than two prey were very scarce. The maximum number of prey in a predator was five, except in samples from October 1987, when small *Sagitta setosa* of about 3 to 4mm length were found to contain up to nine specimens of *Stenosomella*. This was the reason for the high difference between the FCR and NPC for this species in that month, i.e. the higher the difference in value between the FCR and NPC, the higher the frequency or the number of prey found in the predators.

The FR was defined as the number of prey eaten per day (see Feigenbaum and Maris, 1984), and animals fed more heavily at night as evidenced for the higher FCR values (see Figs. 3b to 30b and also Tables 5 to 8). For this reason when only day or only night samples were obtained no values for the FR are presented. Feeding Rates for *Sagitta elegans* ranged from 0.75 prey day⁻¹ to 3.55 prey day⁻¹. Values for *Sagitta setosa* were from 1.38 to 5.35 prey day⁻¹. It is difficult to compare feeding rates between the species, particularly because there are fewer values for *S. setosa*. However it seems that *S. elegans* has lower FR values. It was not possible to find a relation between the prey availability and the Feeding Rates of the animals, and the possible reasons for this finding will be treated in the discussion.

Fig. 3,A,B,C.

Station 1

February 1986.

A) Percentage occurrence of food items in *S. elegans*, as recorded from field samples.
OMNI= Organic Material not identifiable.

B) Food Containing Ratio (FCR) found in analysis of gut contents of *S. elegans* from day-night samples. Surf. (_____) Bott. (-----).

C) Size frequency distribution histogram of *S. elegans* of different maturity stages.

Statistics (All stages)

N = 1291

Mean 12.65 (Length in mm).

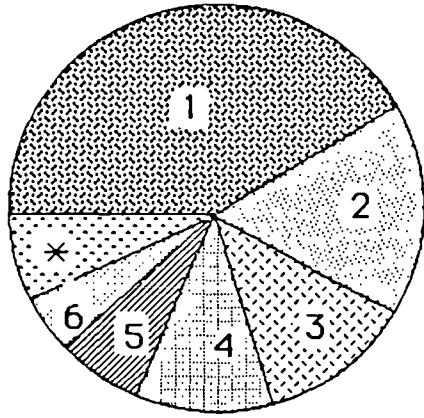
Standard error 0.049 Standard deviation 3.02.

Mean size stage I = 10.14

Mean size stage II = 12.77

Mean size stage III = 15.56

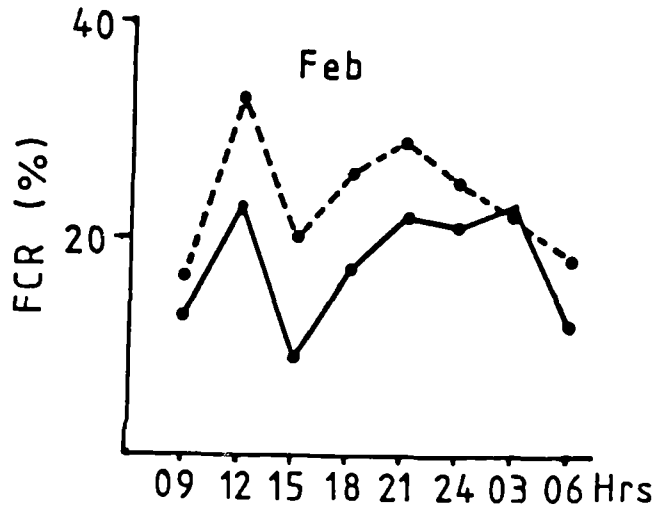
A



Feb.

Items	%
1.- <i>Pseudocalanus</i>	40.1
2.- OMNI	17.7
3.- <i>Oithona</i>	10.4
4.- <i>Sagitta</i>	10.0
5.- Copepod remains	7.0
6.- <i>Centropages</i>	5.4
* Others	9.4
Nauplii	2.3
<i>Temora</i>	2.0
Appendicularia	1.5
<i>Acartia</i>	0.7
Crustacean eggs	0.7
Polychaeta	0.3

B



C

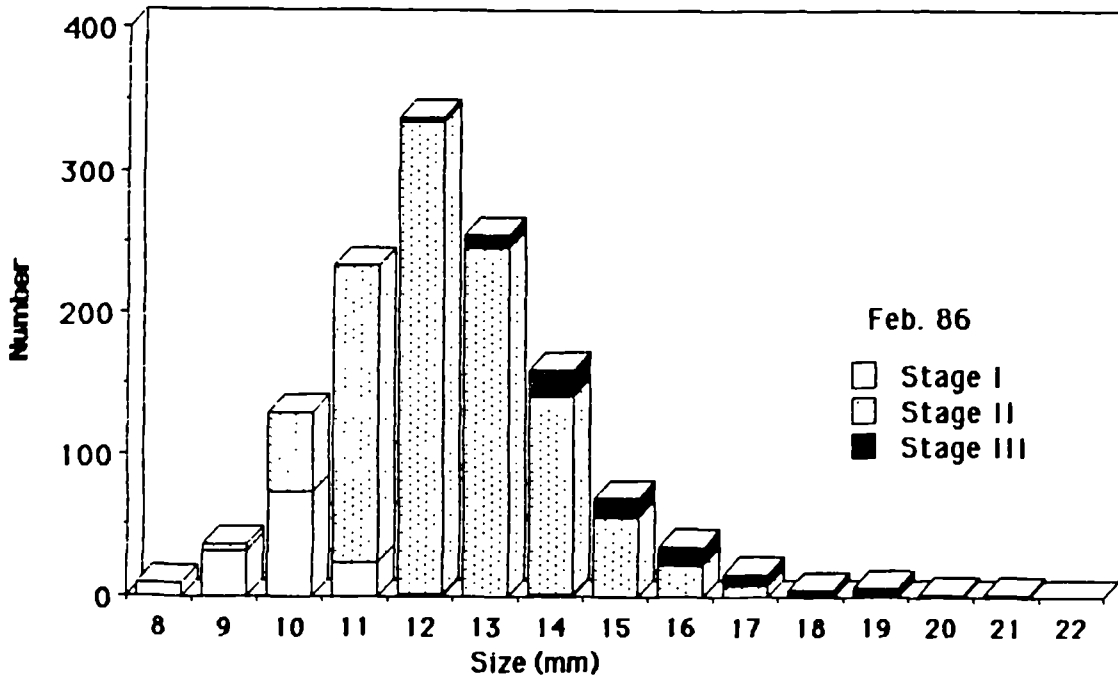


Fig. 4,A,B,C.

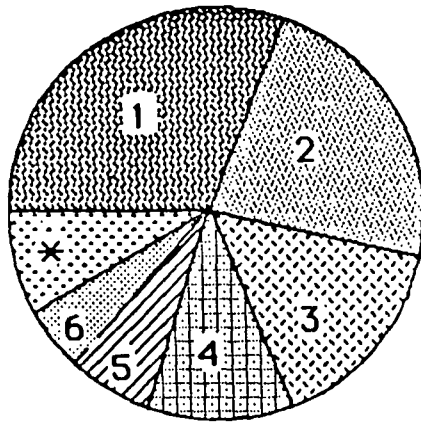
Station 1

April 1986.

- A)** Percentage occurrence of food items in *S. elegans*, as recorded from field samples.
OMNI= Organic Material not identifiable.
- B)** Food Containing Ratio (FCR) found in analysis of gut contents of *S. elegans* from day-night samples. Surf. (_____) Bott. (-----).
- C)** Size frequency distribution histogram of *S. elegans* of different maturity stages.
Statistics (All stages)
N= 690
Mean 3.02 (Length in mm).
Standard error 0.107 Standard deviation 2.80
Mean size stage I = 2.55
Mean size stage II = 12.00
Mean size stage III = 15.66

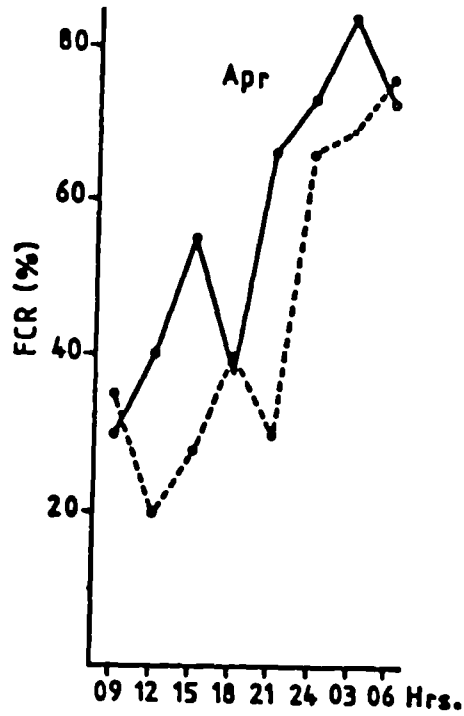
A

Apr.



Items	%
1.- OMNI	36.6
2.-Tintinnids	21.3
3.-Nauplii	15.6
4.- <i>Dinophysis</i>	7.1
5.-Undetermined	6.5
6.-Crustacean eggs	4.1
* Others	8.5
Cirripedia	3.0
<i>Pseudocalanus</i>	2.0
Polychaeta	1.7
<i>Calanus</i>	0.6
<i>Centropages</i>	0.6
Cladocera	0.6

B



C

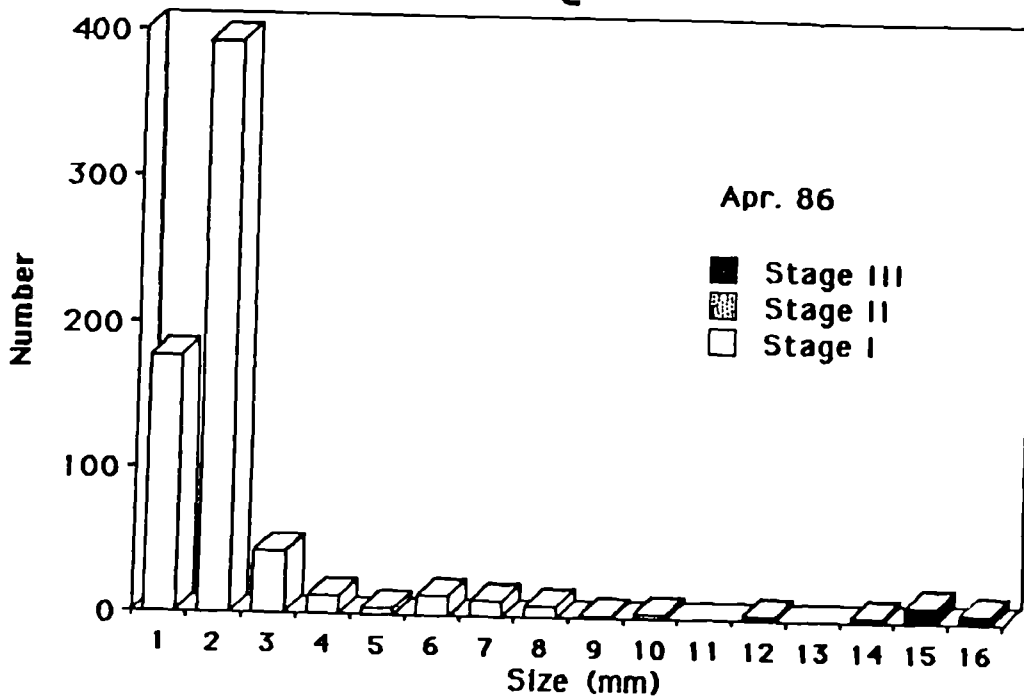


Fig. 5,A,B,C.

Station 1

June 1986.

A) Percentage occurrence of food items in *S. elegans*, as recorded from field samples.
OMNI= Organic Material not identifiable.

B) Food Containing Ratio (FCR) found in analysis of gut contents of *S. elegans* from day-night samples. Surf. (_____) Bott. (-----).

* No sagittas collected.

C) Size frequency distribution histogram of *S. elegans* of different maturity stages.

Statistics (All stages)

N= 1097

Mean 8.53 (Length in mm).

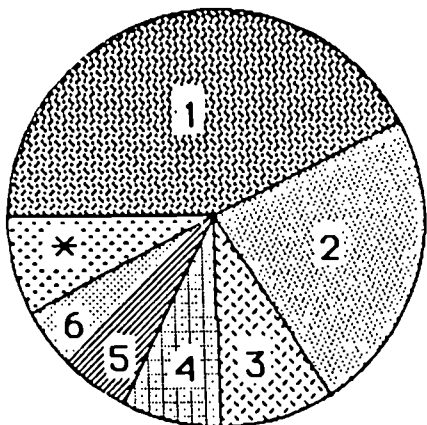
Standard error 0.091 Standard deviation 3.02

Mean size stage I = 7.01

Mean size stage II= 11.37

Mean size stage III= 13.51

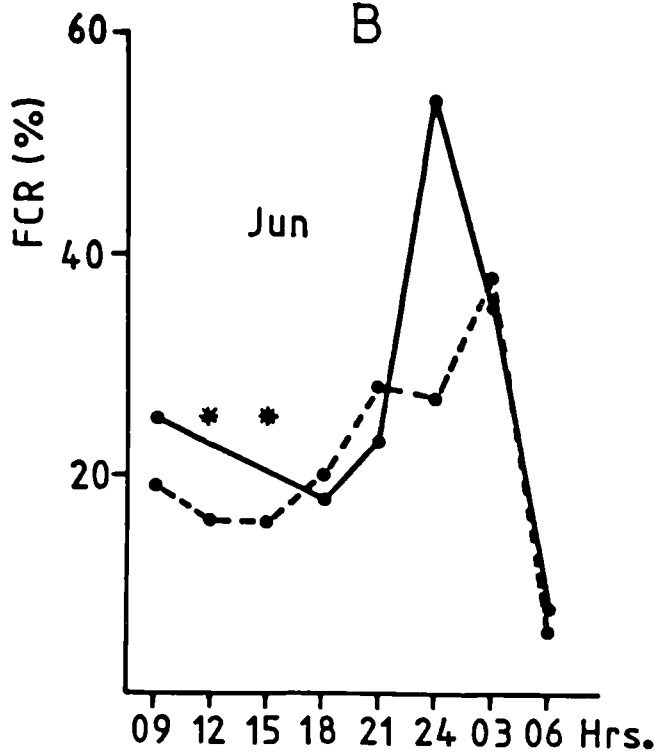
A



Jun.

Items	%
1.- <i>Pseudocalanus</i>	39.0
2.- <i>Centropages</i>	28.3
3.- Nauplii	7.7
4.- <i>Acartia</i>	7.4
5.- OMNI	5.4
6.- <i>Calanus</i>	3.3
* Others	8.9
<i>Temora</i>	3.0
Appendicularia	2.7
Crustacean eggs	1.3
Copepod remains	1.3
Cladocera	0.3

B



C

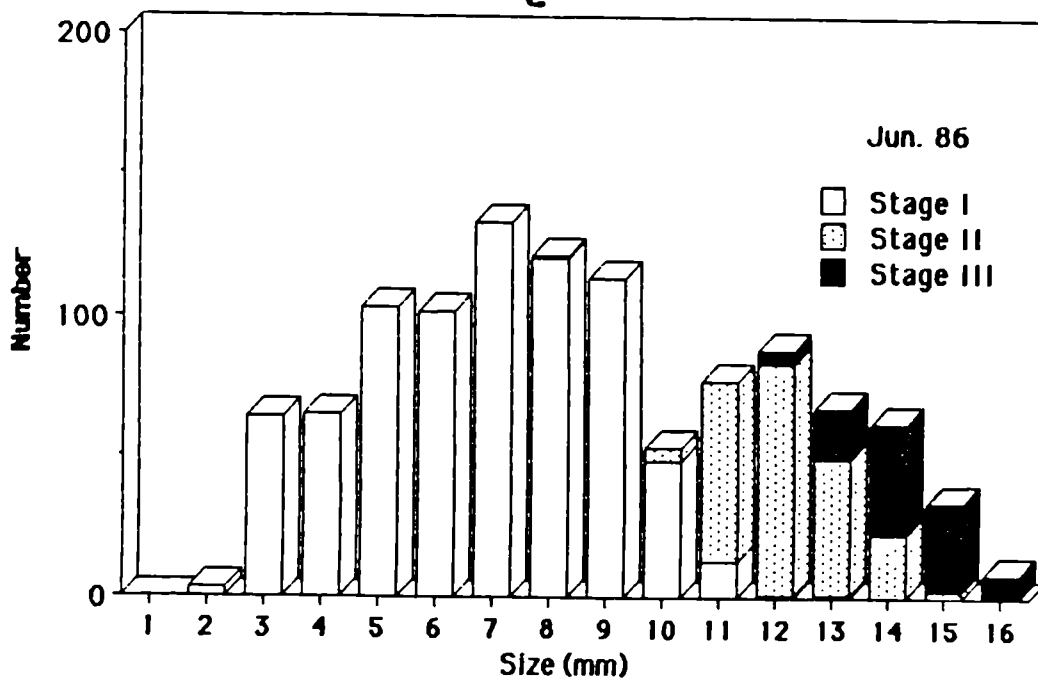


Fig. 6,A,B,C.

Station 1

July 1986.

- A)** Percentage occurrence of food items in *S. elegans*, as recorded from field samples.
OMNI= Organic Material not identifiable.
- B)** Food Containing Ratio (FCR) found in analysis of gut contents of *S. elegans* from day-night samples. Surf. (_____) Bott. (-----).
- C)** Size frequency distribution histogram of *S. elegans* of different maturity stages.
Statistic (All stages)
N= 1390
Mean 7.30 (Length in mm).
Standard error 0.057 Standard deviation 2.14
Mean size stage I = 7.03
Mean size stage II = 9.93
Mean size stage III = 11.57

Jul.

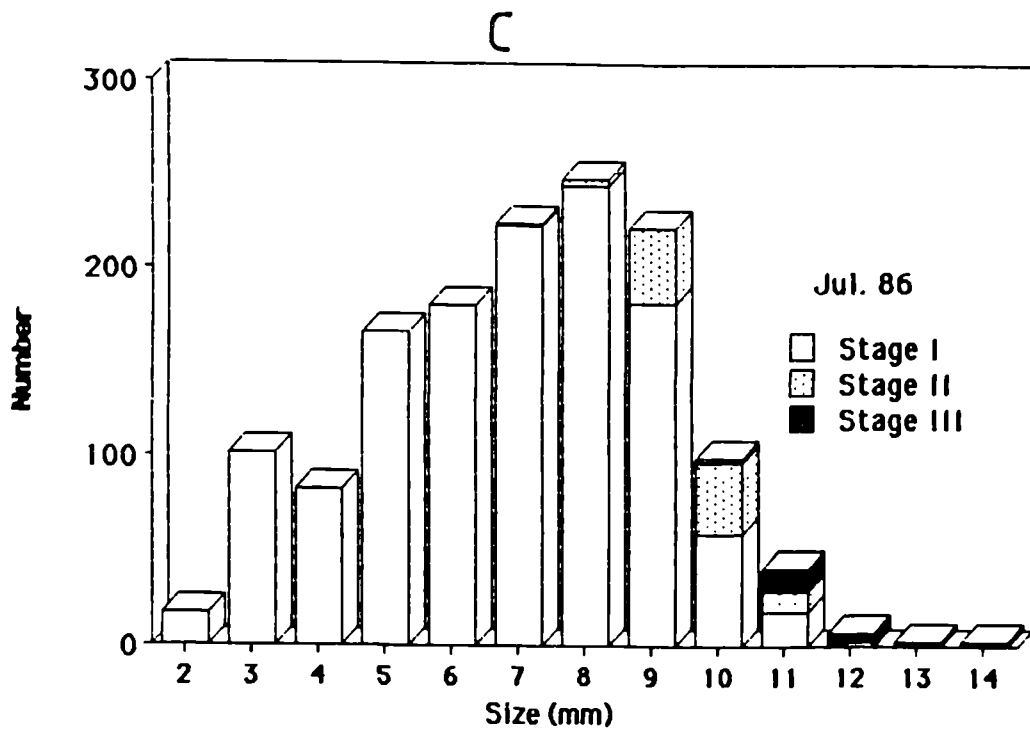
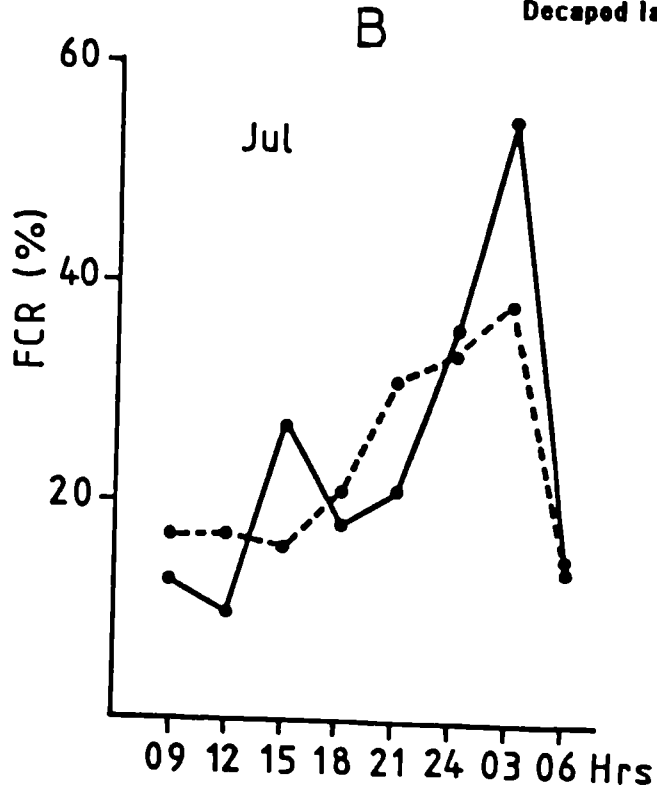
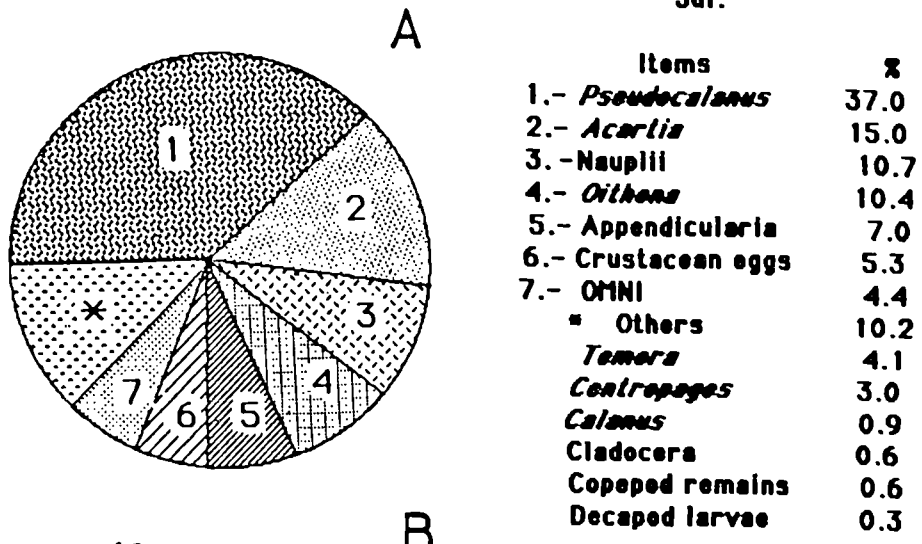
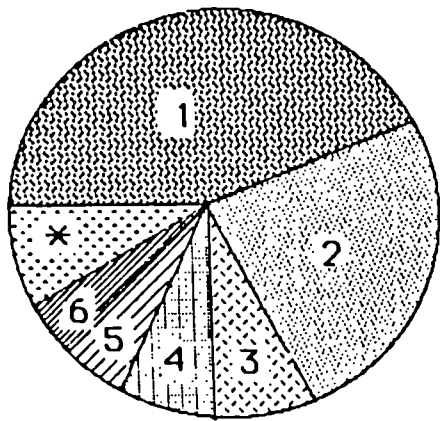


Fig. 7,A,B,C.

Station 1

September 1986.

- A)** Percentage occurrence of food items in *S. elegans*, as recorded from field samples.
OMNI= Organic Material not identifiable.
- B)** Food Containing Ratio (FCR) found in analysis of gut contents of *S. elegans* from day-night samples. Surf. (_____) Bott. (-----).
- C)** Size frequency distribution histogram of *S. elegans* of different maturity stages.
Statistics (All stages).
N= 576
Mean 9.08 (Length in mm).
Standard error 0.084 Standard deviation 2.02
Mean size stage I = 8.90
Mean size stage II = 13.31
Mean size stage III = 14.00



Sep

Items	%
1.- <i>Pseudocalanus</i>	40.7
2.- <i>Acartia</i>	30.7
3.- <i>Oithona</i>	6.1
4.- Appendicularia	5.4
5.- Nauplii	5.4
6.- <i>Centropages</i>	3.0
* Others	8.7
<i>Temora</i>	2.3
<i>Calanus</i>	1.5
OMNI	1.5
Fish eggs	0.7
Crustacean eggs	0.7
Herring	0.7
Copepod remains	0.7

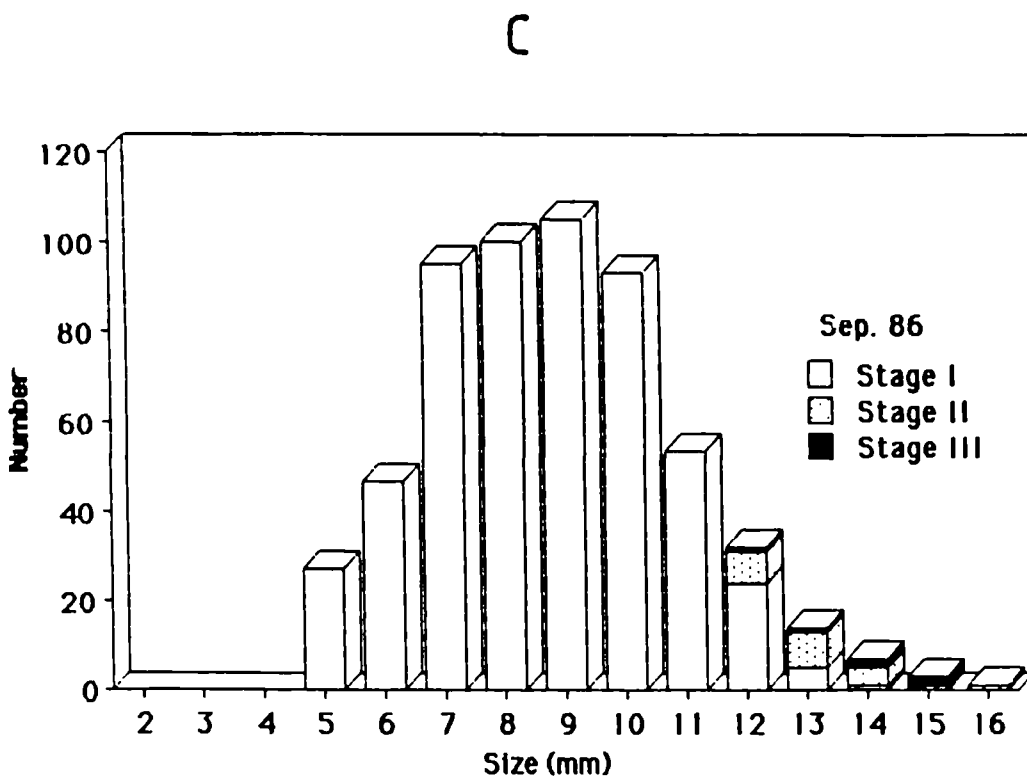
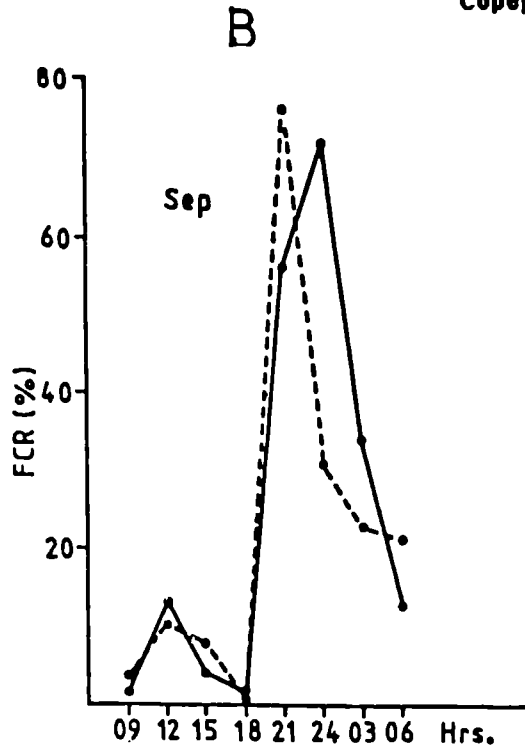


Fig. 8,A,B,C.

Station 1

November 1986.

A) Percentage occurrence of food items in *S. elegans*, as recorded from field samples.
OMNI= Organic Material not identifiable.

B) Food Containing Ratio (FCR) found in analysis of gut contents of *S. elegans* from day samples. Surf. (_____) Bott. (-----).

* No sagittas collected.

C) Size frequency distribution histogram of *S. elegans* of different maturity stages.

Statistics (All stages)

N= 277

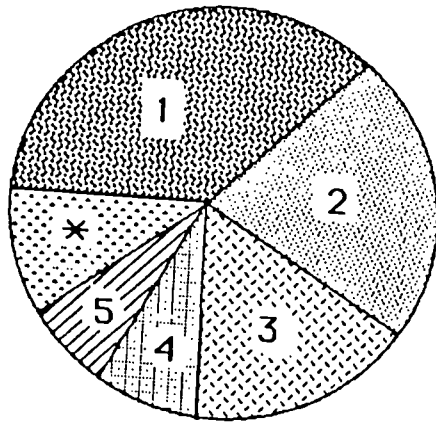
Mean 13.64 (Length in mm).

Standard error 0.091 Standard deviation 1.51

Mean size stage I = 11.00

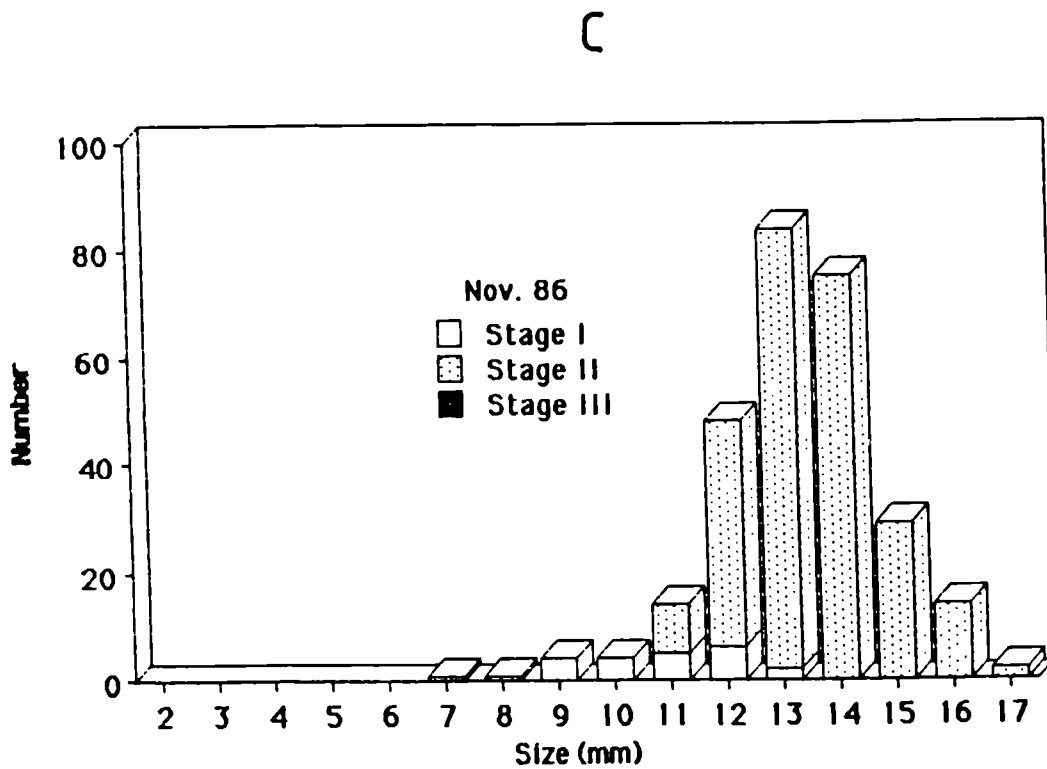
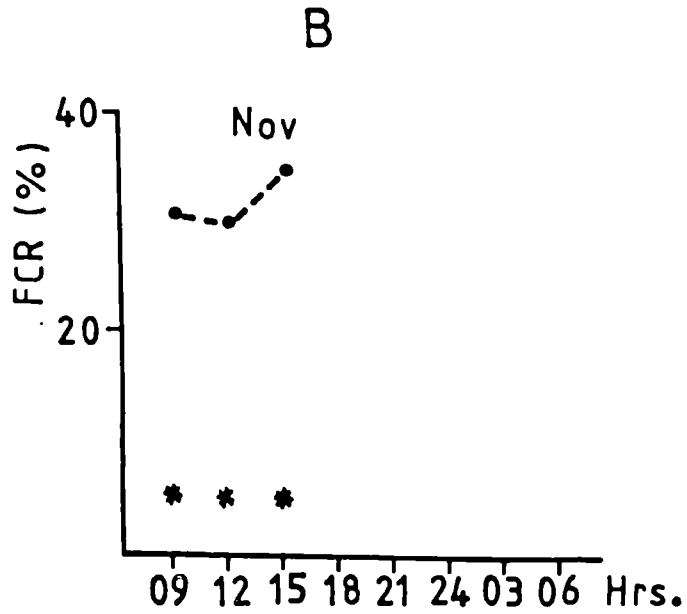
Mean size stage II = 13.87

No stage III recorded.



Nov

Items	%
1.- <i>Pseudocalanus</i>	35.4
2.- <i>Acartia</i>	25.0
3.- <i>Appendicularia</i>	19.0
4.- <i>Oithona</i>	5.4
5.- <i>Temora</i>	4.2
* Others	10.8
Nauplii	2.7
Copepod remains	2.7
OMNI	2.0
Herring	1.8
<i>Calanus</i>	1.3



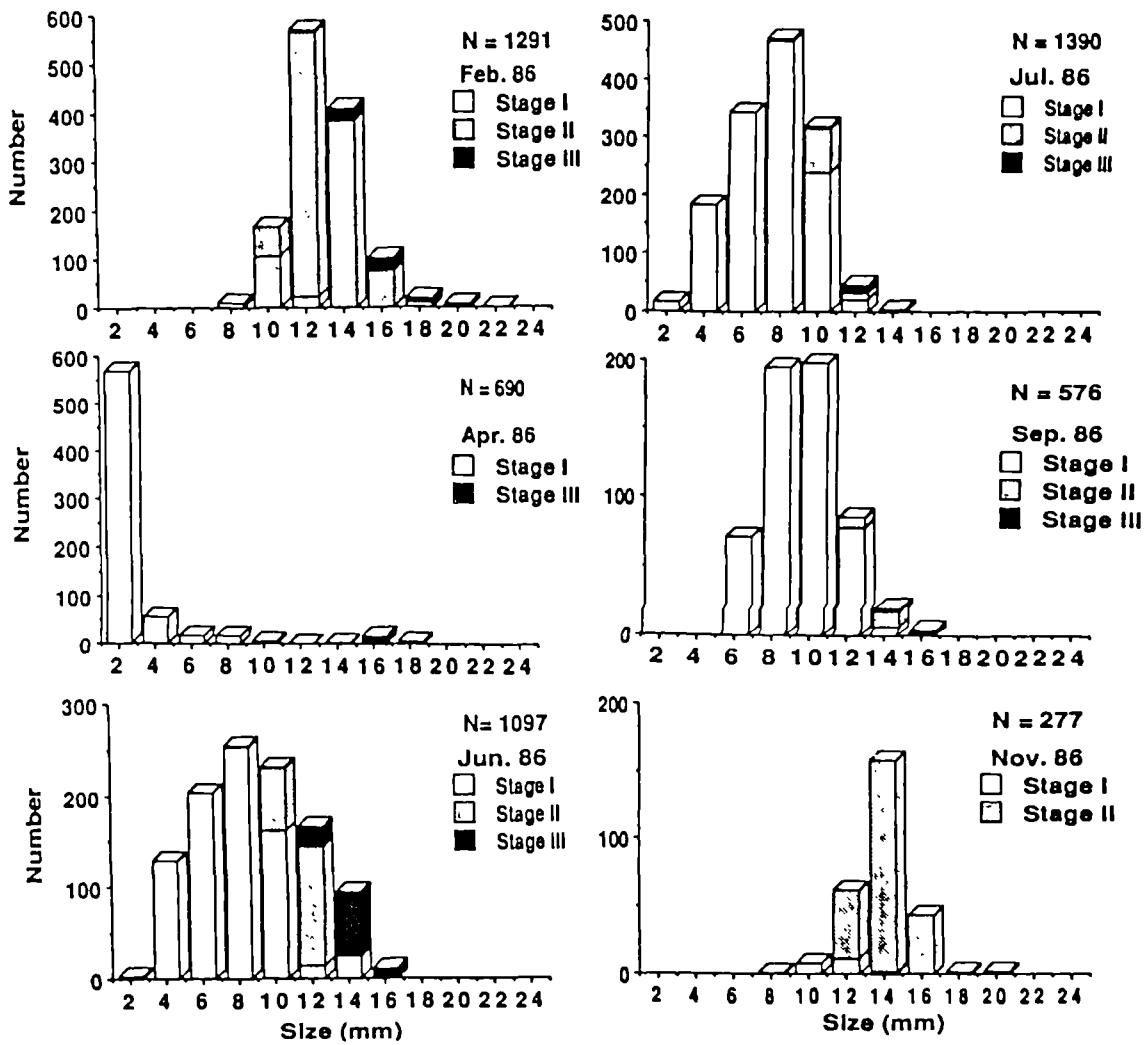


Fig. 9 - Length-frequency and maturity stages of *Sagitta elegans* at station 1, 1986.

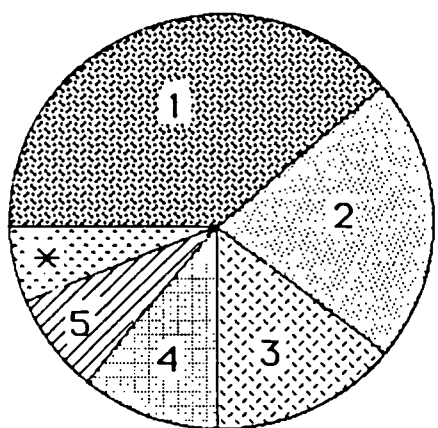
Fig. 10,A,B,C.

Station 1

January 1987.

- A)** Percentage occurrence of food items in *S. elegans*, as recorded from field samples.
OMNI= Organic Material not identifiable.
- B)** Food Containing Ratio (FCR) found in analysis of gut contents of *S. elegans* from day-night samples. Surf. (_____) Bott. (-----).
- C)** Size frequency distribution histogram of *S. elegans* of different maturity stages.
Statistics (All stages)
N= 1717
Mean 14.21 (Length in mm).
Standard error 0.038 Standard deviation 1.58
Mean size stage I = 10.05
Mean size stage II = 13.87
Mean size stage III = 15.62

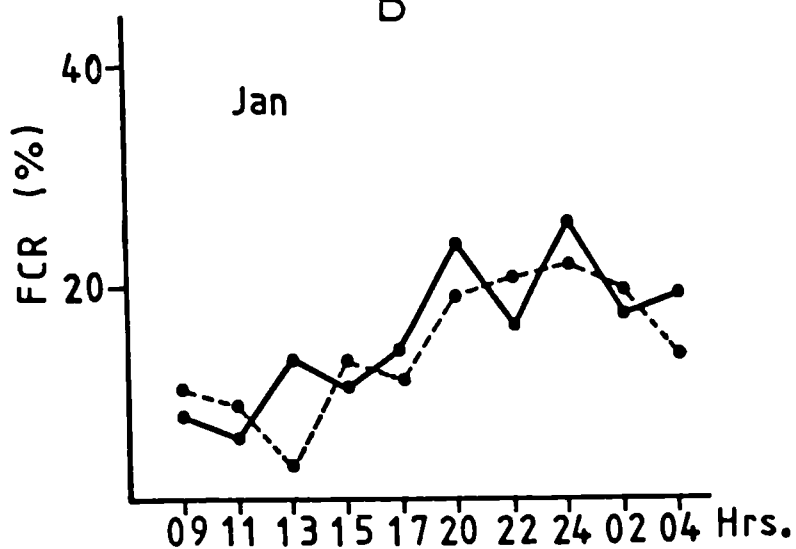
A



Jan.

Items	%
1.- <i>Pseudocalanus</i>	36.0
2.- <i>Acartia</i>	24.7
3.- Appendicularia	16.2
4.- OMNI	11.0
5.- Herring	7.1
* Others	5.0
<i>S. elegans</i>	1.6
Copepod remains	1.4
<i>Calanus</i>	1.2
Nauplii	0.4
Oithona	0.4

B



C

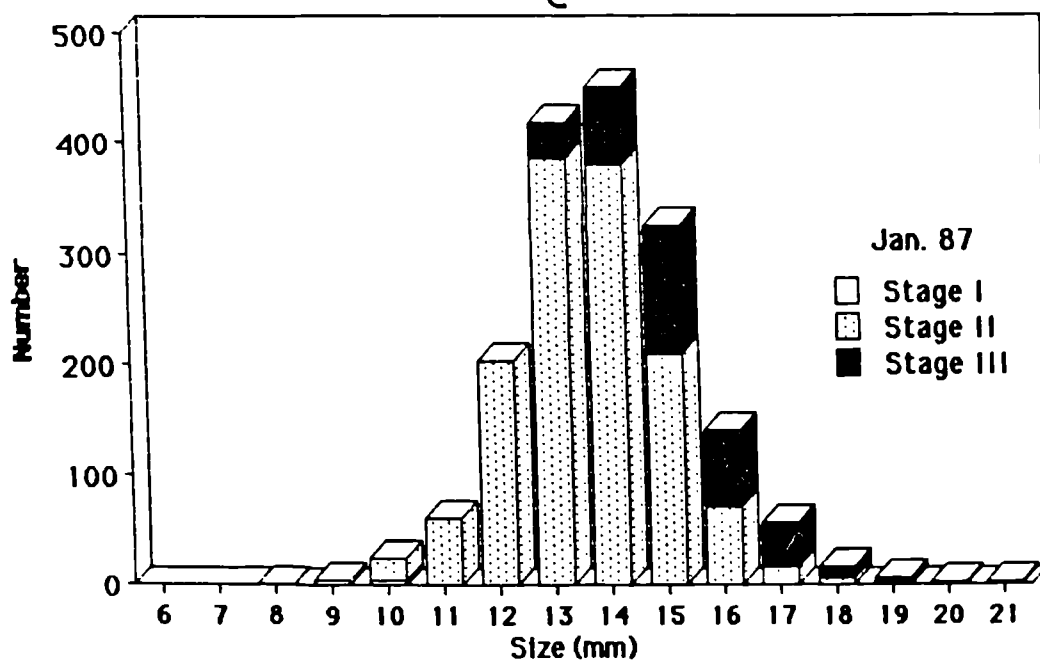


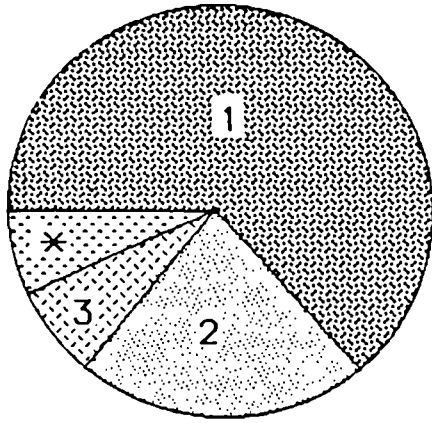
Fig. 11,A,B,C.

Station 1

March 1987.

- A)** Percentage occurrence of food items in *S. elegans*, as recorded from field samples.
OMNI= Organic Material not identifiable.
- B)** Food Containing Ratio (FCR) found in analysis of gut contents of *S. elegans* from day-night samples. Surf. (_____) Bott. (-----).
* No sagittas collected.
- C)** Size frequency distribution histogram of *S. elegans* of different maturity stages.
Statistics (All stages)
N= 725
Mean 14.06 (Length in mm).
Standard error 0.043 Standard deviation 1.17
No gonadic stage I found
Mean size stage II = 11.86
Mean size stage III = 14.11

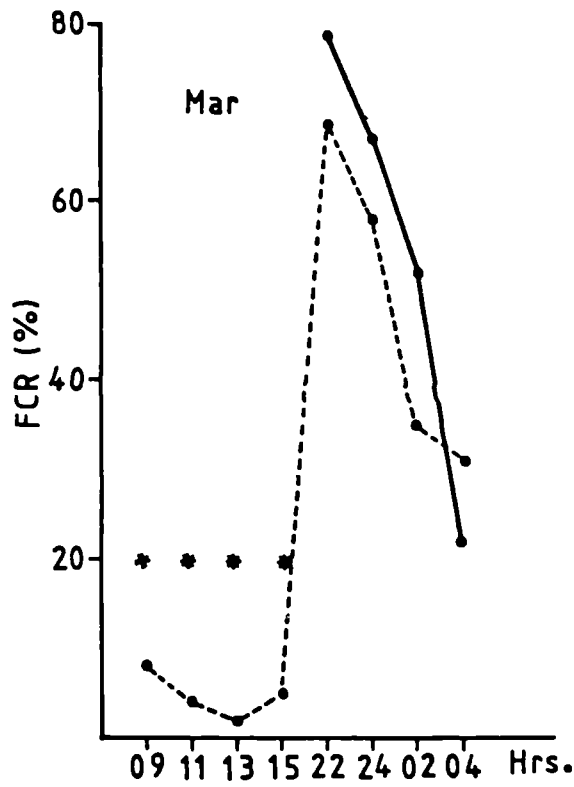
A



Mar.

Items	%
1.- Cirripedia	68.0
2.- <i>Pseudocalanus</i>	21.0
3.- OMNI	5.5
* Others	5.5
Appendicularia	2.3
<i>Oithona</i>	1.1
<i>Calanus</i>	0.4
Copepod remains	0.4
<i>Temora</i>	0.4

B



C

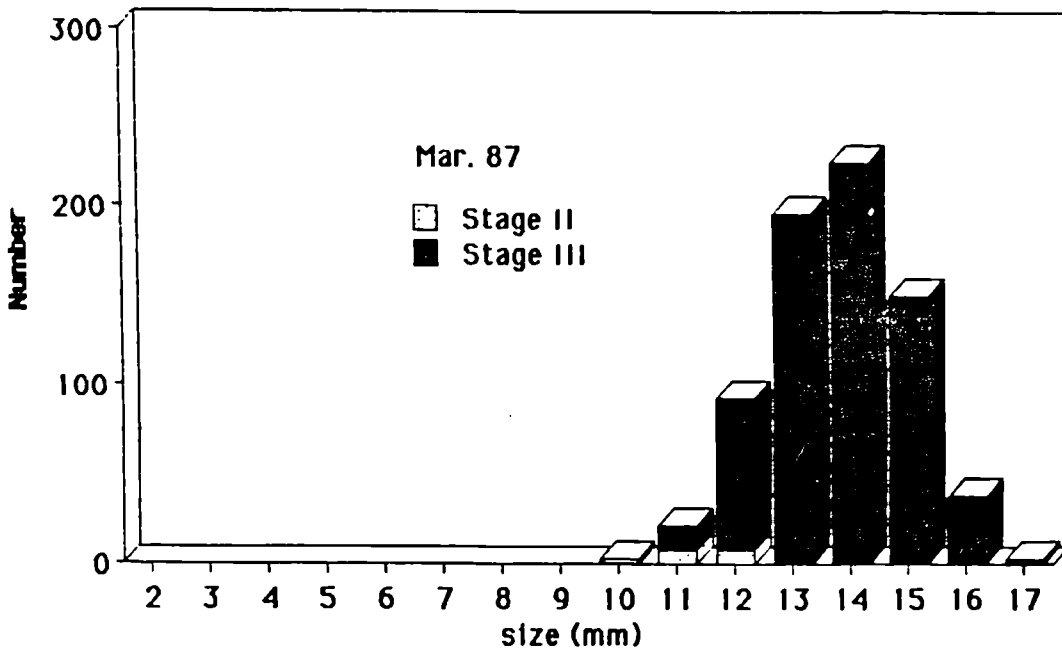


Fig. 12,A,B,C.

Station 1

April 1987.

A) Percentage occurrence of food items in *S. elegans*, as recorded from field samples.
OMNI= Organic Material not identifiable.

B) Food Containing Ratio (FCR) found in analysis of gut contents of *S. elegans* from day-night samples. Surf. (_____) Bott. (-----).

C) Size frequency distribution histogram of *S. elegans* of different maturity stages.

Statistics (All stages)

N= 533

Mean 4.80 (Length in mm).

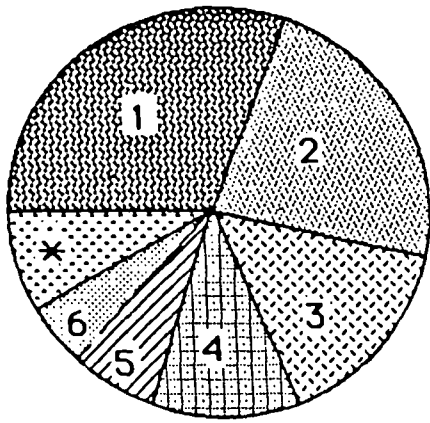
Standard error 0.018 Standard deviation 4.13

Mean size stage I = 3.37

Mean size stage II = 9.36

Mean size stage III = 16.60

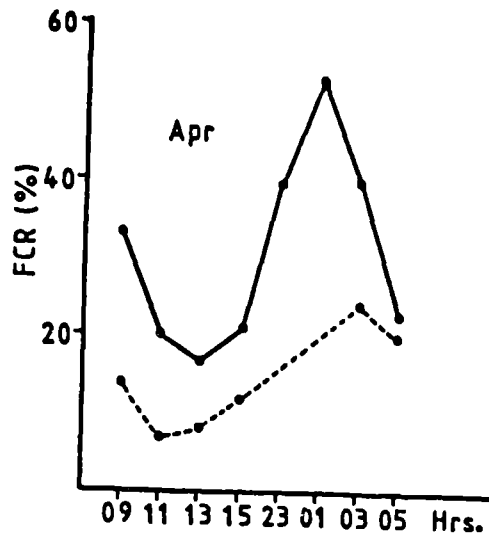
A



Apr.

Items	%
1.- OMNI	27.5
2.- <i>Pseudocalanus</i>	19.0
3.- Nauplii	16.8
4.- <i>Dinophysis</i>	11.4
5.- Copepod remains	7.6
6.- Cirripedia	4.5
* Others	13.2
<i>Calanus</i>	3.8
<i>Centropages</i>	3.8
<i>Temora</i>	3.0
Tintinnids	1.5
<i>Oithona</i>	0.07

B



C

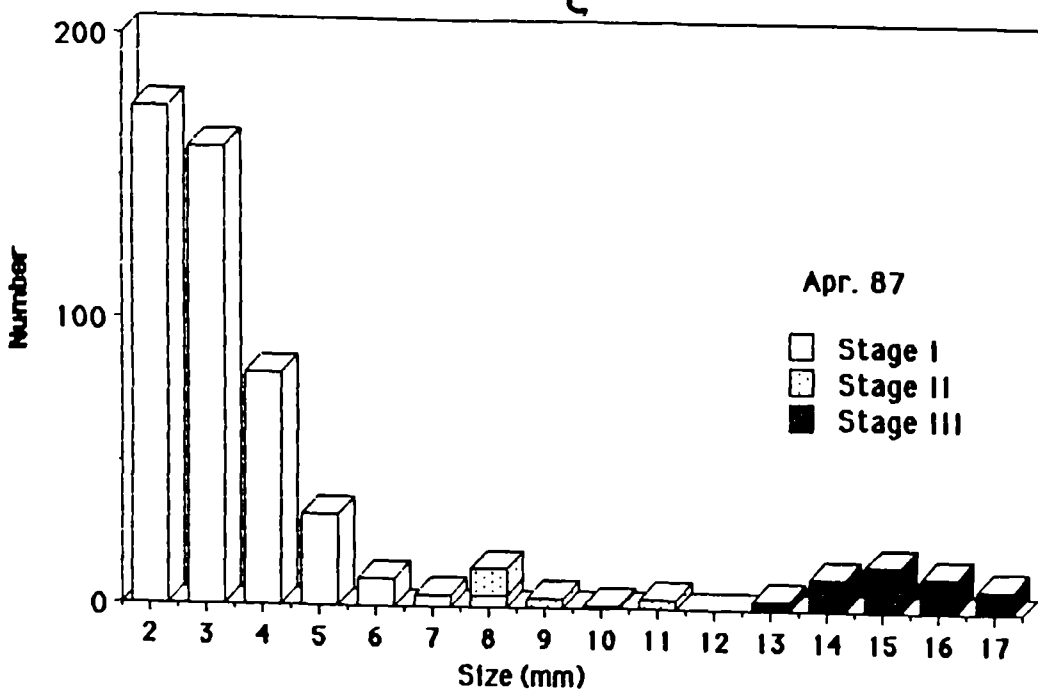


Fig. 13,A,B,C.

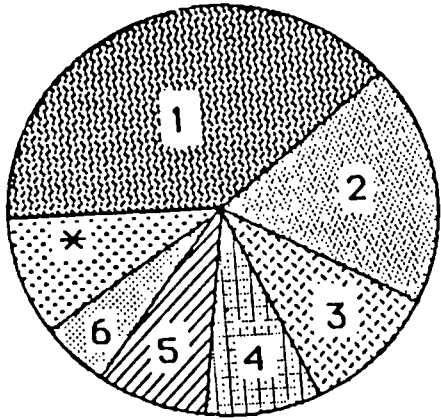
Station 1

May 1987.

- A)** Percentage occurrence of food items in *S. elegans*, as recorded from field samples.
OMNI= Organic Material not identifiable.
- B)** Food Containing Ratio (FCR) found in analysis of gut contents of *S. elegans* from day-night samples. Surf. (_____) Bott. (-----).
- C)** Size frequency distribution histogram of *S. elegans* of different maturity stages.
Statistics (All stages)
N= 520
Mean 10.56 (Length in mm).
Standard error 0.16 Standard deviation 3.62
Mean size stage I = 6.00
Mean size stage II = 10.31
Mean size stage III = 15.25

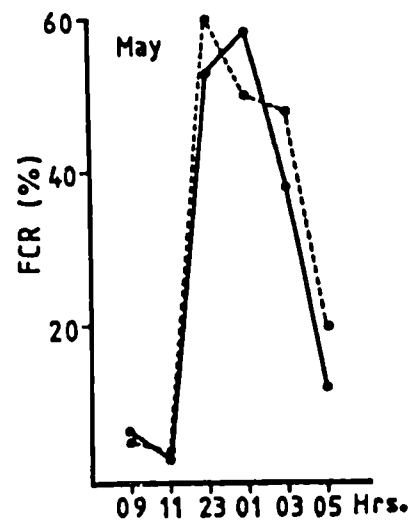
A

May.



Items	%
1.- <i>Pseudocalanus</i>	35.2
2.- <i>Temora</i>	19.9
3.- <i>Acartia</i>	9.9
4.- <i>Centropages</i>	8.8
5.- Cladocera	8.5
6.- <i>Oithona</i>	5.8
* Others	13.0
<i>Calanus</i>	3.5
OMNI	3.5
Copepod remains	2.5
Nauplii	1.1
Cirripedia	0.5

B



C

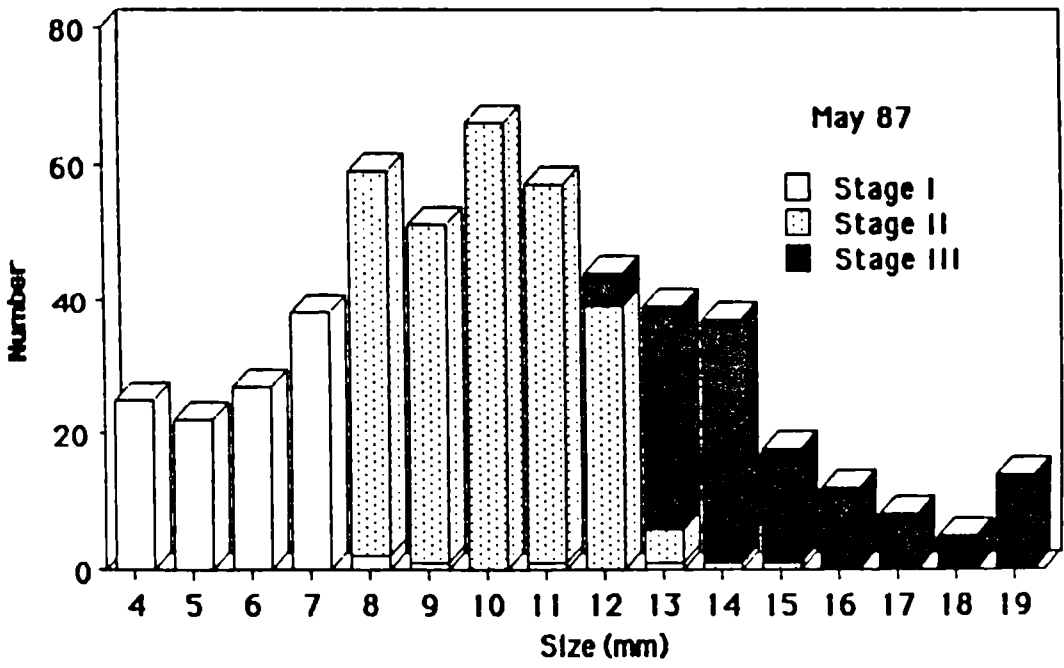


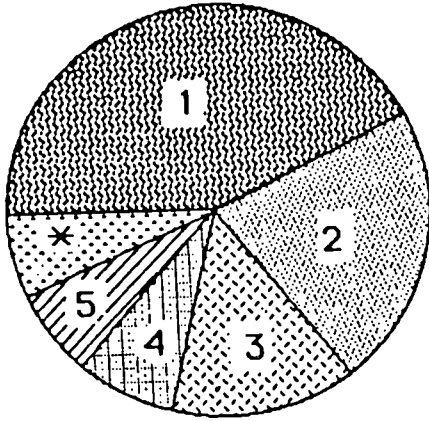
Fig. 14,A,B,C.

Station 1

June 1987.

- A)** Percentage occurrence of food items in *S. elegans*, as recorded from field samples.
OMNI= Organic Material not identifiable.
- B)** Food Containing Ratio (FCR) found in analysis of gut contents of *S. elegans* from night samples. Surf. (_____) Bott. (-----).
- C)** Size frequency distribution histogram of *S. elegans* of different maturity stages.
Statistics
N= 274
Mean 9.00 (Length in mm).
Standard error 0.16 Standard deviation 2.77
Mean size stage I = 5.93
Mean size stage II = 9.85
Mean size stage III = 13.63

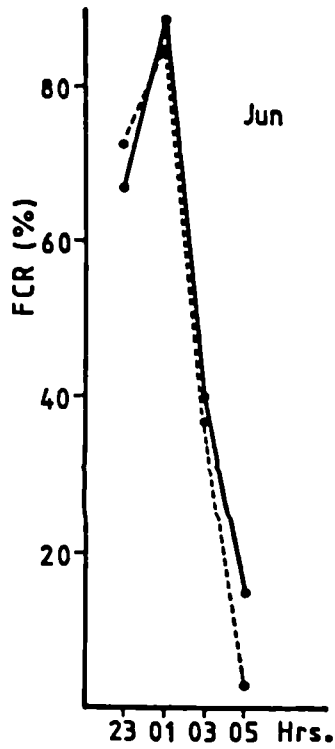
A



Jun.

Items	%
1.- <i>Pseudocalanus</i>	40.0
2. <i>Temora</i>	23.0
3.- <i>Acartia</i>	14.0
4.- Copepod remains	8.8
5.- <i>Centropages</i>	7.4
* Others	1.8
Cladocera	0.6
Amphipoda	0.6
Cladocera	0.6

B



C

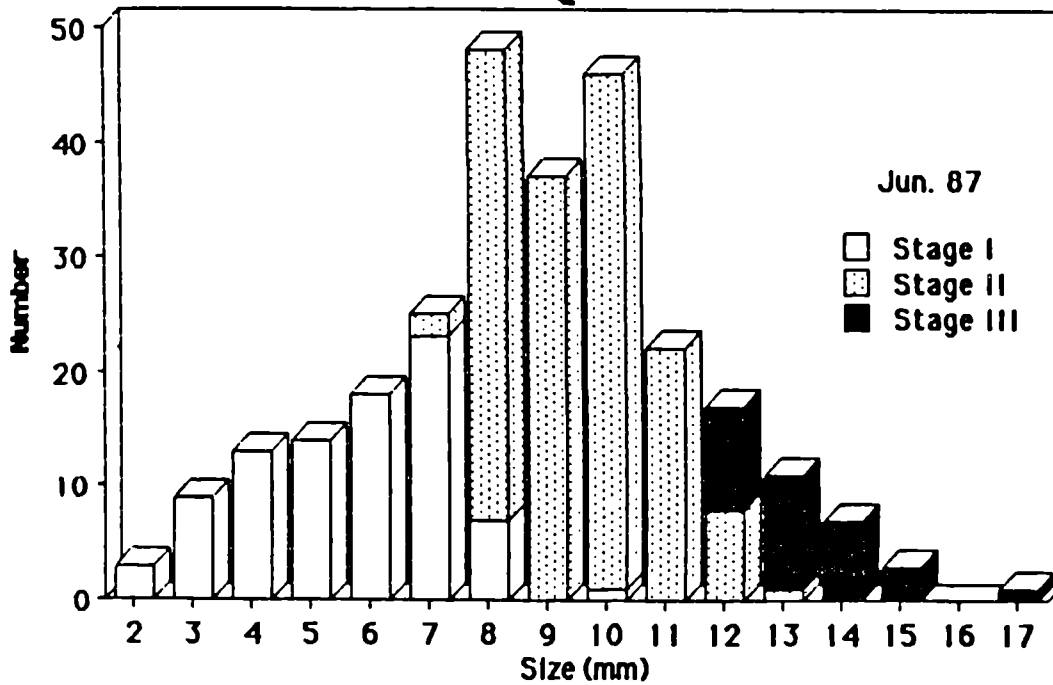


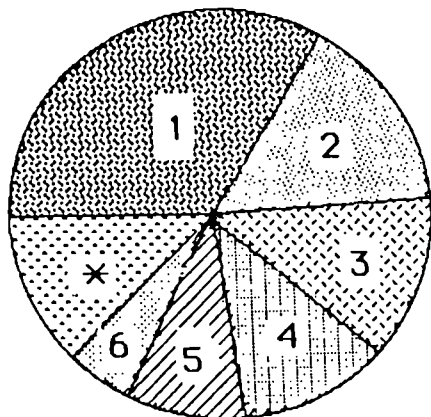
Fig. 15,A,B,C.

Station 1

July 1987.

- A)** Percentage occurrence of food items in *S. elegans*, as recorded from field samples.
OMNI= Organic Material not identifiable.
- B)** Food Containing Ratio (FCR) found in analysis of gut contents of *S. elegans* from night samples. Surf. (_____) Bott. (-----).
- C)** Size frequency distribution histogram of *S. elegans* of different maturity stages.
Statistics (All stages)
N= 372
Mean 5.44 (Length in mm).
Standard error 0.12 Standard deviation 2.42
Mean size stage I = 4.62
Mean size stage II = 9.13
Mean size stage III = 13.20

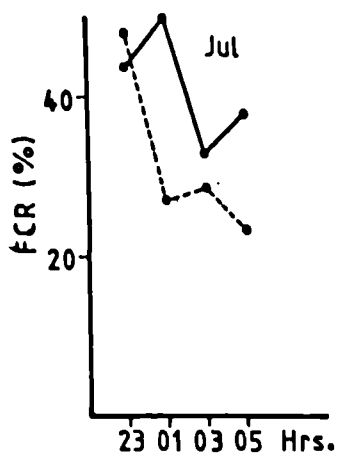
A



Jul.

Items	%
1.- <i>Pseudocalanus</i>	33.0
2.- <i>Acartia</i>	14.6
3.- Copepod remains	11.7
4.- <i>Oithona</i>	11.2
5.- <i>OMNI</i>	11.0
6.- <i>Temora</i>	6.0
* Others	11.7
Appendicularia	5.1
Crustacean eggs	4.4
<i>Centropages</i>	2.2

B



C

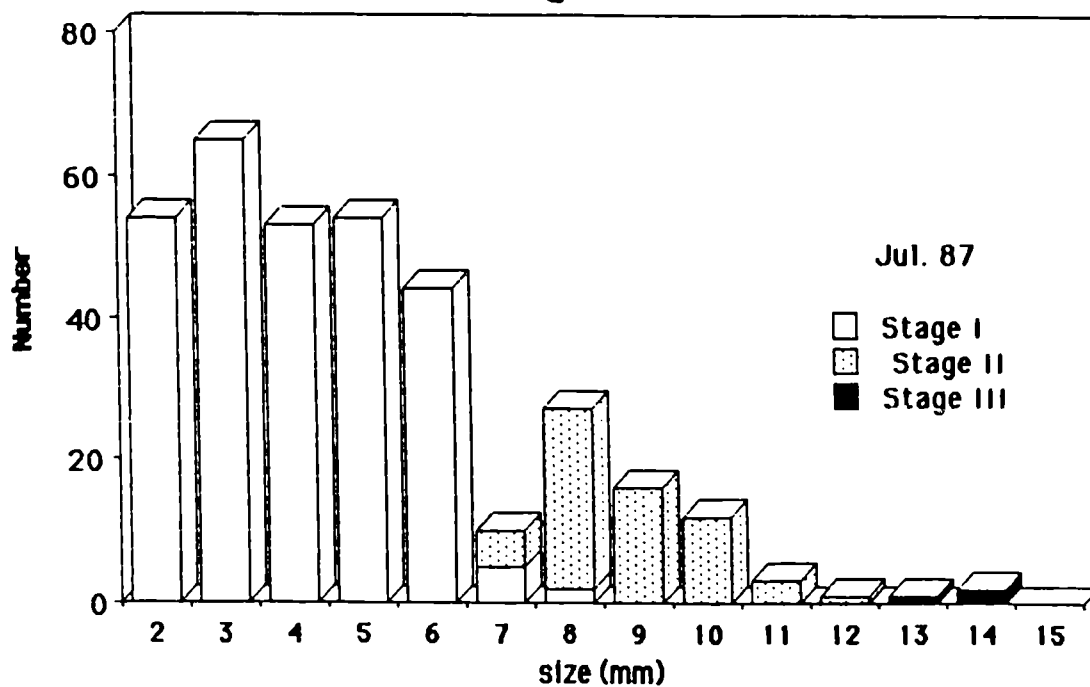


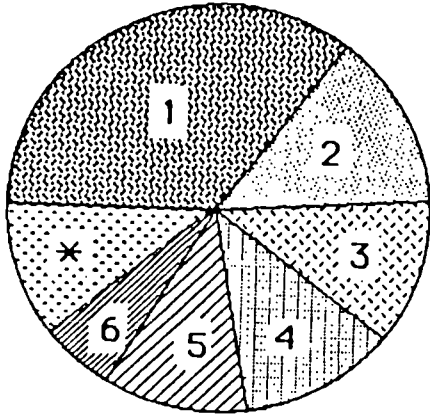
Fig. 16,A,B,C.

Station 1

August 1987.

- A)** Percentage occurrence of food items in *S. elegans*, as recorded from field samples.
OMNI= Organic Material not identifiable.
- B)** Food Containing Ratio (FCR) found in analysis of gut contents of *S. elegans* from day-night samples. Surf. (_____) Bott. (-----).
- C)** Size frequency distribution histogram of *S. elegans* of different maturity stages.
Statistics (All stages)
N= 686
Mean 4.95 (Length in mm).
Standard error 0.06 Standard deviation 1.66
Mean size stage I = 4.83
Mean size stage II = 9.13
Mean size stage III = 12.60

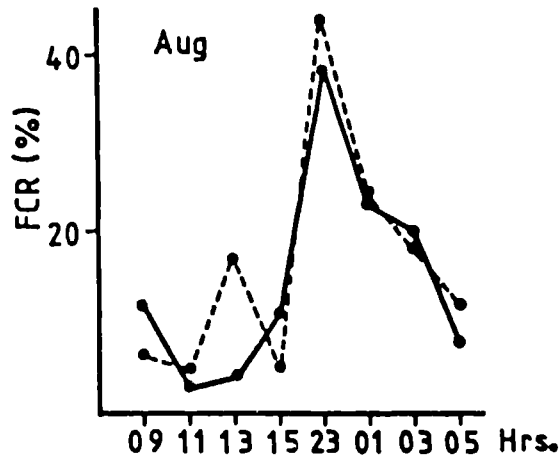
A



Aug.

Items	%
1.- <i>Pseudocalanus</i>	33.0
2.- <i>Oithona</i>	15.1
3.- <i>Temora</i>	12.0
4.- <i>Acartia</i>	11.0
5.- Copepod remains	10.7
6.- Crustacean eggs	7.1
* Others	11.4
OMNI	6.0
<i>Centropages</i>	3.6
Appendicularia	0.9
Dinoflagellates	0.9

B



C

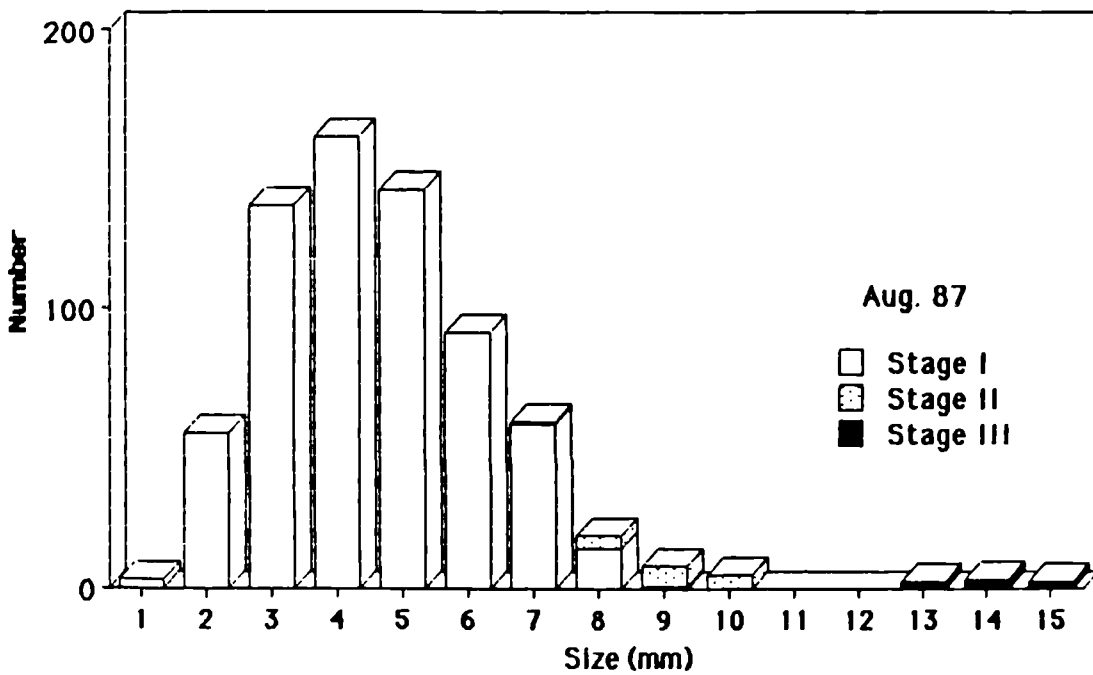


Fig. 17,A,B.

Station 1

September 1987.

A) Food Containing Ratio (FCR) found in analysis of gut contents of *S. elegans* from day samples. Surf. (_____) Bott. (-----).

B) Size frequency distribution histogram of *S. elegans* of different maturity stages.

Statistics (All stages)

N= 285

Mean 9.22 (Length in mm).

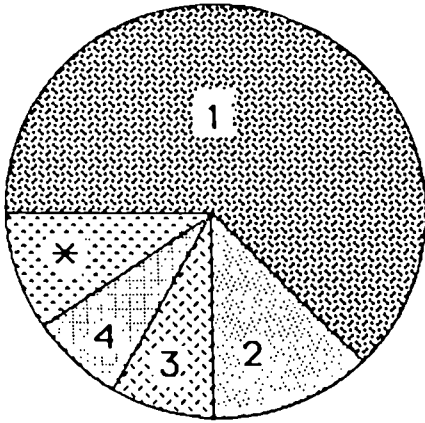
Standard error 0.09 Standard deviation 1.63

Mean size stage I = 9.15

Mean size stage II = 12.24

Mean size stage III = 12.40

A



Sep.	
Items	%
1.- <i>Pseudocalanus</i>	62.0
2.- <i>Acartia</i>	13.8
3.- Nauplii	6.8
4.- Copepod remains	6.8
* Others	10.2
<i>Oithona</i>	5.4
<i>Calanus</i>	2.4
OMNI	2.4

B

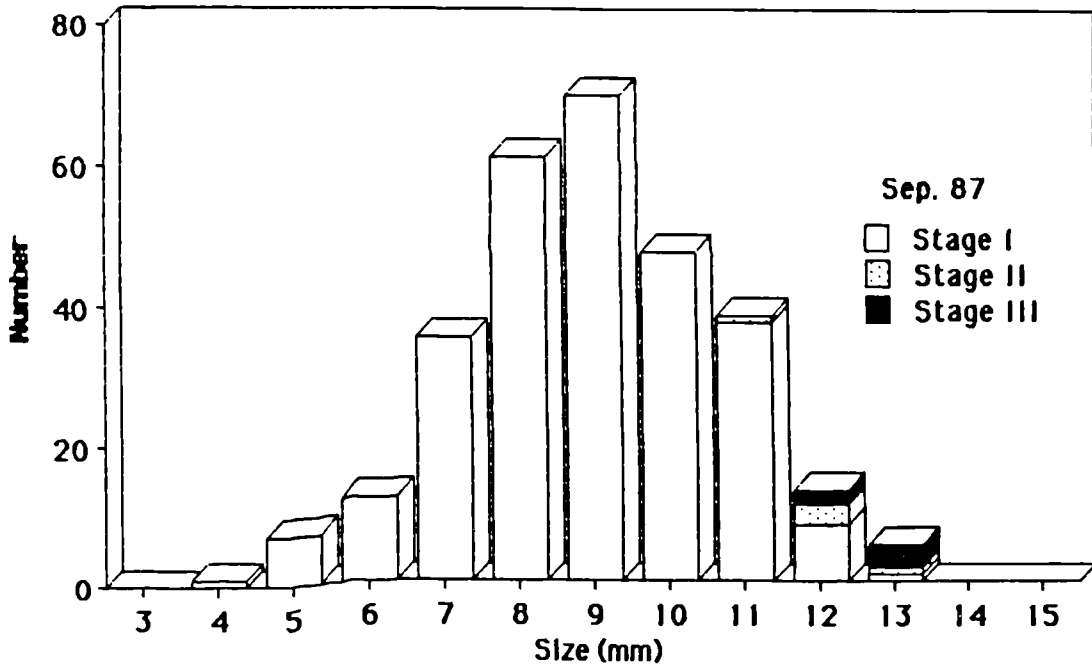
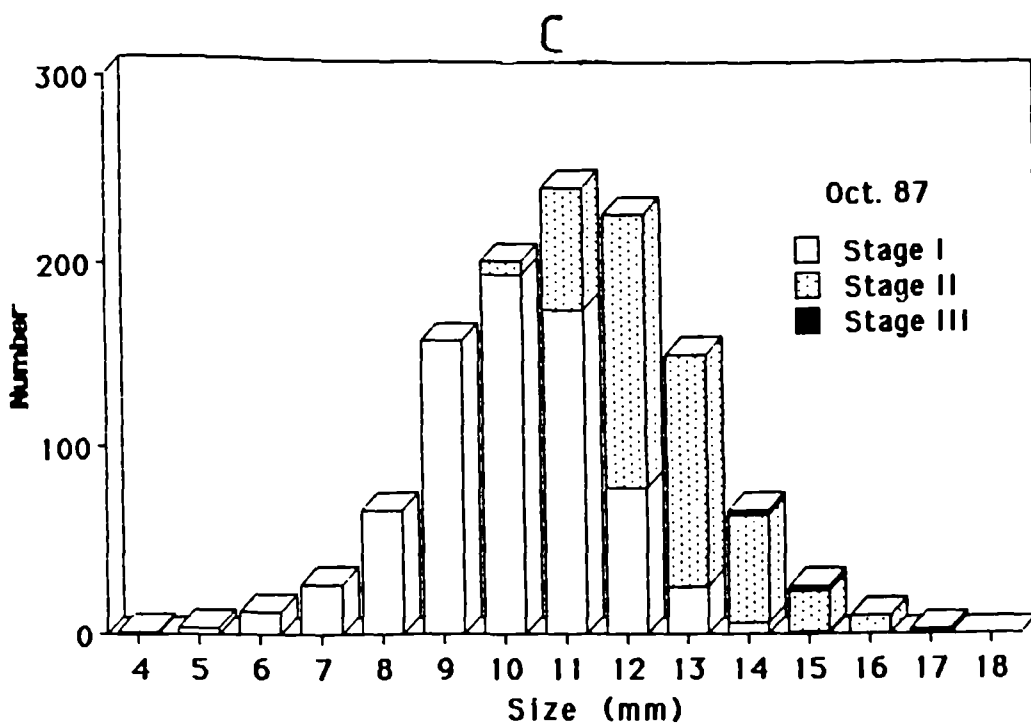
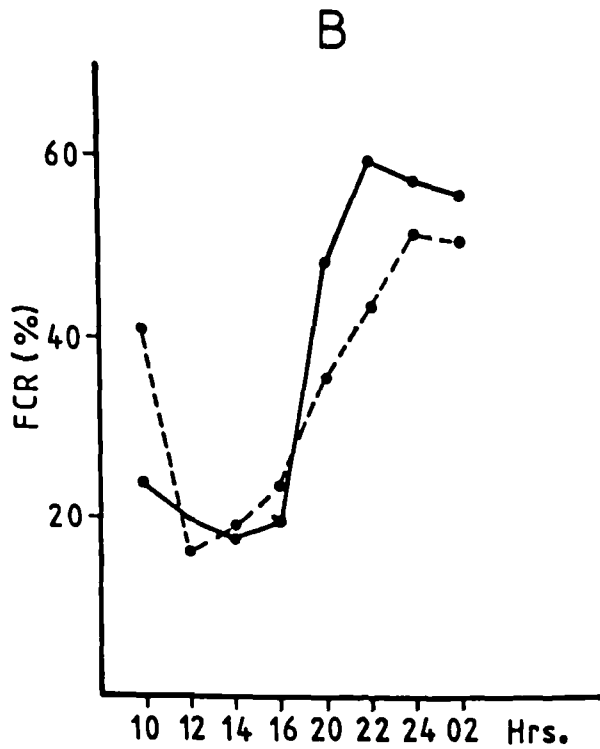
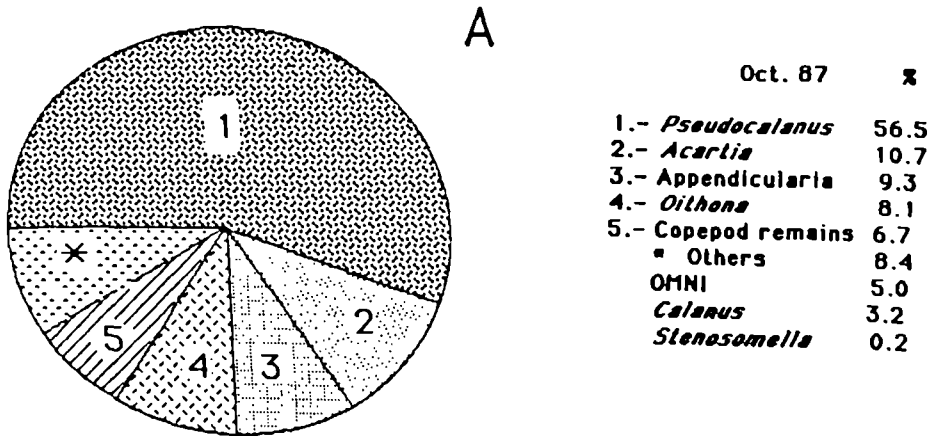


Fig. 18,A,B,C.

Station 1

October 1987.

- A)** Percentage occurrence of food items in *S. elegans*, as recorded from field samples.
- B)** Food Containing Ratio (FCR) found in analysis of gut contents of *S. elegans* from day-night samples. Surf. (_____) Bott. (-----).
- C)** Size frequency distribution histogram of *S. elegans* of different maturity stages.
Statistics (All stages)
N= 1193
Mean 11.30 (Length in mm).
Standard error 0.05 Standard deviation 1.90
Mean size stage I =10.34
Mean size stage II = 12.95
Mean size stage III = 13.40



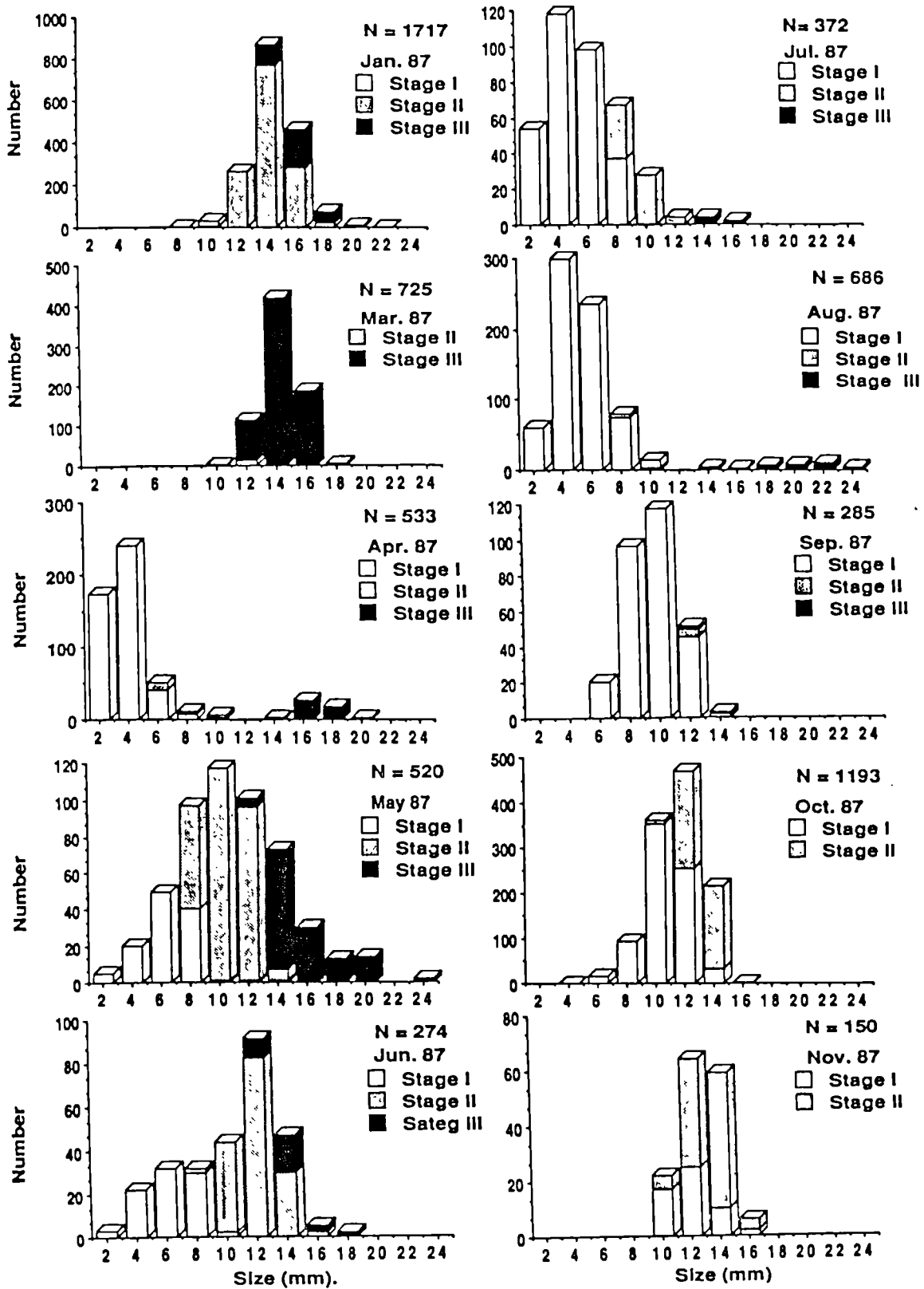


Fig. 19.- Length-frequency and maturity stages of *Sagitta elegans* at station 1, 1987.

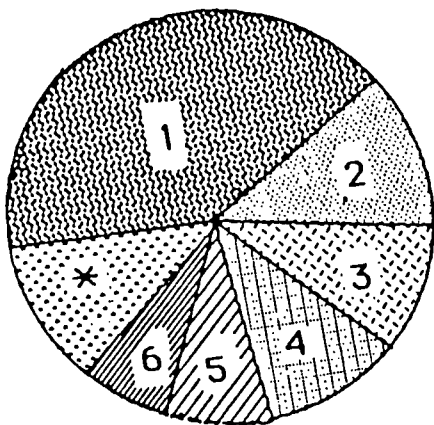
Fig. 20,A,B,C.

Station 2

Feb. Mar. 1986.

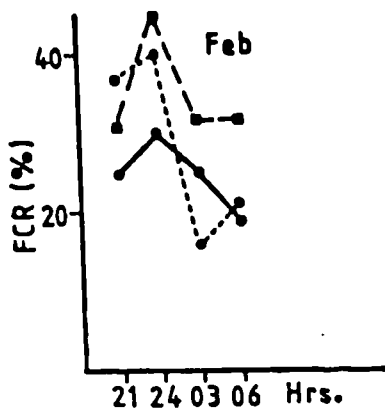
- A)** Percentage occurrence of food items in *S. elegans* as recorded from field samples.
- B)** Food Containing Ratio (FCR) found in analysis of gut contents of *S. elegans* from day-night samples. Surf. (_____) Mid (_ _ _ _)
Bott. (-----)
- C)** Size frequency distribution histogram of *S. elegans* of different maturity stages.
Statistics (All stages)
N= 1611
Mean 12.54 (Length in mm).
Standard error 0.04 Standard deviation 1.54.
Mean size stage I = 10.13
Mean size stage II = 12.38
Mean size stage III = 14.03

A



Feb-Mar Items	%
1.- <i>Pseudocalanus</i>	40.8
2.- Appendicularia	13.6
3.- <i>Calanus</i>	11.8
4.- OMNI	9.4
5.- <i>Oithona</i>	5.2
6.- Copepod remains	5.0
* Others	20.0
Nauplii	3.8
<i>S. elegans</i>	3.6
Polychaeta	2.6
<i>Acartia</i>	2.4
<i>Centropages</i>	2.4
Crustacean eggs	1.6
Cirripedia	1.4

B



C

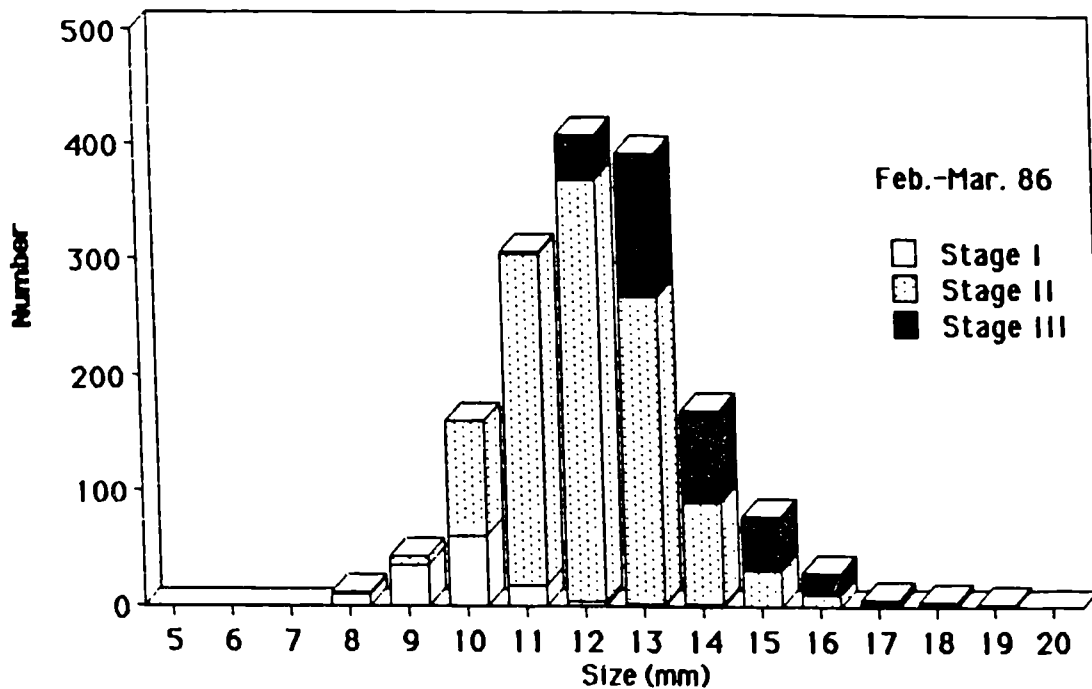
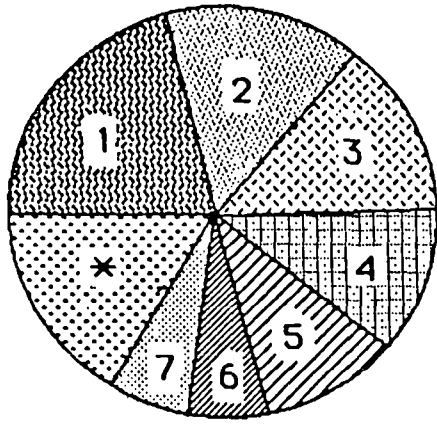


Fig. 21,A,B,C.

Station 2

May 1986.

- A)** Percentage occurrence of food items in *S. elegans*, as recorded from field samples.
- B)** Food Containing Ratio (FCR) found in analysis of gut contents of *S. elegans* from day-night samples. Surf. (_____) Mid (_ _ _ _)
Bott. (-----).
* No sagittas collected.
- C)** Size frequency distribution histogram of *S. elegans* of different maturity stages.
Statistics (All stages)
N= 998
Mean 8.65 (Length in mm).
Standard error 0.13 Standard deviation 4.14
Mean size stage I = 7.15
Mean size stage II = 13.57
Mean size stage III = 17.54



A)

Items	%
1.- <i>Temora</i>	20.1
2.- <i>Pseudocalanus</i>	14.0
3.- Nauplii	13.5
4.- OMNI	12.4
5.- <i>Calanus</i>	10.3
6.- Appendicularia	6.1
7.- <i>Coelropages</i>	5.1
* Others	19.0
<i>Oithona</i>	4.9
Copepod remains	4.6
Cirripedia	3.1
<i>Acartia</i>	3.1
Cladocera	1.7
<i>Microsetella</i>	0.9

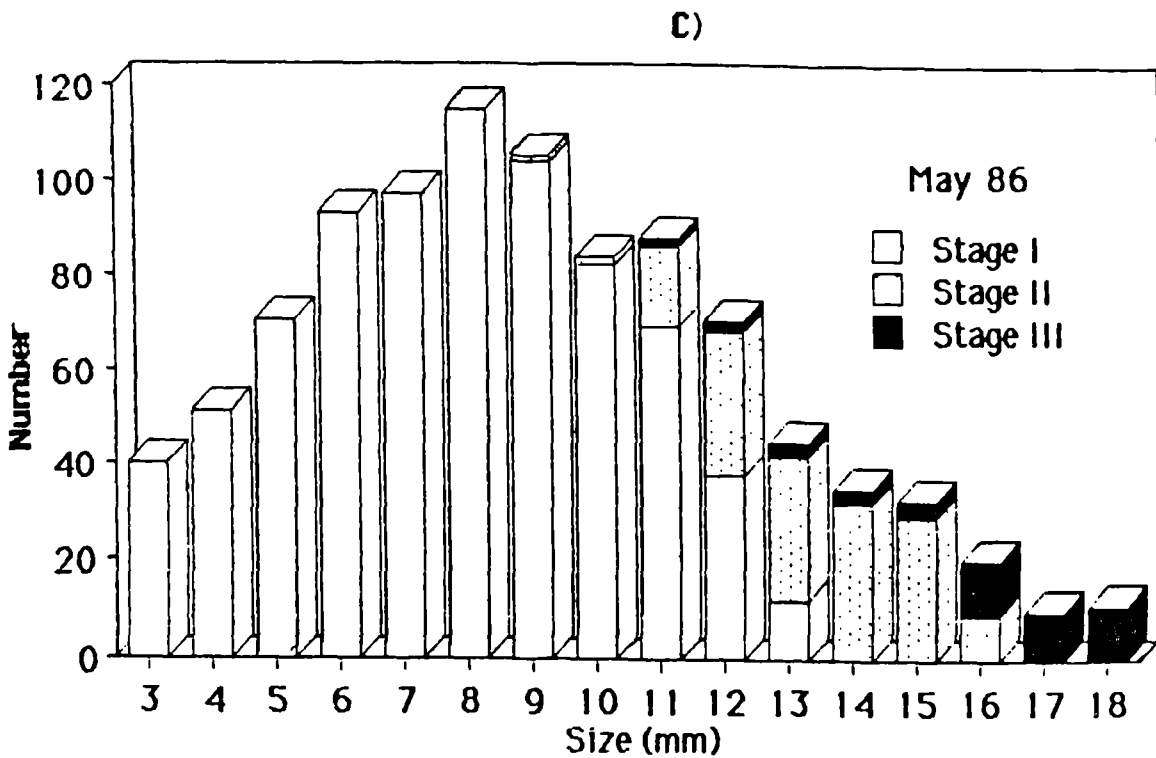
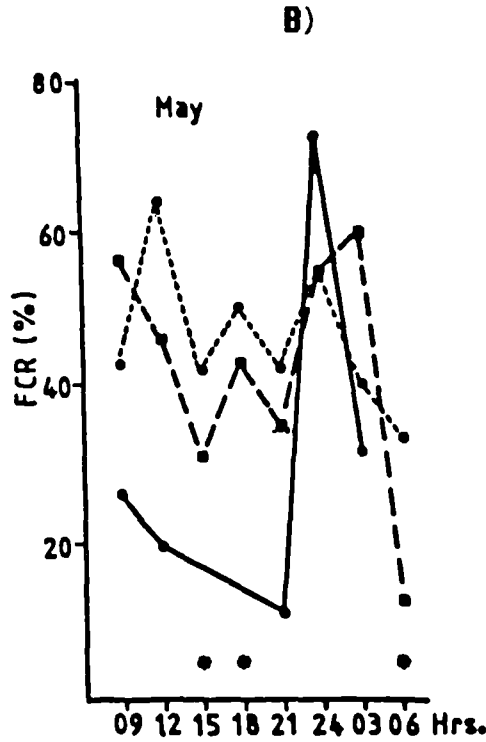


Fig. 22,A,B,C.

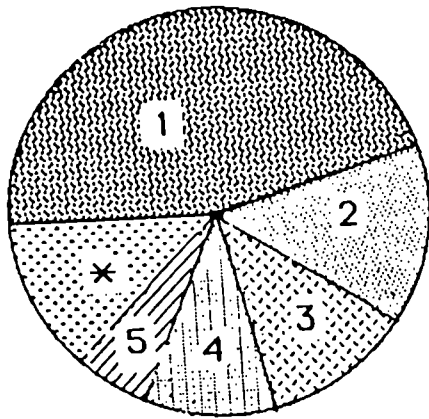
Station 2

July 1986.

- A)** Percentage occurrence of food items in *S. elegans*, as recorded from field samples.
- B)** Food Containing Ratio (FCR) found in analysis of gut contents of *S. elegans* from day-night samples. Surf. (_____) Mid (_ _ _ _)
Bott. (- - - - -).
- C)** Size frequency distribution histogram of *S. elegans* of different maturity stages.
Statistics (All stages)
N= 1788
Mean 11.14 (Length in mm).
Standard error 0.09 Standard deviation 4.03
Mean size stage I = 8.58
Mean size stage II = 12.92
Mean size stage III = 16.50

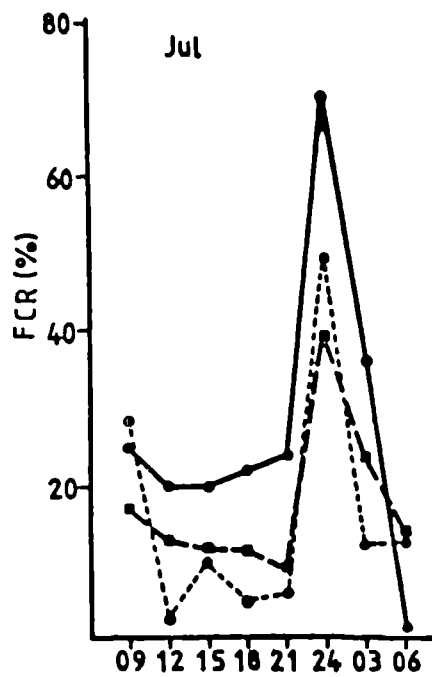
A

Jul.



Items	%
1.- <i>Pseudocalanus</i>	45.0
2.- <i>Acartia</i>	14.1
3.- <i>Oithona</i>	11.8
4.- <i>Calanus</i>	9.9
5.-Copepod remains	5.0
6.-Nauplii	4.2
* Others	10.0
<i>Centropages</i>	3.5
Appendicularia	3.1
<i>Temora</i>	2.4
<i>S. elegans</i>	0.5
Crustacean eggs	0.5

B



C

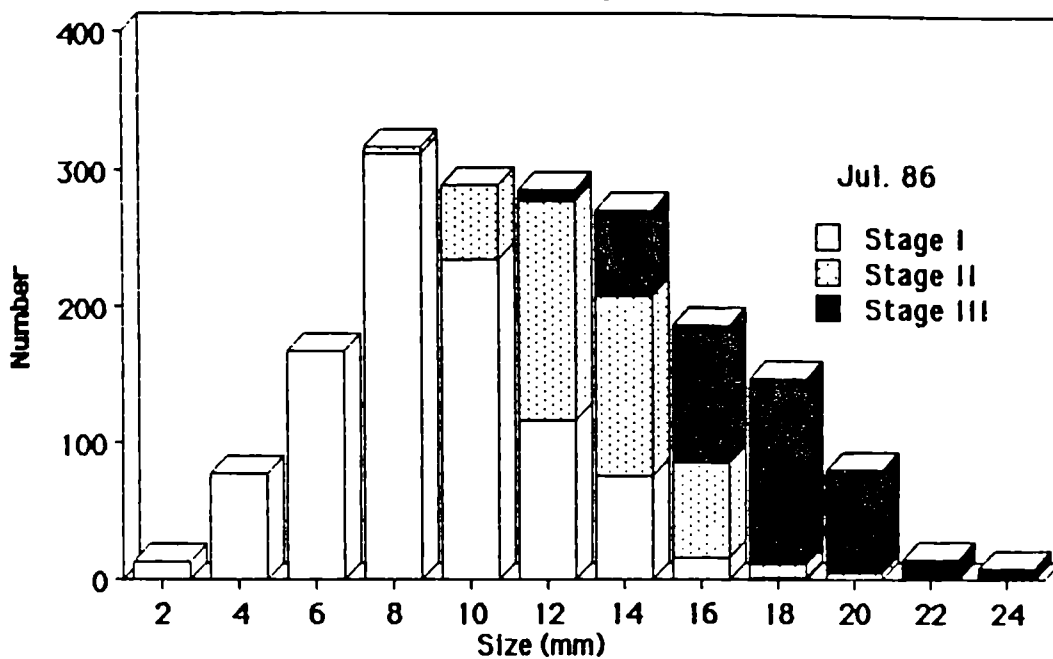


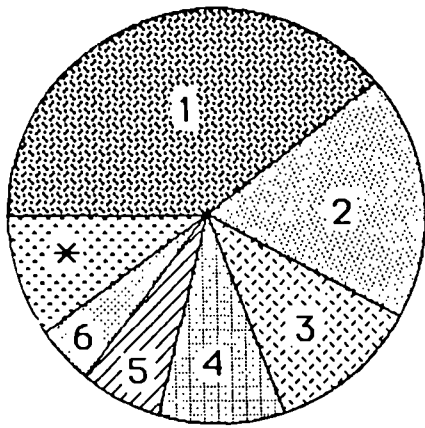
Fig. 23,A,B,C.

Station 2

September 1986.

- A)** Percentage occurrence of food items in *S. elegans*, as recorded from field samples.
- B)** Food Containing Ratio (FCR) found in analysis of gut contents of *S. elegans* from day-night samples. Surf. (_____) Mid (_ _ _)
Bott. (-----).
- * No sagittas collected.
- C)** Size frequency distribution histogram of *S. elegans* of different maturity stages.
Statistics (All stages)
N= 1300
Mean 13.21 (Length in mm).
Standard error 0.05 Standard deviation 1.80
Mean size stage I = 12.34
Mean size stage II = 14.71
Mean size stage III = 16.30

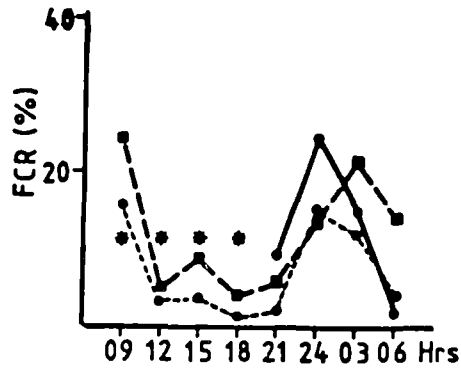
A



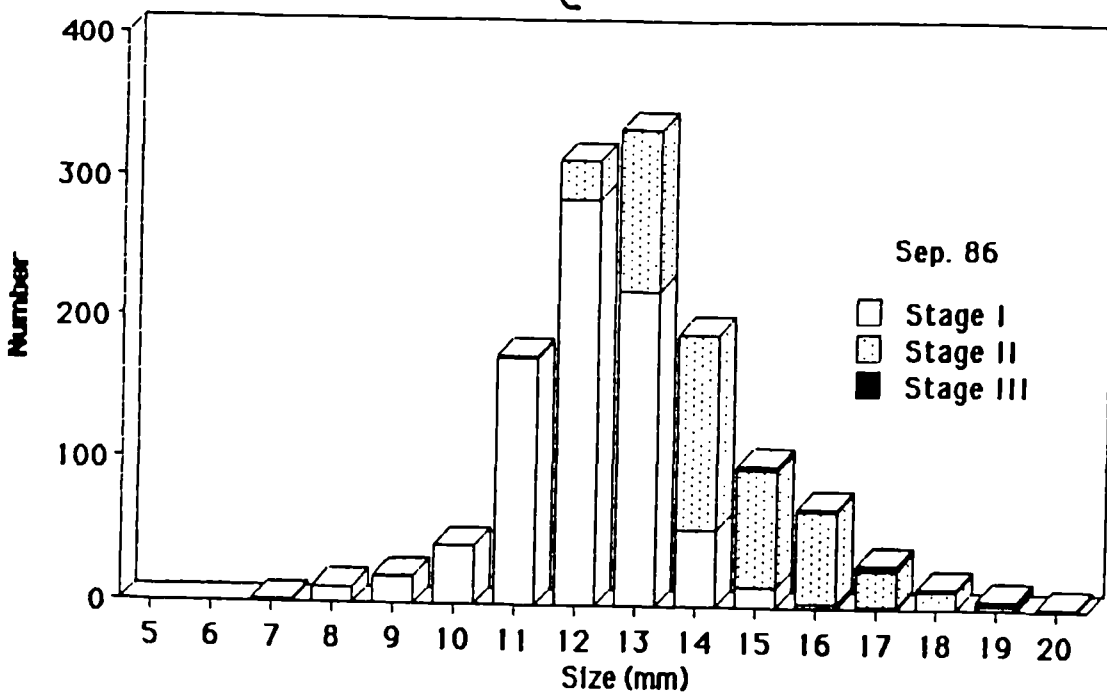
Sep.

Items	%
1.- <i>Pseudocalanus</i>	40.0
2.- <i>Acartia</i>	19.8
3.- OMNI	12.0
4.- <i>Calanus</i>	8.0
5.- Copepod remains	6.3
6.- <i>Oithona</i>	4.0
* Others	9.9
<i>Centropages</i>	3.1
Nauplii	2.3
<i>Temora</i>	2.3
Appendicularia	1.5
Euphausiids	0.8

B



C



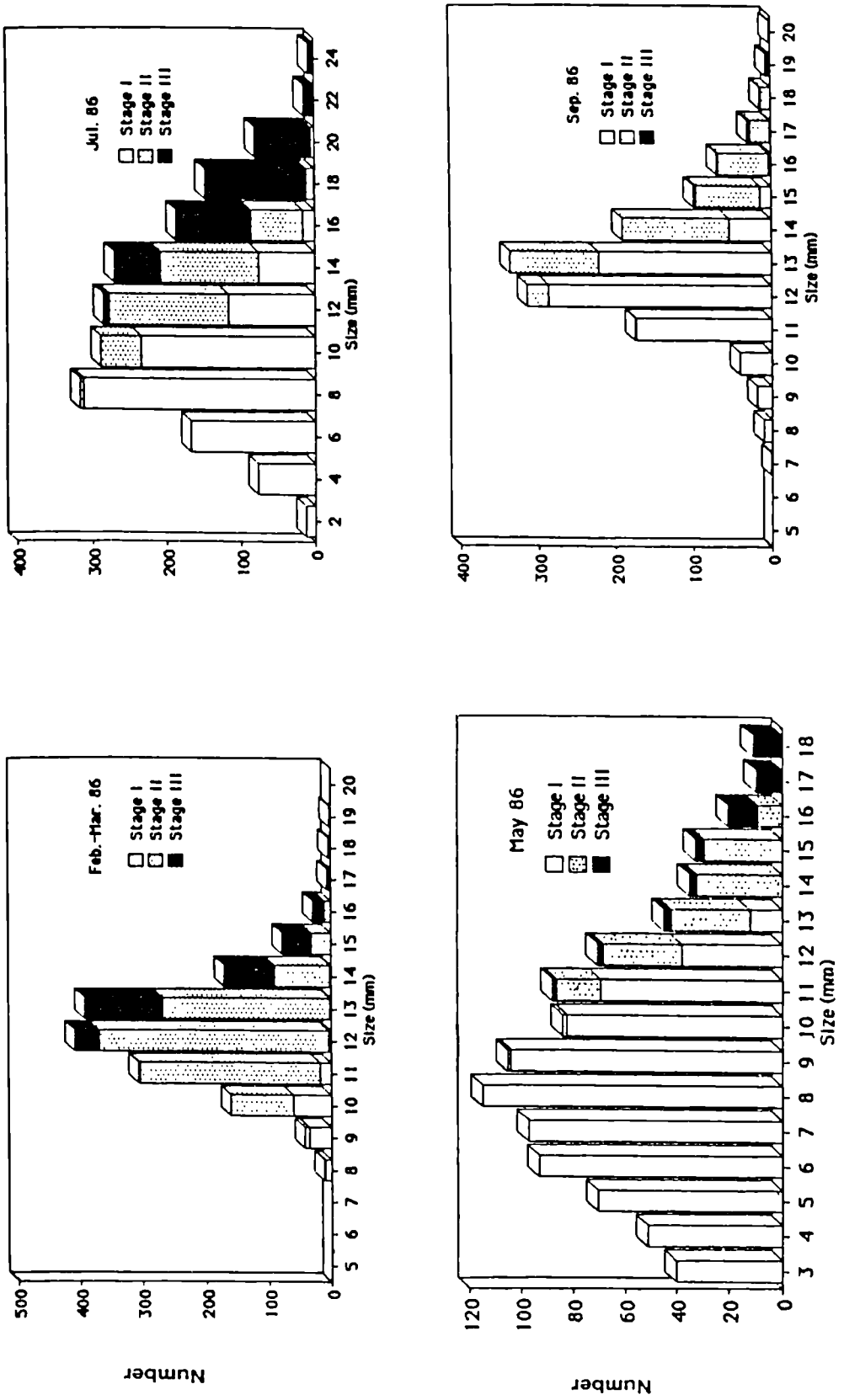


Fig. 24 - Length-frequency and maturity stages of *Sagitta elegans* at station 2, 1986.

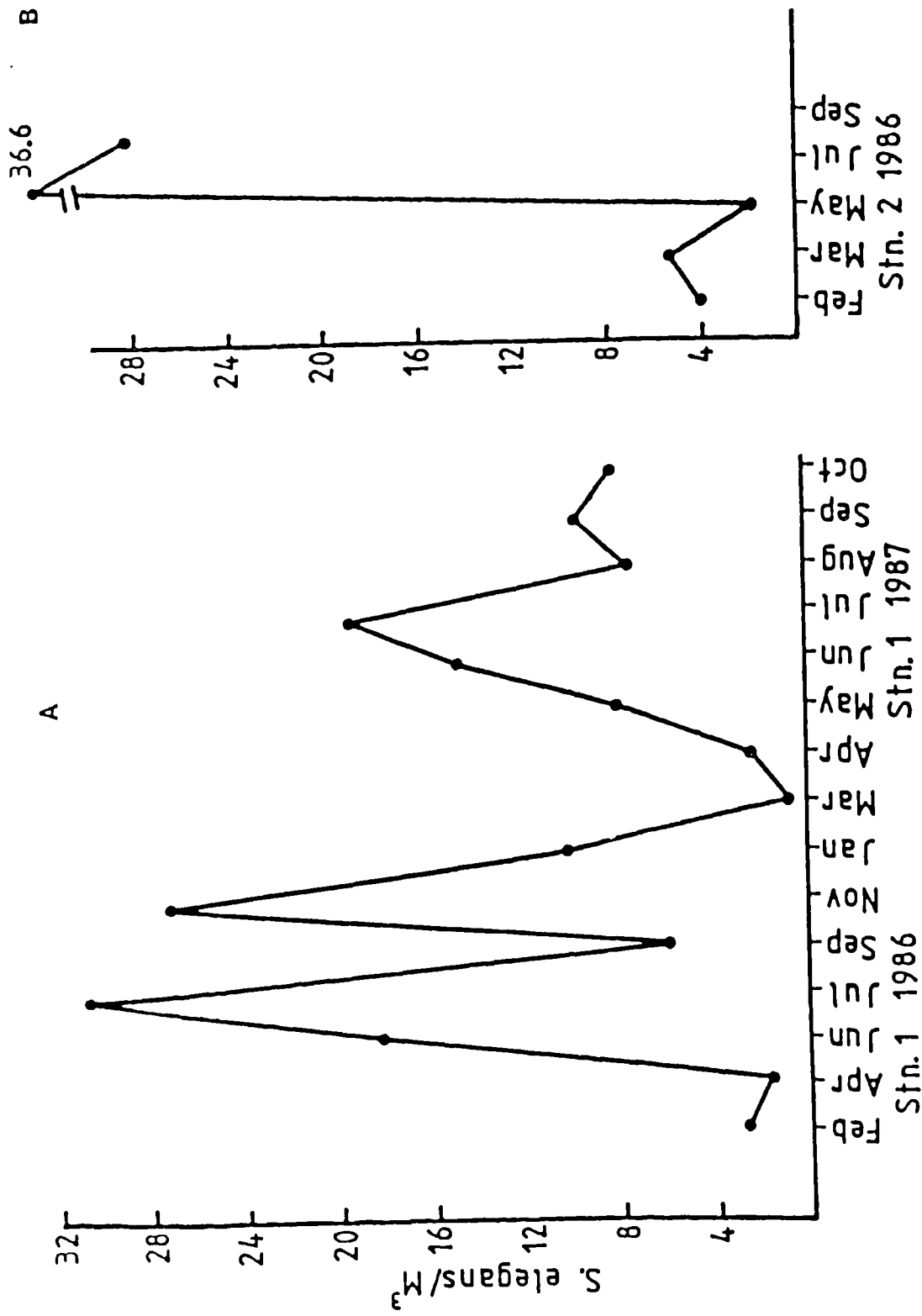


Fig.2.5.- Average seasonal abundance of *S. elegans*
 a) at station 1, 1986-1987 and b) station 2, 1986.

Fig. 26,A,B,C.

Station 1

February 1986.

- A)** Percentage occurrence of food items in *S. setosa*, as recorded from field samples.
- B)** Food Containing Ratio (FCR) found in analysis of gut contents of *S. setosa* from day-night samples. Surf. (_____) Bott. (-----).
- C)** Size frequency distribution histogram of *S. setosa* of different maturity stages.
Statistics (All stages)
N= 1136
Mean 10.94 (Length in mm).
Standard error 0.05 Standard deviation 1.66
Mean size stage I =10.64
Mean size stage II = 12.50
No stage III recorded

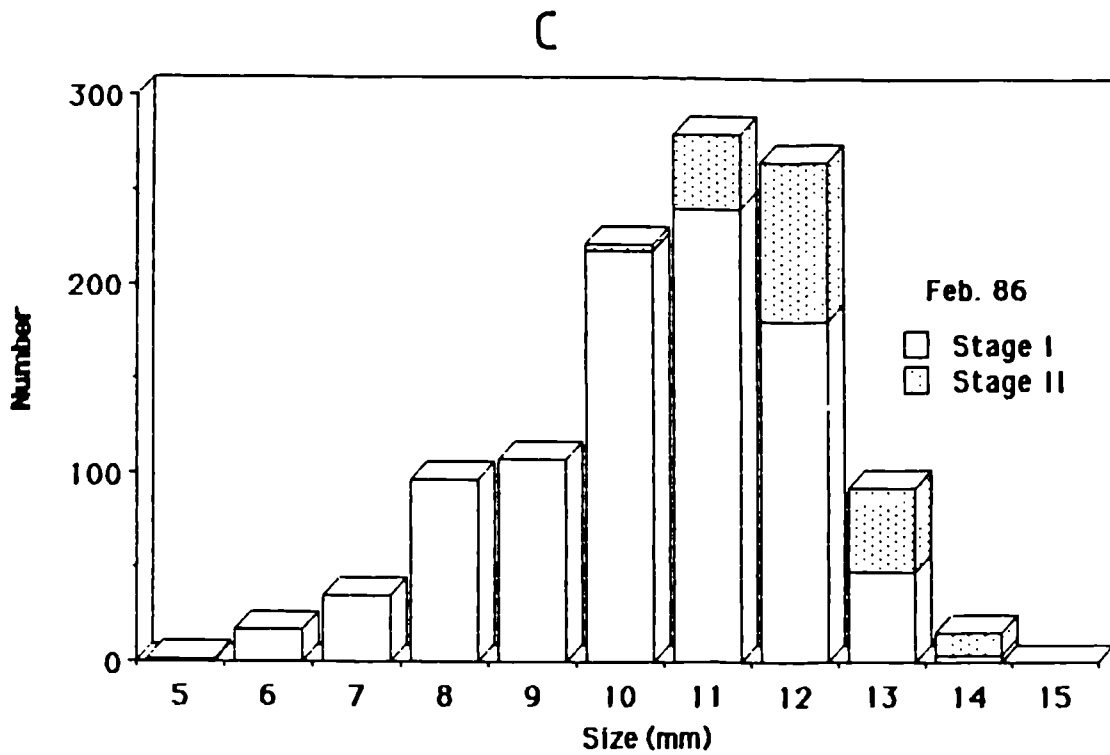
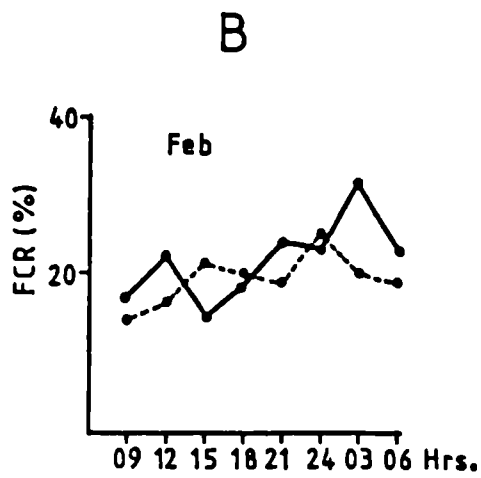
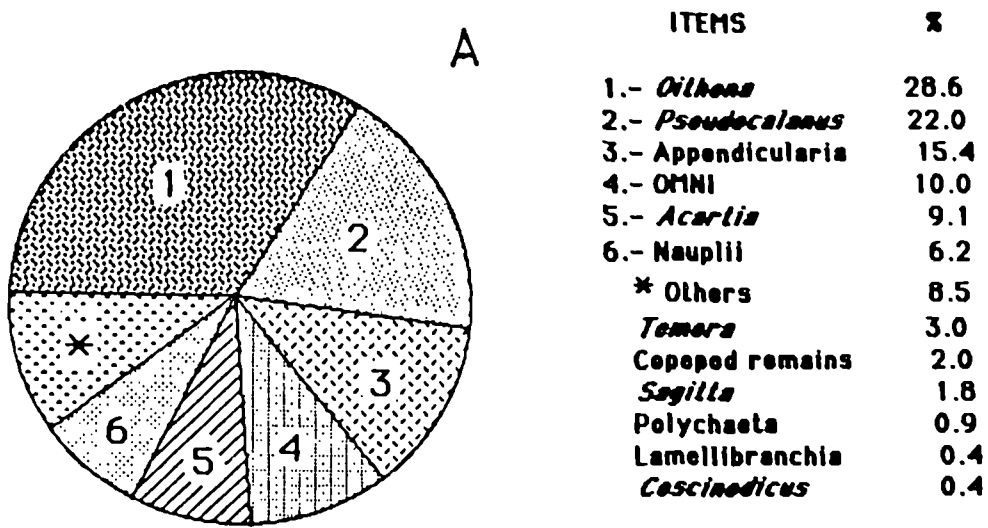


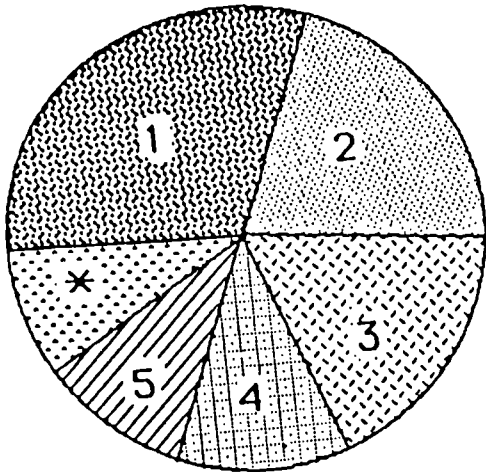
Fig. 27,A,B,C.

Station 1

September 1986.

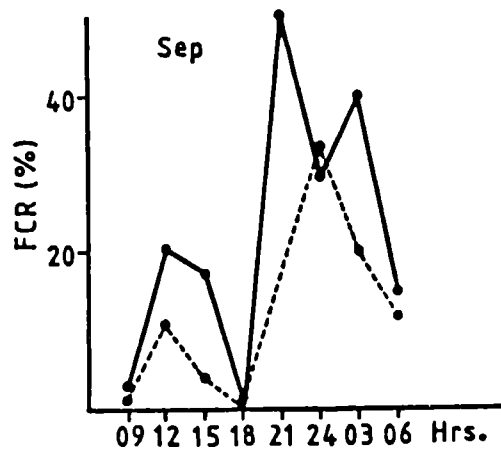
- A)** Percentage occurrence of food items in *S. setosa*, as recorded from field samples.
- B)** Food Containing Ratio (FCR) found in analysis of gut contents of *S. setosa* from day-night samples. Surf. (_____) Bott. (-----).
- C)** Size frequency distribution histogram of *S. setosa* of different maturity stages.
Statistics (All stages)
N= 696
Mean 8.59 (Length in mm).
Standard error 0.08 Standard deviation 2.17
Mean size stage I = 6.63
Mean size stage II = 8.75
Mean size stage III = 11.13

A



Items	%
1.- Appendicularia	29.4
2.- <i>Acartia</i>	23.0
3.- <i>Pseudocalanus</i>	20.3
4.- Nauplii	11.6
5.- <i>Oithona</i>	10.0
* Others	5.3
OMNI	4.4
Copepod remans	0.9

B



C

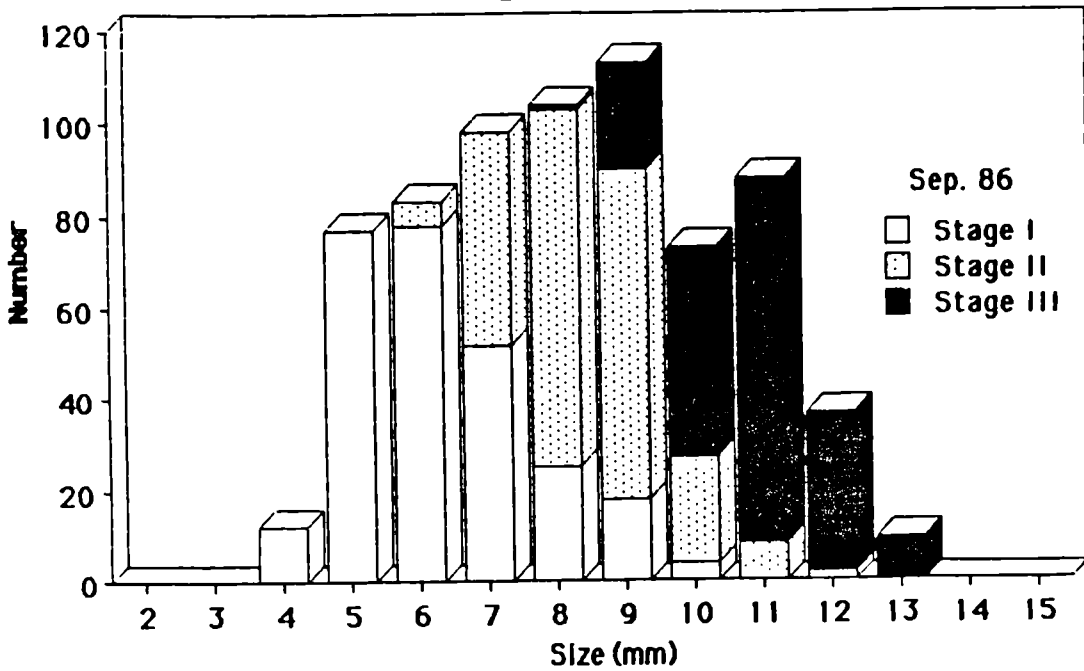


Fig. 28,A,B,C.

Station 1

November 1986.

A) Percentage occurrence of food items in *S. setosa*, as recorded from field samples.

B) Food Containing Ratio (FCR) found in analysis of gut contents of *S. setosa* from day samples. Surf. (_____) Bott. (-----).

* No sagittas collected.

C) Size frequency distribution histogram of *S. setosa* of different maturity stages.

Statistics (All stages)

N= 172

Mean 10.49 (Length in mm).

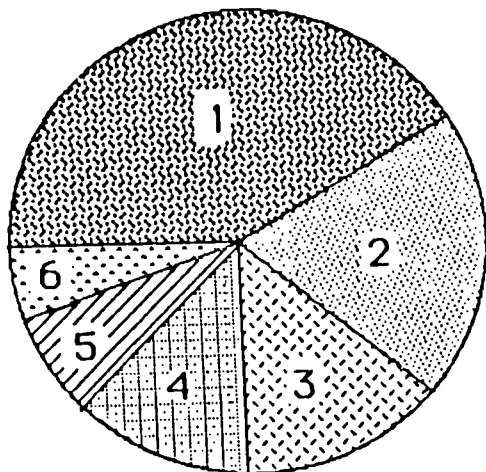
Standard error 0.15 Standard deviation 2.03

Mean size stage I = 9.85

Mean size stage II = 12.30

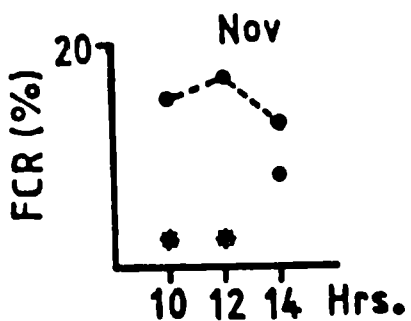
Mean size stage III = 13.73

A



Items	%
1.- Appendicularia	36.7
2.- <i>Acartia</i>	22.0
3.- Nauplii	17.0
4.- <i>Pseudocalanus</i>	16.3
5.- Dinoflagellates	6.0
6.- OMNI	2.0

B



C

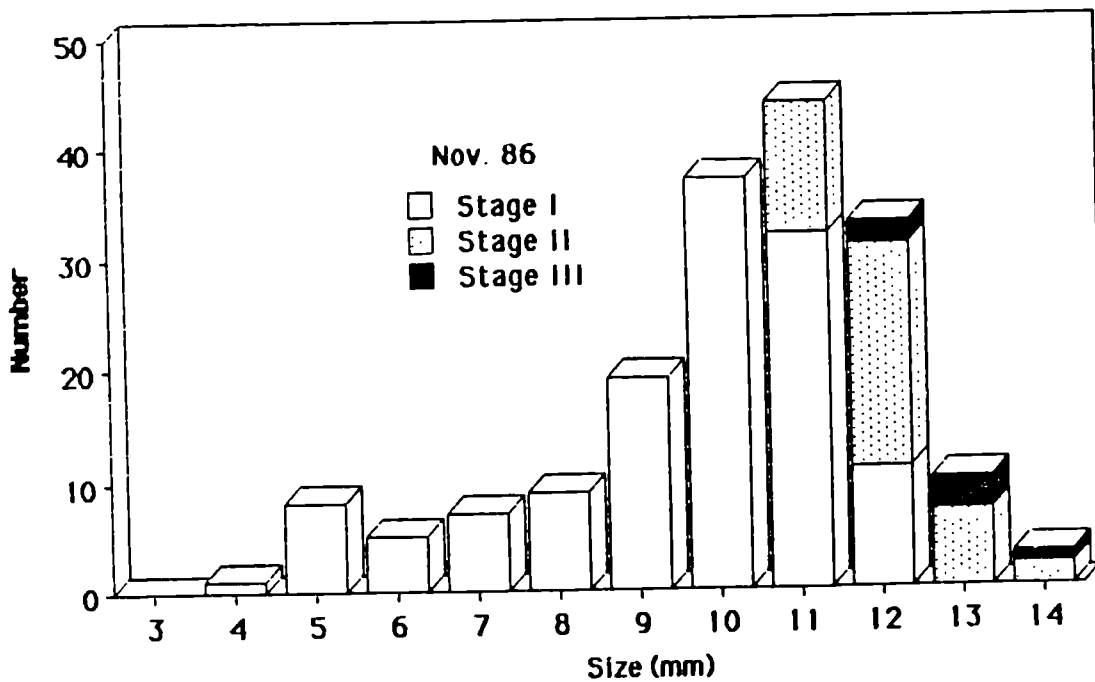
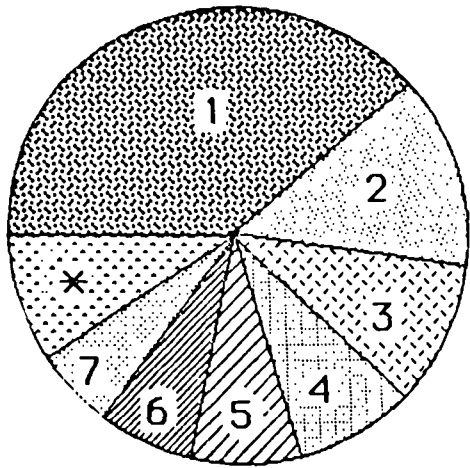


Fig. 29,A,B,C.

Station 1

January 1987.

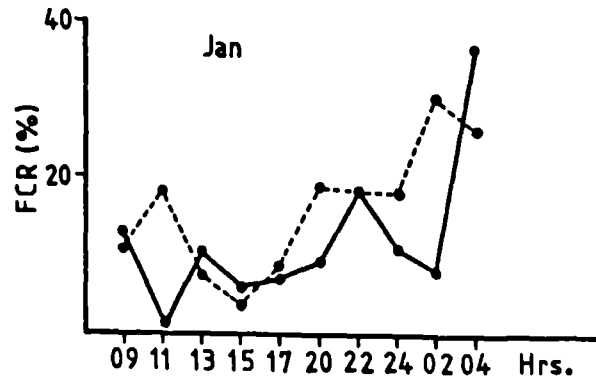
- A)** Percentage occurrence of food items in *S. setosa*, as recorded from field samples.
- B)** Food Containing Ratio (FCR) found in analysis of gut contents of *S. setosa* from day-night samples. Surf. (_____) Bott. (-----).
- C)** Size frequency distribution histogram of *S. setosa* of different maturity stages.
Statistics (All stages)
N= 1050
Mean 11.50 (Length in mm).
Standard error 0.04 Standard deviation 1.28
Mean size stage I = 11.25
Mean size stage II = 13.23
No stage III recorded.



A

Jan 87 Items	%
1.- Appendicularia	41.0
2.- Nauplii	11.8
3.- <i>Pseudocalanus</i>	9.6
4.- <i>Oithona</i>	7.4
5.- Copepod remains	7.0
6.- Herring	6.0
7.- OMNI	6.0
* Others	10.8
<i>Acartia</i>	5.2
Polychaeta	2.2
Crustacean eggs	2.0
<i>Coscinodiscus</i>	1.5

B



C

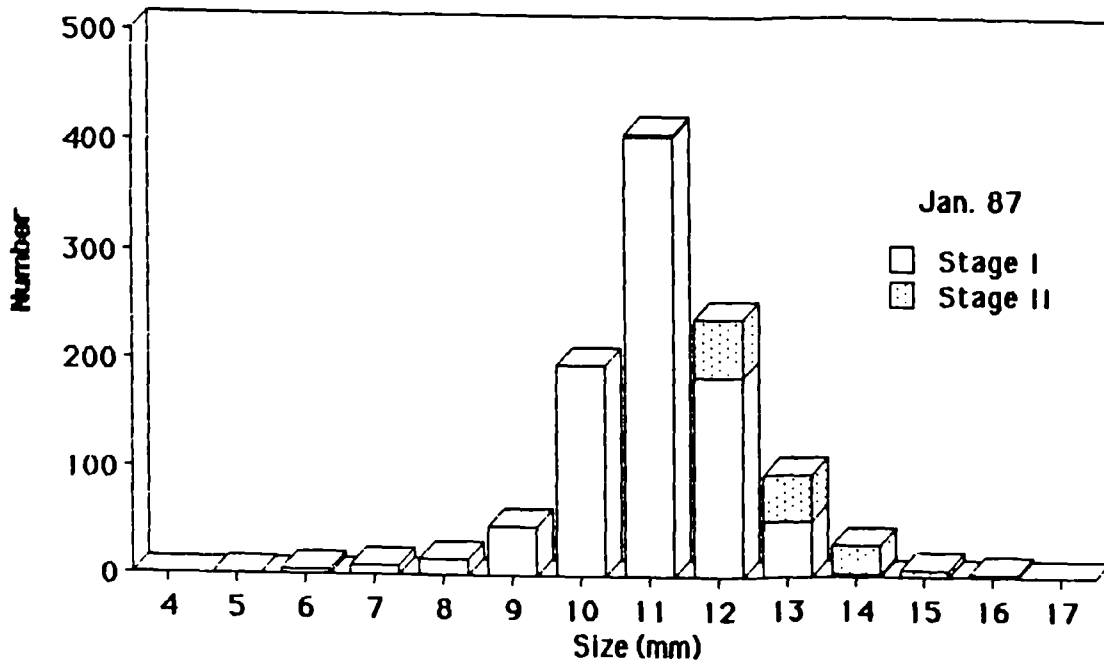


Fig. 30, A,B,C.

Station 1

October 1987.

- A)** Percentage occurrence of food items in *S. setosa*, as recorded from field samples.
- B)** Food Containing Ratio (FCR) found in analysis of gut contents of *S. setosa* from day-night samples. Surf. (_____) Bott. (-----).
- C)** Size frequency distribution histogram of *S. setosa* of different maturity stages.
- Statistics
N= 972
Mean 8.85 (Length in mm).
Standard error 0.07 Standard deviation 2.43
Mean size stage I = 6.70
Mean size stage II = 10.26
Mean size stage III = 12.42

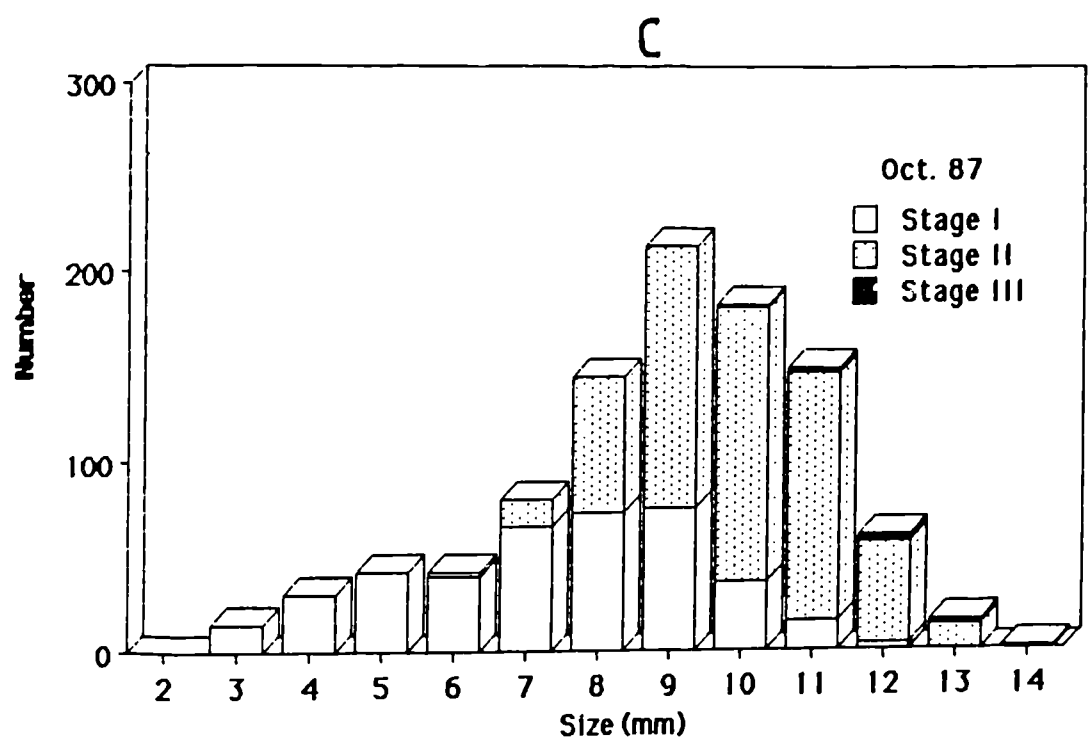
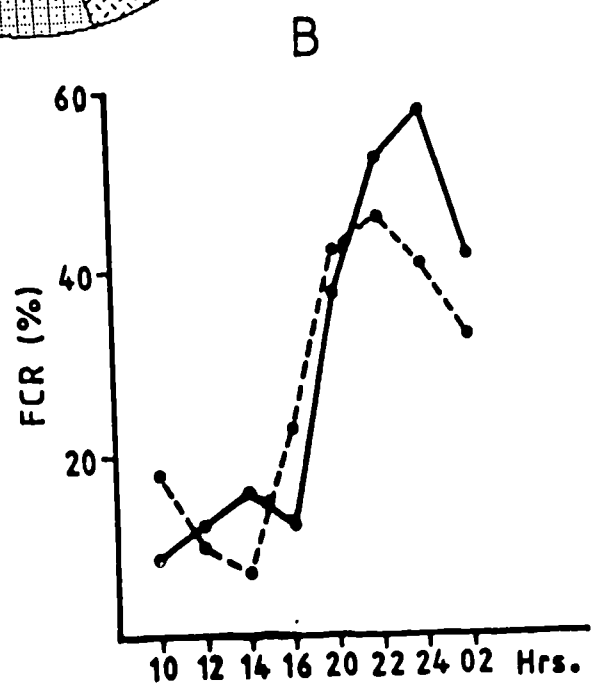
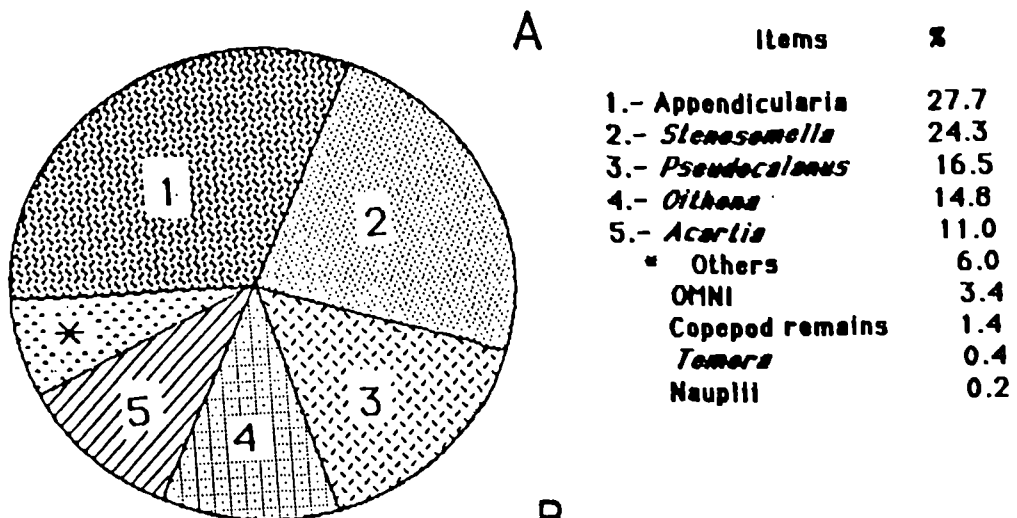


Fig. 31.

Station 1

November 1987.

Size frequency distribution histogram of *S. setosa* of different maturity stages.

Statistics (All stages)

N= 235

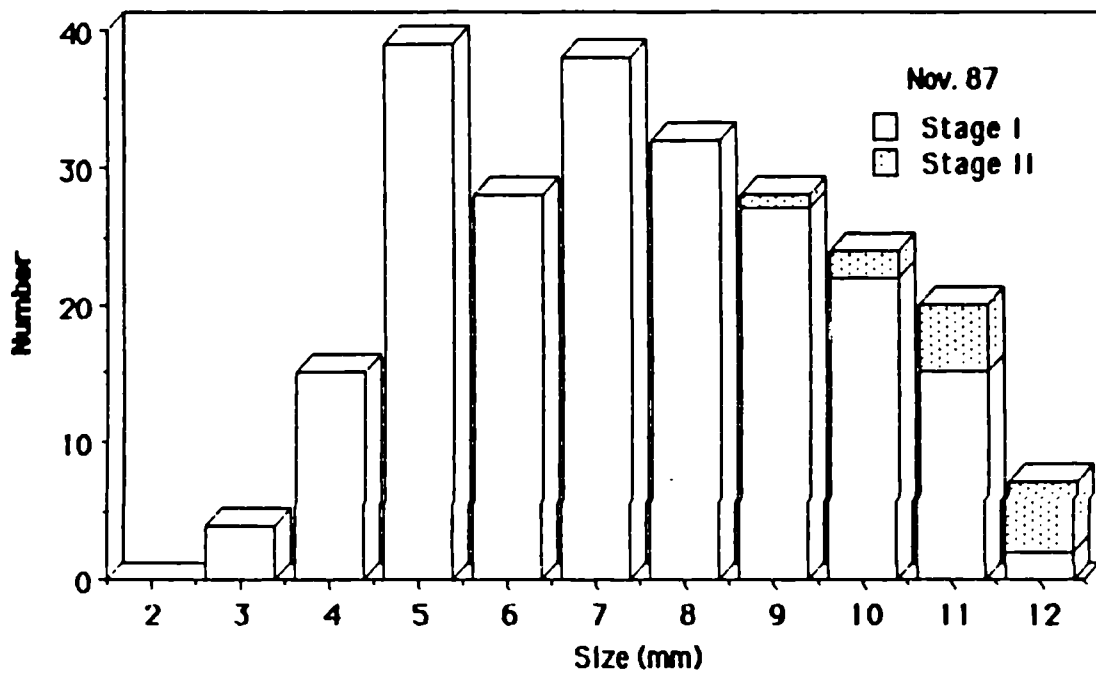
Mean 7.81 Mode 5.60 (Length in mm).

Standard error 0.14 Standard deviation 2.21

Mean size stage I = 7.60

Mean size stage II = 11.38

No stage III recorded



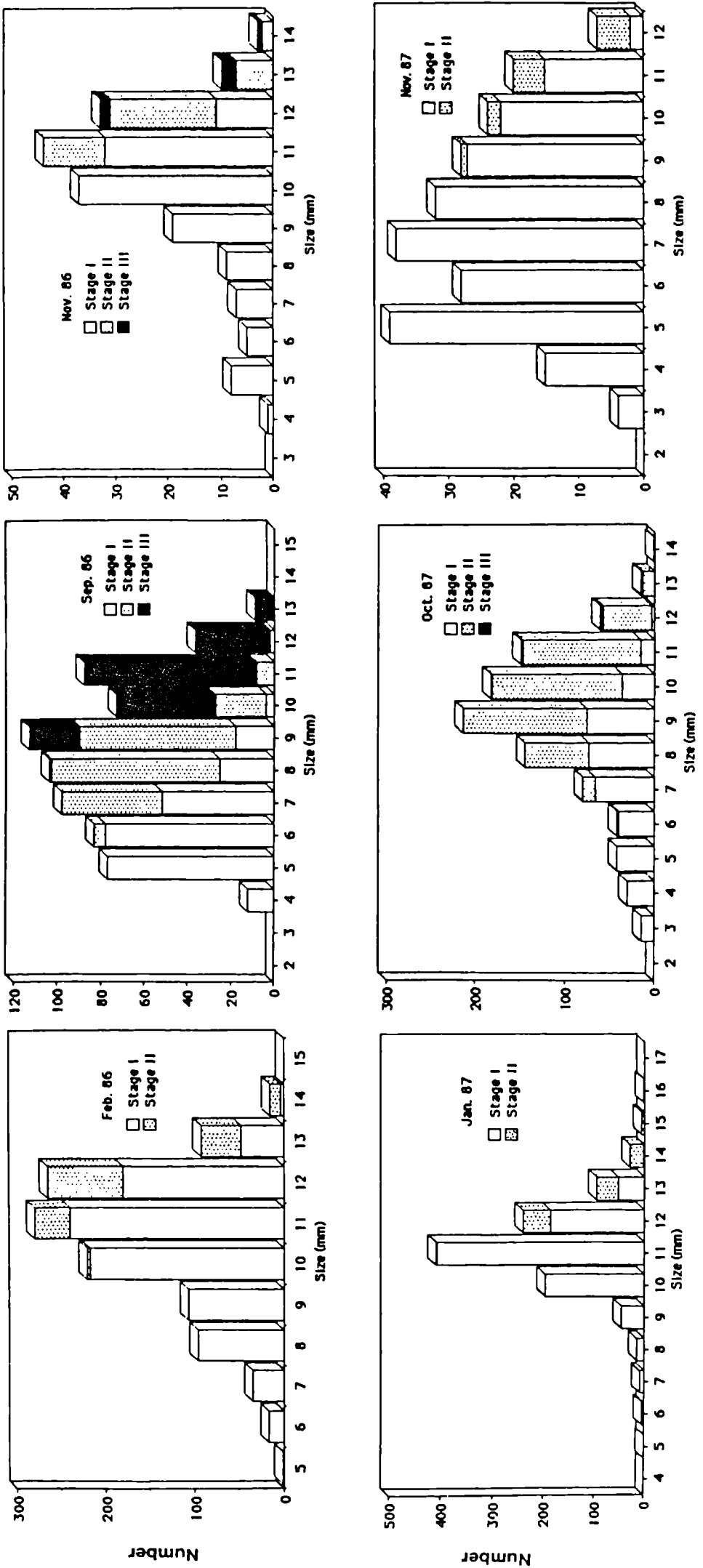


Fig. 32.- Length -frequency and maturity stages of *Sagitta setosa* at station 1, 1986-1987.

Fig. 33.

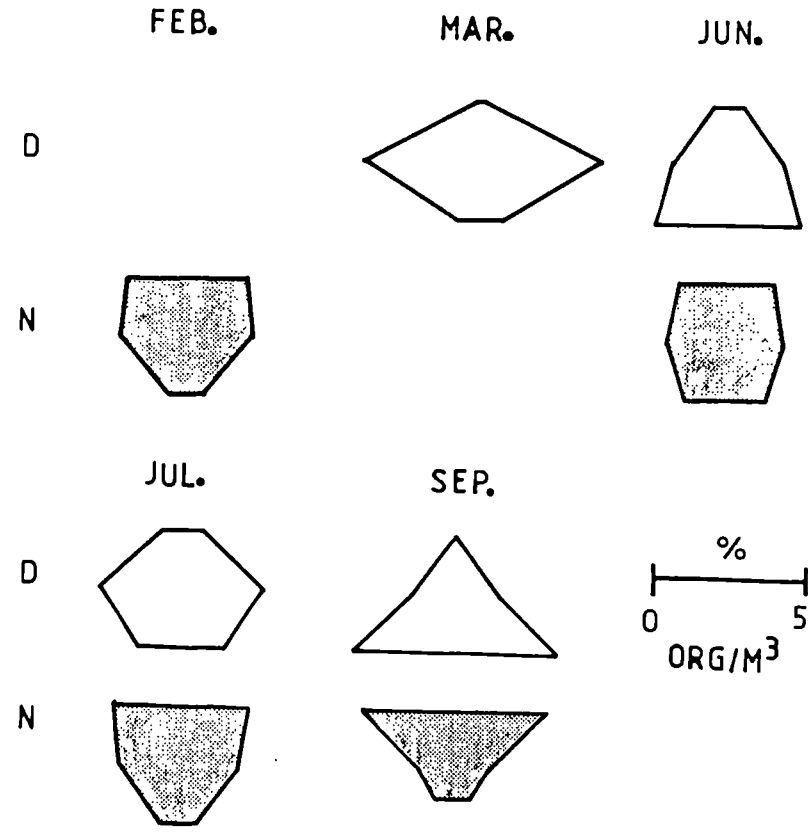
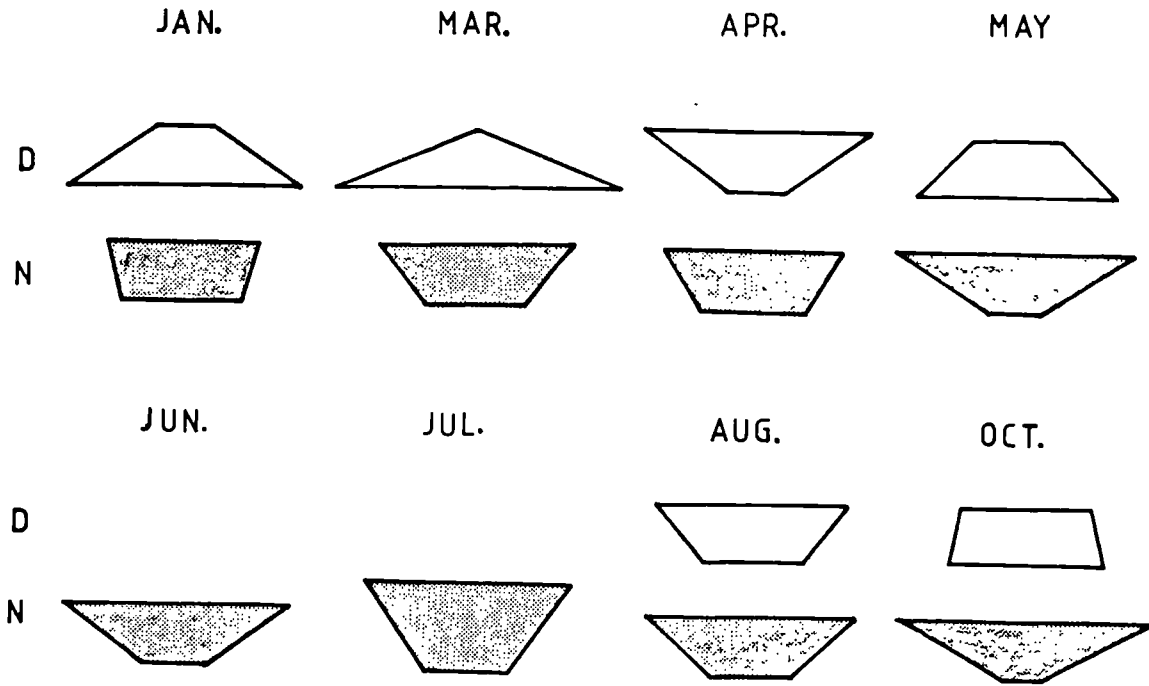
A) Diel vertical migration of *S. elegans* at station 1, 1987.

B) Diel vertical migration of *S. elegans* at station 2, 1986.

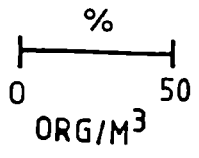
D= day N= night

Depths are: for station 1, surface and near bottom, for station 2, surface, midwater and near bottom.

A



B



	09 Hrs		12 Hrs		15 Hrs		18 Hrs		21 Hrs		24 Hrs		03 Hrs		06 Hrs		Σ
	S	B	S	B	S	B	S	B	S	B	S	B	S	B	S	B	
<i>S. setosa</i>	0.7	0.5	0.4	2.0	2.0	2.0	1.0	4.0	0.1	0.3	0.5	1.0	0.5	0.5	0.3	0.4	3
<i>S. elegans</i>	0.2	0.4	0.2	4.0	3.0	10.0	1.0	3.0	0.1	7.0	0.3	3.0	5.0	5.0	1.0	4.0	8.2
<i>Calanus</i>	0.03	0.2	0.04	0.3	0.3	1.0	0.1	0.08	0.4	0.1	0.5	0.1	0.2	0.1	1.0	0	0.8
<i>Acartia</i>	2.6	20.0	9.0	2.0	10.0	10.0	15.0	14.0	7.0	8.0	14.0	1.0	3.0	3.0	4.0	2.0	23.5
<i>Centropages</i>	2.2	10.0	3.0	0	5.0	1.0	11.0	1.0	2.0	1.0	2.0	0	0.4	0	0	0	7
<i>Pseudocalanus</i>	0.8	16.0	4.0	34.0	4.0	18.0	9.0	14.0	12.0	21.0	7.0	26.0	4.0	27.0	5.0	19.0	40.8
<i>Temora</i>	0.4	12.0	3.0	4.0	2.0	2.0	3.0	0	9.0	2.0	4.0	2.0	2.0	3.0	6.0	3.0	10.5
<i>Oithona</i>	0.4	0	2.0	0	0.4	1.0	0	0	0	0	0	0	0	0	0	0	0.6
<i>Polychaeta</i>	0	0	1.0	0	0.4	2.0	0	1.0	0	2.0	1.0	2.0	1.0	0	0.5	1.0	2.2
<i>Clypea harenagus</i>	0	0	0	0	0	0	0	0.3	0.08	0	0	0.05	0	0	0	0	0.3
<i>Appendicularia</i>	0	0			0	0	0	1.0	1.0	0.4	2.0	0	7.0	1.0	1.0	2.0	2.8

Table 9.- Plankton composition and abundance (Org/M³) at station 1, in February 1986. S=Surface B=Bottom. Day samples 9-11-86; night samples 20-21-11-86.

	09 Hrs		12 Hrs		15 Hrs		18 Hrs		21 Hrs		24 Hrs		03 Hrs		06 Hrs		Σ
	S	B	S	B	S	B	S	B	S	B	S	B	S	B	S	B	
<i>S. elegans</i>	5.0	0.1	0.3	0.4	1.4	2	2	1	2	1	2	3	1	3	3	1	0.2
<i>Calanus</i>	29.0	3.0	2	17	11	31	11	41	17	28	28	30	22	18	6	41	2.2
<i>Cirripedia</i>	202	206	175	52	175	218	241	111	193	119	197	113	210	79	175	254	18.9
<i>Pseudocalanus</i>	48	198	35	175	22	198	88	87	175	187	243	198	338	179	70	286	17.5
<i>Acartia</i>	2.0	36	39	52	48	44	66	52	193	131	110	103	57	99	35	190	8.7
<i>Polychaeta</i>	79	158	53	48	79	87	48	32	48	64	39	95	219	40	48	87	8.5
<i>Temora</i>	162	266	101	143	70	397	254	317	228	444	201	159	131	357	548	619	30.5
<i>Centropages</i>	26	32	53	16	52	40	87	24	88	111	61	56	9	87	136	56	6.4
<i>Hydrozoa</i>	13	0	13	0	4	0	65	16	13	8	4	8	0	0	9	0	1
<i>Appendicularia</i>	13	0	15	0	9	20	9	0	4	0	5	12	0	12	13	0	0.7
<i>Cladocera</i>	4	0	9	8	13	19	0	4	70	56	44	32	4	32	79	79	3.1
Fish eggs	4	3	0	0	6	2	4	0	0	3	0	0	3	0	0	0	0.1
Fish larvae	4	12	0	0	0	0	4	0	3	5	0	0	0	0	0	8	0.2
<i>Bryozoa</i>	4	0	5	0	0	0	4	0	0	12	0	20	0	4	0	0	0.3
<i>Oithona</i>	4	0	0	0	0	0	0	4	0	6	0	0	0	0	0	0	0.09
Decapods	0	4	9	0	13	4	0	0	18	8	0	12	9	3	4	16	0.7
Nauplii	0	0	0	0	0	4	18	8	4	0	0	0	0	0	0	0	0.2
Gasteropods	0	4	0	0	0	4	0	5	0	0	0	0	0	0	0	0	0.09

Table 10.- Plankton composition and abundance (Org/M³) at station 1, in April 1986. S=Surface B=Bottom. Day samples 14-IV-86; night samples 24-25-IV-86.

	09 Hrs		12 Hrs		15 Hrs		18 Hrs		21 Hrs		24 Hrs		03 Hrs		06 Hrs		Σ
	S	B	S	B	S	B	S	B	S	B	S	B	S	B	S	B	
<i>S. elegans</i>	3	18	0	8	0	2	14	35	15	13	59	2	56	11	2	54	1
<i>Calanus</i>	97	258	1	109	0	29	54	396	570	158	186	79	22	10	263	436	10
<i>Temora</i>	48	317	18	412	0	151	17	349	1947	270	219	448	1127	476	1228	1126	30
<i>Pseudocalanus</i>	66	698	18	452	9	59	109	539	890	301	447	206	298	198	359	1269	22
<i>Cladocera</i>	13	4	9	56	6	190	17	20	9	0	0	12	22	63	0	0	1.5
<i>Appendicularia</i>	31	83	9	135	0	87	4	59	10	24	61	135	87	135	30	39	3.4
<i>Centropages</i>	9	87	22	64	0	83	30	111	35	24	482	158	87	71	153	79	5.5
<i>Acartia</i>	110	539	48	48	12	40	1644	635	833	587	122	139	22	31	912	992	25
<i>Decapods</i>	0	20	0	8	0	4	3	24	57	8	9	4	0	0	13	39	0.7
<i>Hydrozoa</i>	0	0	0	0	0	8	0	12	0	0	9	0	4	12	0	0	0.1
<i>Fish eggs</i>	0	0	0	0	0	0	4	0	0	0	0	0	17	0	0	0	0.07
<i>Polychaeta</i>	0	0	2	0	0	0	0	12	0	0	4	0	0	0	0	8	0.06
<i>Oithona</i>	0	6	0	0	0	3	0	8	9	0	0	2	0	0	0	0	0.04
<i>Cirripedia</i>	0	0	0	0	0	0	0	12	0	0	0	0	5	0	4	8	0.1

Table 11.- Plankton composition and abundance (Org/M³) at station 1, in June 1986. S=Surface B=Bottom. Day samples 11-VI-86; night samples 15-16-VI-86.

	09 Hrs		12 Hrs		15 Hrs		18 Hrs		21 Hrs		24 Hrs		03 Hrs		06 Hrs		Σ
	S	B	S	B	S	B	S	B	S	B	S	B	S	B	S	B	
<i>S. elegans</i>	50	20	44	68	36	161	38	19	5	9	14	13	6	7	2	8	3.8
<i>Calanus</i>	17	14	11	1	22	6	13	12	5	2	2	1	0.5	0	1	3	0.8
<i>Temora</i>	263	143	48	39	0	107	114	95	210	4	254	238	101	20	92	70	13.6
<i>Acartia</i>	272	238	430	139	1482	139	701	504	123	158	66	43	30	119	232	166	36.6
<i>Cladocera</i>	44	39	17	0	0	4	35	39	35	22	4	0	4	1	30	14	2
<i>Decapods</i>	17	55	13	24	35	16	4	12	44	27	70	83	9	4	57	45	3.9
<i>Pseudocalanus</i>	482	180	26	238	0	440	140	508	267	317	26	55	4	59	237	547	26.7
<i>Centropages</i>	26	10	30	24	219	39	22	12	0	8	13	8	0	8	5	0	3.2
<i>Appendicularia</i>	44	24	9	20	0	43	38	27	44	35	26	12	118	47	83	60	4.7
<i>Oithona</i>	0	0	0	0	0	0	4	8	5	4	8	8	0	0	8	5	0.4
<i>Polychaeta</i>	0	4	0	0	0	6	0	0	43	8	0	5	0	0	7	4	0.6
<i>Echinoderma</i>	0	0	0	4	0	0	4	0	0	0	22	4	197	12	52	19	2.3
<i>Hydrozoa</i>	9	0	8	10	0	16	4	3	0	4	3	8	6	3	13	5	0.6
<i>Fish larvae</i>	0	0	0	0	0	12	0	0	5	4	0	0	0	0	2	0	0.2
<i>Ctenophora</i>	0.4	0	0	0	0	2	0	0	0	3	0	0	4	0	0	0	0.07

Table 12.- Plankton composition and abundance (Org/M³) at station 1, in July-August 1986. S=Surface B=Bottom. Day samples 29-VII-86; night samples 1-2-VIII-86.

	09 Hrs		12 Hrs		15 Hrs		18 Hrs		21 Hrs		24 Hrs		03 Hrs		06 Hrs		Σ
	S	B	S	B	S	B	S	B	S	B	S	B	S	B	S	B	
<i>S. elegans</i>	24	2	4	7	8	12	4	1	4	0.2	6	1	2	1	1	1	0.4
<i>S. setosa</i>	25	2	7	28	19	31	7	2	1	0.06	1	2	3	0.3	0.2	0.5	0.7
<i>Calanus</i>	29	20	18	15	28	44	45	6	56	0.5	11	7	13	8	10	5	1.6
<i>Pseudocalanus</i>	188	170	44	99	17	119	61	158	298	103	241	79	131	218	201	178	12
<i>Temora</i>	70	71	30	59	19	127	35	47	105	4	26	27	35	27	131	158	5
<i>Acartia</i>	1732	2341	526	516	1316	595	2561	952	728	278	254	317	526	39	351	468	69.6
<i>Decapods</i>	35	27	22	19	26	16	44	8	26	12	8	8	0	7	9	4	1.4
<i>Hydrozoa</i>	22	4	3	16	17	2	16	20	0	0	0	0	9	0	0	0	0.5
<i>Cladocera</i>	35	24	0	19	0	0	35	20	8	4	0	0	0	8	18	4	0.9
<i>Centropages</i>	13	8	26	12	8	27	0	0	17	0	22	35	9	5	10	0	1
<i>Oithona</i>	4	0	5	12	17	16	0	15	0	0	16	0	4	9	0	12	0.5
<i>Appendicularia</i>	30	31	22	43	105	67	17	40	136	51	48	67	92	71	26	39	4.5
<i>Sagitta</i> spp.	1	5	11	12	14	21	10	0.4	0	0	1	0	0	0	0	0	0.3
<i>Polychaeta</i>	0	0	0	8	0	8	0	4	3	0	4	0	0	0	0	0	0.1
<i>Clupea harengus</i>	0	0	0	0	0	0	0	3	0	0	8	9	22	33	67	26	0.8
<i>Amphipoda</i>	0	0	0	6	0	0	0	0	0	5	13	4	9	24	0	12	0.3

Table 13.- Plankton composition and abundance (Org/M³) at station 1, in September 1986. S=Surface B=Bottom. Day samples 17-IX-86; night samples 23-24-IX-86.

	10 hrs.		12 hrs.		14 Hrs.		Σ
	S	B	S	B	S	B	
<i>S. setosa</i>	0.07	5.0	0	13	0.1	2.8	0.4
Herring	0.9	1.6	0.2	0.4	0.3	0.2	0.1
Calanus	1.7	22.8	1.0	15	3.7	11	2.5
<i>Pseudocalanus</i>	33	40	16.5	120	0	165	17
<i>Temora</i>	8.7	47.7	8.7	4	162	12	11
Cladocera	4.4	0	0	0	0	0	0.2
Centropages	13.1	0	0	0	0	4	0.8
Amphipods	4.4	8	0	0	0	0	0.5
Decapods	4.4	4	0	4	0	0	0.5
<i>Acartia</i>	98.4	357	14.7	324	0	331	51.2
<i>S. elegans</i>	0	103	0	28	0.8	33	7.5
Appendicularia	0	47.4	44	43	4.4	4	6.5
Oithona	0	4	2	4	0	4	0.6
Polychaeta	0	4	0	12	0	0	0.7

Table 14.- Plankton composition and abundance (Org/M³) at station 1, in November 1986. S=Surface B=Bottom. Day samples 4-XI-86.

	09 Hrs		11 Hrs		13 Hrs		15 Hrs		17 Hrs		20 Hrs		22 Hrs		24 Hrs		02 Hrs		04 Hrs		Σ
	S	B	S	B	S	B	S	B	S	B	S	B	S	B	S	B	S	B	S	B	
Pseudocalanus	6	49	10	11	5	18	5	24	35	20	6	19	9	9	26	11	20	18	11	20	32
Acartia	7	12	6	7	5	10	6	11	11	21	4	8	8	4	7	7	5	7	9	12	16
Appendicularia	7	12	7	8	4	8	3	6	3	5	1	2	1	1	5	4	3	4	0	35	11
Oithona	3	0	0	0.2	1	1	0.5	1	0	2	0	0	0.2	0.1	0.5	0.2	0.2	0.4	0	0	1
Lamellibranchia	1	2	0.4	1	1	0.7	1	2	0	0	0	0	0	0	0.5	0.3	0	0	0.2	0	1
Polychaeta	6	2	0.6	0.4	3	0.4	2	0.4	1	3	0.5	0.5	1	2	2	1	1	0.7	0	1	2.8
Calanus	0.3	0	0.6	2	1	2	1	2	4	3	2	1	1	0.3	3	1	2	0.2	2	1	2.9
S. setosa	0.1	0	0.2	2	2	1	0.5	1	0.2	0.3	0.2	0.1	0.3	0.1	0.4	0.6	0.5	0.2	2	3	1.4
S. elegans	0.2	18	2	8	3	12	2	24	18	7	8	4	19	7	26	16	15	5	3	5	19
Harpacticoids	0	2	0	0.2	0	0.2	0.2	0.2	0	0	0	0	0	0	0	0	0.1	0	0	0.2	0.3
Centropages	0	0	1	0	0	0	0.2	0	0	0	0	0	0.2	0.1	1	0	0	0	0.2	0	0.3
Temora	0	0	0.4	0.4	0	0	0	0.4	1	0	0	0	0.2	0.3	0.1	0.4	0.5	0.7	1	1	0.6
Amphipoda	0	0	0	0.2	0	0.2	0	0.4	0	3	0	2	0.1	0.1	0	1	0.1	1	0	0.7	0.9
Clupea harengus	0	0	0	0.1	0.1	0.1	0.5	3	0	2	0.5	4	0.04	0.1	0.2	43	11	19	3	13	9.7

Table 15.- Plankton composition and abundance (Org/M³) at station 1, in January 1987. S=Surface B=Bottom. Day samples 30-1-87; night samples 28-29-1-87.

	09 Hrs		11 Hrs		13 Hrs		15 Hrs		22 Hrs		24 Hrs		02 Hrs		04 Hrs		Σ
	S	B	S	B	S	B	S	B	S	B	S	B	S	B	S	B	
Cirripedia	35	23	58	78	90	26	34	26	206	158	316	160	158	50	83.3	35	36.6
Pseudocalanus	22	49	9	109	6	52	21	34	83	103	61.4	103	51	108	53	10.5	20.8
Decapods	2	5	3	7	2	4.2	1	1.4	24.6	15.8	15	35	15.5	6	5.5	2	3.4
Temora	3	0.4	1.6	4	1.6	5.7	1	4	12.3	2	4.4	8	10	7	8.8	8	2
Appendicularia	5	10	9.4	22	33	20	72	88	16.6	17.3	39.4	43.6	52.2	30	56	5.3	12.4
Oithona	11	2	2.6	18	2.6	4	10.5	2.4	9.6	3.7	4.4	14.3	5.5	6	7.7	2	2.5
Acartia	5	2	6	4	5	1	2.6	3.3	1.7	6.3	9.6	6.3	6.6	4	6.6	8	1.8
Calanus	7	3	1.6	8	3	8.5	2.6	5	20	8.4	4.4	14.3	14.4	6	9	8	3
S. elegans	0	0.3	0.04	1.4	0	0.5	0	0	21	0.5	9.6	1.6	8.8	1	1.4	0.6	1
Hydrozoa	0.4	1	0.5	1	1	0.2	0.5	1	1	0	1.7	0	0	0	1	0	0.2
Bryozoa	1	2.4	0	0	0	1	5.7	3.3	1	0.5	0.8	1.6	8.8	2	2.2	3	0.7
Fish eggs	2	1	2	3.3	2.6	1.4	4.2	4.3	2.6	1	2.6	2.4	7.7	4	8.8	5	1.3
F. larvae	1	0.4	0	0	1	1	0.5	0.4	0.8	0.5	3.5	3.1	2.2	2	5.5	2	0.6
Harpacticoids	0.4	6	3	7	0	1.4	0.5	0	0.8	2.6	0.8	4.7	0	3	0	1	0.5
Polychaeta	2	1.4	8	14	1.6	6	7	7.6	0.8	5.2	4.4	9.5	8.8	3	6.6	5	2
Echinodermata	7	1.4	0.5	0.4	17	28	134	54	0	11	30.7	60.3	17.7	11	44.4	5.3	10.6
Cladocera	0.4	0	0	0	0.5	0	0.3	0	0	0	0	0.8	0	0	1	0	0.1
Euphausiids	0	0	0	0	0	0	0	0	0	0	2.6	0.8	2.2	1	1	0.3	0.2

Table 16.- Plankton composition and abundance (Org/M³) at station 1, in March 1987. S=Surface B=Bottom. Day samples 23-III-87; night samples 23-24-III-87.

	09 Hrs		11 Hrs		13 Hrs		15 Hrs		23 Hrs		01 Hrs		03 Hrs		05 Hrs		Σ
	S	B	S	B	S	B	S	B	S	B	S	B	S	B	S	B	
<i>Pseudocalanus</i>	96.6	443	58.4	99	169	126	160	176	168	174	64.6	80	233	200	136	300	22.5
<i>Appendicularia</i>	89	172	49.2	59	55.4	75.5	96	44	141	58	61.5	71.4	53.7	74.3	135	59	10.8
<i>Temora</i>	94	363	70.7	118	188	112	150	118	160	232	157	174	346	120	183	165	23.1
<i>Acartia</i>	51	158	55.4	56	61	78	57.6	59	51	8.7	37	28.5	42	37	108	76.4	8.1
<i>Cirripedia</i>	50	160	55.4	67	77	84	93	50	89.6	43.4	49	28.5	89.5	34.3	170	118	10.6
<i>Calanus</i>	33	67.7	12.3	8.8	24.6	14	23.2	15	173	23	83	48.5	47	25.7	20.3	26.4	5.4
<i>Centropages</i>	68	80	43	27	46	28	64	21	32	29	30.7	23	47.7	28.5	34	12	5.1
<i>Bryozoa</i>	0	37	0	13.3	6.1	19.6	12.8	9	25.6	23.2	37	17.1	6	43	40.6	18	2.6
<i>Oithona</i>	25.4	49	6	0	6.1	11.2	13	6	38.4	11.6	24.6	11.4	12	5.7	6.7	12	2
<i>Hydrozoa</i>	2.5	4.6	3	1	6.1	0.5	3.2	0	6.4	3	3	0.5	6	5.7	13.5	1	0.5
<i>Euphausiids</i>	2.5	6.1	0.6	0.5	1.2	0	0	6	6.4	1	7.3	6	0.6	2.8	6.7	0.6	0.4
<i>Polychaeta</i>	5	37	3.7	5.3	18.4	14	6.4	9	12.8	5.8	3	5.7	18	1	7	0.6	1.3
<i>Echinodermata</i>	18	0	9.2	0	6.1	0	0	6	83.2	8.7	46	14.3	6	5.7	27	6	1.9
<i>S. elegans</i>	5	1.8	1.4	0.5	3	0.5	4	1	4.8	0.1	2.3	0.1	2	0.7	2.5	6	0.3
<i>Decapods</i>	10.2	12.3	0	5.3	18.4	14	6.4	18	6.4	3	6	1.7	24	8.5	13.5	11.7	1.3
<i>Cladocera</i>	5	37	6	2.6	9.2	8.4	12.8	0	8.3	8.7	60	5.7	24	2.8	27	6	1.8
<i>Fish eggs</i>	5.1	0.7	3	0.5	2.4	2.8	3.2	6	5.1	1.4	6	1.7	3	2.8	7	1	0.4
<i>F. larvae</i>	0	0	0.6	0.5	0	1.4	0	0	0	0	0	1.1	0.6	0	6	0	0.1
<i>Haracticoida</i>	0	3	3	1	0	4.2	0	6	0.6	0	0	2.8	0	2.8	6.7	0	0.2
<i>Nauplii</i>	12.7	18.4	0	0	0	0	6.4	0	3.2	5.8	24.6	0	6	2.8	0	0	0.5
<i>Metridia</i>	2.5	0	0	0	0	0	0	3	0	0	2	0	0	0	3.4	0	0.1
<i>Lamellibranchia</i>	0	1.6	0	5.6	0	0.3	0	0	0	1.4	0.6	0.5	0	2.8	0	6	0.1
<i>Gasteropoda</i>	2.5	0	3	2.6	3	1.1	0	3	0	0	0.6	0	0	0	0	11.7	0.2

Table 17.- Plankton composition and abundance (Org/M³) at station 1, in April 1987. S=Surface B=Bottom. Day samples 27-IV-87; night samples 28-29-IV-87.

	09 Hrs		11 Hrs		23 Hrs		01 Hrs		03 Hrs		05 Hrs		Σ
	S	B	S	B	S	B	S	B	S	B	S	B	
<i>Cladocera</i>	1700	1800	5818	714	3707	1571	3200	714	3600	815	8660	1636	38.3
<i>Temora</i>	690	1680	182	2000	4276	1857	2640	1685	3200	1538	2500	2436	27.9
<i>Pseudocalanus</i>	440	840	91	428	1172	928	3300	685	1600	630	500	745	12.8
<i>Acartia</i>	270	400	782	400	1413	471	1220	257	110	292	1300	927	8.8
<i>Centropages</i>	240	280	55	357	258	143	220	214	800	153	520	363	4
<i>Appendicularia</i>	250	320	309	328	741	428	900	114	500	338	240	309	5.4
<i>Oithona</i>	20	0	36.3	0	138	114	120	18	100	30.7	8	0	0.6
<i>Cirripedia</i>	50	24	3.6	29	35	0	60	0	0	15	6	21	0.2
<i>Calanus</i>	6	16	3.6	7	86	64	120	28	17	2.7	6	11	0.4
<i>S. elegans</i>	1.4	2.8	1.4	4	14	6.7	50	3.4	9.2	1.2	0.6	4	0.1
Fish eggs	1	0	0	1	0	0	0	4.3	10	0	2	0	0.02
F. larvae	4	0.8	9.1	0	8.6	0.7	20	0	20	3	10	7	0.09
Decapods	7	16	0	43	34.5	29	2	28	60	15	20	73	0.3
Euphausiids	1	0	0	0	8.6	7	20	0	6	0	0	0	0.04
Bryozoa	0	8	0	0	0	0	0	0	0	0	0	19	0.01
Hydrozoa	0	80	0	1	8.6	1.4	40	0	6	46	80	19	0.3
Polychaeta	0	0	0	1	0	0	20	0	0	0	4	0	0.02
Metridia	0	0	0	0	103	2.8	40	1.4	0	1.5	0	0	0.1

Table 18.- Plankton composition and abundance (Org/M³) at station 1, in May 1987. S=Surface B=Bottom. Day samples 25-V-87; night samples 25-26-V-87.

	23 Hrs		01 Hrs		03 Hrs		05 Hrs		\bar{x}
	S	B	S	B	S	B	S	B	
<i>Temora</i>	5285	3247	3100	5250	2596	1565	1853	3708	42.8
<i>Pseudocalanus</i>	2268	2165	4133	1275	1000	1250	956	3041	26
<i>Acartia</i>	1517	1855	1466	1437	1346	2025	1764	2300	22
<i>Centropages</i>	357	422	417	587	385	375	382	458	5.4
<i>Cladocera</i>	89	175	100	89	211	312	44	291	2.1
<i>Appendicularia</i>	18	20.6	33	25	19	37.5	73	8.3	0.3
<i>Calanus</i>	23	14	10	12.5	9.6	8.7	3.6	16.6	0.1
<i>Decapods</i>	26.7	20.6	33	7.5	13.4	37.5	29	41	0.3
<i>S. elegans</i>	26.7	8.2	30	2.5	34.6	6.2	1.7	9.1	0.2
<i>Polychaeta</i>	1.8	31	33	38	0	0	3	0	0.1
<i>Cirripedia</i>	1.8	10.3	0	0	3.8	1.2	0	8.3	0.03
<i>Euphausiids</i>	1.8	0	3.3	1.2	0	0	0	0	0.009
<i>Metridia</i>	0	10.3	13	0	2	0	0	0	0.02
<i>Bryozoa</i>	0	10.3	0	0	0	0	0	0	0.01
<i>Fish larvae</i>	0	8.2	0	2.5	5.7	3.7	3	0	0.03
<i>F. eggs</i>	0	0	0	5	0	3.7	3	0	0.01
<i>Oithona</i>	0	0	16.6	0	0	0	14.7	0	0.04
<i>Amphipoda</i>	0	0	0	12.5	0	0	0	0	0.01
<i>Hydrozoa</i>	0	0	16.6	1.2	12	1.2	1.4	0	0.03

Table 19.-Plankton composition and abundance (Org/M³) at station 1, in June 1987. S=Surface B=Bottom. Night samples 10-11-VI-87.

	23 Hrs		01 Hrs		03 Hrs		05 Hrs		\bar{x}
	S	B	S	B	S	B	S	B	
Pseudocalanus	1962	1740	1320	1381	1030	1094	1323	509	32.2
Temora	781	770	340	538	360	421	571	552	13.5
Acartia	952	1770	1280	1309	930	814	1333	1556	31
Oithona	76	246	40	102	58	28	238	261	3.2
Decapods	72	77	40	73	69	28	209	44	1.9
Cladocera	209	184	160	116	232	280	409	160	5.4
Centropages	114	107	120	116	69	126	238	291	3.6
Appendicularia	38	200	240	436	197	84	362	363	5.9
Hydrozoa	19	0	20	29	11	0	95	15	0.5
Nauplii	4.7	15	20	0	0	28	66.6	7	0.4
Calanus	26	12	20	8	5	2.6	28	20	0.3
S. elegans	47.6	19	12.5	6	4	1.4	49.5	15	0.4
Polychaeta	42.8	0	12	43	46	5.2	47	7	0.6
Fish larvae	4.7	0	0	4.7	6	2.8	9.5	0	0.08
F. eggs	4.7	77	0	3.6	0	1.4	0	0	0.2
Bryozoa	2.4	1.5	2	0	0	0	9.5	1.4	0.05
Lamellibranchia	0	1.5	0	7	6	1.4	0	1.4	0.05

Table 20.- Plankton composition and abundance (Org/M³) at station 1, in July 1987. S=Surface B=Bottom. Night samples 16-17-VII-87.

	10 Hrs		12 Hrs		14 Hrs		16 Hrs		23 Hrs		01 Hrs		03 Hrs		05 Hrs		\bar{x}
	S	B	S	B	S	B	S	B	S	B	S	B	S	B	S	B	
<i>Pseudocalanus</i>	293	545	94	919	100	894	80	842	1700	1795	800	847	1120	1600	513	756	24.5
<i>Temora</i>	352	436	2263	257	1150	433	120	968	620	400	830	160	949	711	410	1467	22
<i>Acartia</i>	784	591	442	827	900	1054	700	800	400	1200	270	659	480	800	564	933	21.7
<i>Cladocera</i>	234	618	84	597	580	1035	60	1389	750	782	950	508	1514	302	1025	729	21.2
<i>Appendicularia</i>	96	109	73.6	230	170	169	60	185	120	124	80	75	149	106	102	178	3.8
<i>Decapoda</i>	26.6	90	42	37	50	56	20	76	150	53	120	66	160	133	51	44	2.2
<i>Centropages</i>	53.3	64	21	73	80	94	100	59	10	62	50	37.6	21	35	20.5	44	1.5
<i>Oithona</i>	32	18	10.5	46	70	103	30	84	70	20	100	66	53	44	113	36	1.8
<i>Calanus</i>	16	5.4	48	11	38	10	5	3.1	12	6	4	7.5	24	6.6	4.5	4.8	0.4
<i>S. elegans</i>	8	3	30	9	10	5	2.2	4.2	6	4.4	3	3	21	4.4	3	5.5	0.2
Fish Larvae	0	1	0	3.6	0	2	4	2.5	2	9	0	3	10.6	2.6	2.3	2.6	0.08
<i>Polychaeta</i>	5.3	36	4.2	1.8	20	3	3	4.2	2	3.5	10	3	21	0	20.5	27	0.3
<i>Nauplii</i>	10.6	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0.04
<i>Hydrozoa</i>	1	0	0	7	15	19	3	1.7	0	9	1	2	5.3	1.5	5	9	0.1

Table 21.- Plankton composition and abundance (Org/M³) at station 1, in August 1987. S=Surface B=Bottom. Day samples 5-VII-87; night samples 6-7-VIII-87.

	10 Hrs		12 Hrs		14 Hrs		16 Hrs		20 Hrs		22 Hrs		24 Hrs		02 Hrs		Σ
	S	B	S	B	S	B	S	B	S	B	S	B	S	B	S	B	
Pseudocalanus	390	286	353	400	210	200	295	154	711	466	720	270	916	249	533	150	32.4
Acartia	341	301	294	377	168	250	244	192	489	526	1000	200	816	266	700	250	33
Appendicularia	87.8	98.1	200	103	126	155	80	77	400	126	360	75	308	89	213	80	13.2
Calanus	105	37.7	270	171	273	122	71	27	155	20	144	60	63	20	100	8.7	8.4
Euphausiids	19.5	0.7	4.7	3.4	10.5	10.0	1.7	0	0.8	0	0.8	0	0	0	0	0	0.2
Decapods	9.7	3.7	23.5	8.5	10.5	10.0	4.2	0	13.3	3.3	8.6	5	16	8.8	6.6	1.5	0.6
Metridia	9.7	7.5	0	2	23.6	10.0	8.4	3.8	17.7	0	24	2	5.8	0	3.3	0.5	0.6
Oithona	9.7	45.2	47	68.5	31.5	38.0	12.6	5.7	177	67	224	50	216	44	133	10	6
Herring	0.6	0.2	0.2	0.1	0.4	0	0.1	0	0	0.4	0.3	0.1	0.2	0	0.2	0	0.01
Isias	4.8	7.5	11.7	0	0	0	0	0	8.8	0	0	0	0	8.8	0	0	0.2
S. elegans	3.1	5.2	5.3	5.1	6.3	8.5	8.4	7.7	17.7	1.2	36	3.7	6.6	3.5	13.3	0.7	0.6
S. setosa	0.9	2.0	1.1	0.8	1.1	1.0	1	2.7	4.4	2.5	18	1.2	4.1	1.7	3.3	0.2	0.2
Temora	0.9	7.5	58.8	57	0	20	29	19.2	26.6	13.3	32	20	25	8.8	33.3	15	1.9
Polychaeta	0.9	0.7	0	1	1.3	0	0	0	4.4	1.6	8	0	0.8	0.8	0.6	5	0.1
Fish larvae	0.9	0.7	0	2	0	10.0	0	0.7	0	1.3	0	0	0	0	0	0	0.02
Candacia	0	0	5.9	1	0	0	4.2	3.8	2.2	0	16	0	0.8	0	0	0	0.1
Centropages	0	0	0	0	2.6	0	12.6	0	3.3	0.6	16	0	0	0.8	6.6	0	0.2
Amphipods	0	0	0	1	0	0.1	0	0.7	36	50	24	80	9.1	62.1	2.6	55	1.6

Table 22.- Plankton composition and abundance (Org/M³) at station 1, in October 1987. S=Surface B=Bottom. Day samples 21-X-87; night samples 22-23-X-87.

	10 Hrs			12 Hrs			21 Hrs			24 Hrs			03 Hrs			06 Hrs			Σ
	S	M	B	S	M	B	S	M	B	S	M	B	S	M	B	S	M	B	
<i>S. elegans</i>	0.07	23.3	3.6	0.3	4	1.5	1.3	4.6	1.2	4.7	1.6	1.5	2.3	4	1	12.4	11	2	8.1
<i>Acartia</i>	22	0	0.6	4.4	0.9	0	4.4	1.3	2.1	0.8	3	0	2	0.3	1.2	1.2	6.4	1.5	5
<i>Calanus</i>	13	13	1.8	19.8	8.3	3	0.7	4.6	0.6	0.8	2	1.3	1.1	5.3	1.3	3.5	12.7	1.4	9.6
<i>Appendicularia</i>	33	97.4	18.2	53	52	3.6	0.8	19	9	3.1	7	12	1.5	0.5	13.5	2.6	4.5	12	34.9
Fish eggs	9	6.5	0	6.2	1.3	0.6	0	0.6	0.3	0.4	0.6	0	0.4	0	1.2	0	0	0	2.7
<i>F. larvae</i>	0	9.7	0.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Cirripedia</i>	3.1	0	0	0	0.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3
<i>Polychaeta</i>	0	48.7	3	1.8	4.8	0.6	0	5.2	2.1	0.4	10	2.7	0.2	22	11.4	6.6	11.5	3	13.3
<i>Pseudocalanus</i>	0	26	5.4	6.2	4	6	2.6	13	19.7	2.7	11.7	13.6	1.5	9.7	15.7	7.5	13	11	17
<i>Cladocera</i>	0	9.7	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	1
<i>Echinoderma</i>	4.5	6.5	6.0	7.1	0	2.4	0	0	2.4	4.0	2	0	0	0	0	0	0	0	3.5
<i>Hydrozoa</i>	0	3.3	0	0	0.3	0	0	1.3	0.3	0	0	0	0	0	0	0	0.3	0	0.5
<i>Nauplii</i>	0	0	1.2	0	1.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3
<i>Temora</i>	0	0	0	0.8	0.9	0	0.4	0	0	0	0	0	0	0	0	0.4	0.3	0	0.2
<i>S. setosa</i>	0.04	0.06	0.03	0.07	0.03	0.04	0.1	0.1	0.3	0.07	0.04	0.03	0.1	0.1	0.06	0.1	0.07	0.03	0.1
<i>Oithona</i>	0	0	0	0	1.6	0	0	0	1.2	0	0	1.3	0	0	3.6	0	0	2.4	1.1
<i>Euphausiids</i>	0	0	0	0	0	0	0.8	8	0.3	0.8	1.2	0	1.3	1.4	0	0.8	0	0	0.6

Table 23. - Plankton composition and abundance (Org/M³) at station 2, in February-March 1986. S= Surface M= Midwater B= Bottom. Day samples 17-111-86 night samples 22-23-11-86.

	09 Hrs			12 Hrs			15 Hrs			18 Hrs			21 Hrs			24 Hrs			03 Hrs			06 Hrs			Σ
	S	M	B	S	M	B	S	M	B	S	M	B	S	M	B	S	M	B	S	M	B	S	M	B	
Calanus	34	241	72.7	28	162	127	3529	373	284	661	608	1525	184	142	102	92	95	42	33	114	110	5.1	125	107	32
Pseudocalanus	17.7	49	11.8	11	98	141	92	250	101	73	114	127	357	149	93	132	107	70.6	127	63.3	136	7.3	31.6	85	9.2
Scarcia	40	6.5	15	33	6.3	2.8	99	3.1	4.5	103	126	17	228	127	70.6	26	19	34	37	3.1	25.4	14.7	22	65	4.2
Memora	66.3	162	103	0	215	557	7.3	218	181	1176	76	45	1213	231	85	283	241	175	592	63.3	141	55	171	175	23
Appendicularia	8.8	6.4	30.3	22	114	48	0	60	68	206	50	37	257	57	34	84.5	47	19.7	275	53.8	51	294	88.6	56	7
Adocera	199	19.4	12	1360	31	22	294	123	28	816	28.5	17	283	111	90	125	54	42	290	28	39	1544	69.6	104	21
Centropages	4.4	0	12	7.3	9.5	17	25	35	25	81	57	5.6	92	76	25	18	0	2.8	51.4	9.5	2.8	18.4	6.3	20	2
Virripedia	4.4	3.2	9	0	28	11.3	0	9.5	0	0	0	0	3.6	1.5	0	11	0	0	0	3.1	0	0	0	0	0.3
Asteropoda	1	0	3	0	0	0	0	3.1	0	11	0	0.6	0	0	0	0	0	0	0	0	0	7.3	0	0	0.0
C. elegans	2.2	3.2	0.7	0.7	2.6	1.7	0	1.6	4	0	2	1.7	2	6.3	2.2	4.4	1.1	0.8	0	0.6	2.8	0	0.4	4.5	0.1
Hydrozoa	4.4	0	0	0	0	2.8	0	3.2	0	0	0	0	0	0	0	3.6	0	0	0	0	0	3.6	0	0	0.1
Decapods	0	3.2	0	7.3	0	0	0	0	0	0	0	0	3.6	0	0	0	0	0	0	0	0	0	0	0	0.1
Jithona	0	4	6	7.3	0	2.8	7.3	22	17	11	12.6	8.4	0	16	14	0	22	2.8	0	9.5	8.4	0	6.3	14	0.7
Polychaeta	0	0	3	0	0	0	0	0	0	0	0	0	0	3.1	0	0	0	0	0	0	5.6	0	0	0	0.0
Caprellii	0	0	9.1	0	3.1	4.2	0	3.1	0	0	0	0	0	0	0	0.9	0	0	3.6	12.6	0	0	9.5	0	0.1
Bryozoa	0	0	0	3.2	6.3	8.4	0	0	0	0	9.5	17	0	0	0	3.6	3.1	2.8	18.4	9.5	36.7	11	3.1	11.3	0.5
Chinodermata	0	0	0	0	3.1	0	0	3.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
Cyphosittids	0	0	3	0	3.1	0	0	9.5	11.3	11	31	8.5	0	0	0	11	0	2.8	11	0	5.6	3.6	0	5.6	0.4

Table 24.-Plankton composition and abundance (Org/M³) at station 2, in May-June 1986. S= Surface M= Midwater B= Bottom. Day samples 29-V-86 night samples 6-7-VI-86.

	09 Hrs			12 Hrs			15 Hrs			18 Hrs			21 Hrs			24 Hrs			03 Hrs			06 Hrs			Σ
	S	M	B	S	M	B	S	M	B	S	M	B	S	M	B	S	M	B	S	M	B	S	M	B	
Acartia	913	310	78.8	758	169	6	409	156	133	44	79.3	91	263	135	65	2325	247	42	2444	139	26	952	336	162	37
Calanus	51	210	185	46	99.7	46.5	55.5	149	285	88	59.5	195	39.4	51.2	121	317	190	101	174	127	54	143	160	177	13
Pseudocalanus	277	702	167	139	464	33.3	139	513	273	39.4	635	212	1219	494	212	960	291	82	270	136	33.3	794	769	547	33.8
S. elegans	11	114	14.5	15.8	52	7.2	31.7	130	82	13.1	15.8	51.5	8.7	32	17	95.2	56.7	10.6	31.7	34.8	7.2	3.2	16	28.2	3.1
Decapods	39.7	6.3	0	16	6.4	0	0	0	0	0	0	0	2.2	0	2.8	0	3.1	0	2	3.1	1.8	0	0	0	0.3
Appendicularia	8	9.5	3	8	3.2	0	0	6.5	6	61.4	15.8	15	17.5	3.2	0	4	6.3	1.8	0.5	0	0	15.8	0	3	0.6
Temora	619	117	18.2	51.6	13	0	305	84.4	103	48.2	87.3	64	35	3.2	0	15.8	19	3.6	79.3	9.4	0.6	31.7	22.4	0	7.4
Centropages	111	22	12	16	19.4	0	83.3	20	27	4.4	8	3	74.5	8.6	5.6	59.5	3.1	48.4	24	9.5	3	47.6	12.8	3	2.3
Oithona	0	12.6	6	0	19.4	0.7	0	20	0	8.8	12	3	8.7	6.4	8.4	23.8	12.6	4.0	8	3.1	0.6	47.6	16	21	0.9
Euphausiids	0	3.1	3	0	0	0	0	0	6	4.4	4	72.7	4.8	0	11.3	12	6.3	1.2	12	6.3	1.3	0	6.4	29.4	0.7
Metridia	0	3.1	0	0	0	0.7	0	1	0	1.1	0	0	0	0	0	2	0	0	0.5	0	0.6	0	0	0	0.02
Isias	0	3.1	0	0	3.2	0.7	0	0	0	1.1	0	0	0	0	0	1	0	0	1	0	0.6	0	0	0	0.02
Hydrozoa	0	0	3	0	0	0	0	0	0	4	0	4	0	4.4	0	0	9.5	0	2	0	0	0	0	0	0.09
Cladocera	0	0	3	0	0	0	0	0	0	4	0	4	3	1.1	0	0	0	0	2	0	0	0	0	6	0.07
Polychaeta	0	1.4	0	0	0	0	0	1	0	7.9	0	0	6.4	8.6	4	22	1.2	0.8	3.1	0	0	0	0	6	0.02

Table 25.- Plankton composition and abundance (Org/M³) at station 2, in July-August 1986. S= Surface M= Midwater B= Bottom. Day samples 30-VII-86 night samples 4-VIII-86.

	09 Hrs		12 Hrs		15 Hrs		18 Hrs		21 Hrs		24 Hrs		03 Hrs		06 Hrs		Σ									
	S	M	B	S	M	B	S	M	B	S	M	B	S	M	B	S		M	B							
Acartia	114	292	52	70	122	28	109	73	33	246	127	54	175	26	13.6	131	41.6	11	35	51	5	212	49	24	29.4	
Pseudocalanus	24	308	33	4	151	339	0	35.7	36	0	62	39.5	22.7	167	32	5.6	121	78	6	10.3	0	18	0.6	0.4	0.2	34.7
Temora	2.2	0	3	0	0	4	0	0	0	0	0	0	0	0	0	1.5	0	0	0.4	10.3	0	0.2	0	0	0	0.1
Polychaeta	2.2	3.2	0	0	0	0	0	0	0	0	0	0	1	0	0	0.8	0	0	0.2	0	0	2.8	0	0	0	0.1
Centropages	2.2	22.7	18	4.3	0	0	0	3.2	6	0	0	0	3	0	0	0.6	0	0	0.2	1	0	0.8	1.2	0.4	0.9	
Calanus	0.2	29	161	0	139	365	0	37.4	18	0.1	13	19.5	10.4	57	7.7	6.6	22.6	6.5	8	19	1.1	11.2	40	19		
Euphausiids	0	6.5	6	0	3	12	0	0	6	0	1.6	2.8	8.7	4.2	0	13	26	0	17.5	11	9	0	1.2	12	2	
S. elegans	0	0.3	54	0	39	72.3	0	58.2	50	0	7.8	54	247	28	6.7	4.5	21.5	15	2.2	24	7.27	24.6	15	12	12	
Appendicularia	0	26	0	0	0	0	0	0	0	0	0.6	0	0.3	0	0	0	0	1	0.4	0	0	0.6	0	0.4		
Cladocera	0	19.4	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	
S. setosa	0	0	0	0	9.1	0	0	0.2	0	0	0.2	0	0.1	0	0	0.4	0	0	0.2	0.4	0	0	0.3	0	0.1	
Oithona	0	0	0.3	0	0	0	0	0	0	0	0	0	13	0	0	0	6	1.4	0.4	9	0	0	0	3	0.3	
Metridia	0	0	0.3	0	0	0	0	0	0	0	0	0	4.4	0	0.2	0	0	0	0	0	0	0	0	0	0.07	

Table 26. - Plankton composition and abundance (Org/M³) at station 2, in September 1986. S= Surface M= Midwater B= Bottom. Day samples 16-IX-86 night samples 18-19-IX-86.

7.0.

Feeding experiments.

7.1.

Selection.

Experiments for the selection of prey and daily predation were carried out only for *Sagitta elegans* as this species is relatively abundant in Port Erin Bay throughout the year and catching the specimens was relatively easy with a minimum of handling. The results are presented in Tables 27 and 28.

Experiments 1 to 6 were made with a single species as prey and they showed that the predation rates were similarly high for *Centropages* and male *Acartia*, followed by *Pseudocalanus*, female *Acartia* and the lowest consumption by the predators was for *Temora*. The rest of the experiments were carried out with more than one species, and results were consistent regarding high predation for most of the items offered. They also showed that *Temora*, *Isias* and *Oikopleura* (only one experiment each with the two latter species) were less favoured as prey. *Acartia*, when offered as male or as copepodite stage IV and V, was readily eaten, however, when female *Acartia* was given instead, the predation rate decreased. *Centropages* was usually the species most predated, although sometimes more *Oithona* were taken. Note that all *Oithona* specimens given were adults, in an effort to make them size-comparable with the other species.

Temora was without doubt the least consumed prey, whether offered as a single species or in a mixture with other prey items.

7.2.

Daily ration.

The daily ration experiments were carried out with those copepod species to be well predated by the sagittas, i.e. *Pseudocalanus*, *Oithona* and *Centropages*.

Results indicate that predation increased with increases in the density of prey offered. However, when prey density reached 100 organisms per litre or more, the predation rate became erratic, showing no further regular increment when higher densities of food were provided.

Table 27.- Prey electivity experiments for *Sagitta elegans*
IV-V= Copepodite stages. Ad = Adults.
F= Females M= Males.

Experiment No.	Sagittas		Vol. (cc)	Food items provided			Items eaten \bar{x}
	No.	Size(mm)		Mean	(Stage)	Species	
1	16	7.8-10.2	9.2	2000	(IV-V)	Centrop. (50)	72
2	9	7.4-11.0	9.4	2000	(IV-V)	Centrop. (20)	60
3	16	7.2-9.6	9.4	2000	(IV_Ad.)	Pseudoc. (100)	31
4	15	9.6-13.4	11.0	2000	(IV-Ad.)	Temora (100)	12
5	6	10.0-11.8	10.9	2000	(Ad.)	Acartia (F) (50)	28.5
					(Ad.)	Acartia (M) (50)	71.5
6	11	8.4-10.0	9.4	2000	(Ad.)	Acartia (F) (100)	27.9
					(Ad.)	Acartia (M) (100)	72.1
7	10	6.0-8.0	6.9	2000	(IV-V)	Pseudoc. (50)	31
					(Ad)	Oithona (50)	69
8	15	9.6-13.4	11.0	2000	(Ad.)	Pseudoc. (25)	40.0
					(Ad.)	Centrop. (25)	60.0
9	10	9.0-10.8	10.0	2000	(IV-V).	Pseudoc. (50)	50
					(Ad.)	Oithona (50)	50
10	16	6.2-11.0	8.8	2000	(IV-Ad.)	Temora (100)	10.3
					(IV-Ad.)	Centrop. (100)	89.7
11	14	6.0-8.6	7.4	2000	(Ad.)	Oithona (25)	45.6
					(IV-V)	Centrop. (25)	30.0
					(IV-V)	Pseudoc. (25)	24.3
12	15	10.0-15.4	12.3	2000	(Ad.)	Temora (40)	2.7
					(Ad.)	Pseudoc. (40)	25.0
					(Ad.)	Centrop. (40)	33.3
13	7	9.0-11.0	10.4	2000	(IV-Ad.)	Temora (20)	8.0
					(Ad.)	Isias (20)	12.0
					(IV-Ad.)	Pseudoc. (20)	40.0
					(IV-Ad.)	Centrop. (20)	40.0
14	10	6.0-10.6	8.2	2000	(IV-V)	Pseudoc. (20)	16.0
					(Ad.)	Oithona (20)	24.0
					(IV-V)	Temora (20)	10.0
					(IV-V)	Acartia (20)	16.0
					(IV-V)	Centrop. (20)	34.0
15	17	7.8-10.4	9.1	2000	(IV-V)	Temora (25)	8.0
					(IV-V)	Pseudoc. (25)	21.1
					(Ad.)	Oithona (25)	24.4
					(IV-V)	Acartia (25)	30.8
						Appendicularia (25)	15.5
16	8	7.0-11.0	9.7	2000	(IV-V)	Temora (20)	0
					(IV-V)	Pseudoc. (20)	28.3
					(IV-V)	Acartia (20)	14.2
					(IV-V)	Centrop. (20)	23.0
					(Ad.)	Oithona (20)	34.4
17	7	7.0-11.2	9.9	2000	(IV-Ad.)	Temora (20)	0
					(IV-Ad.)	Pseudoc. (20)	21.5
					(IV-V)	Acartia (20)	36.2
					(V-Ad.)	Centrop. (20)	8.9
					(Ad.)	Oithona (20)	33.3

Experiment No.	No. of Sagittas	Vol. (cc)	Prey (Org./L)	Daily ration	Food Unavailable
1	9	2000	10	1.3	0
2	15	2000	25	2.3	0
3	14	2000	37.5	3.3	0
4	7	2000	40	3.5	2
5	16	2000	50	3.9	2
6	8	2000	50	4.1	4
7	10	2000	50	4.2	0
8	7	2000	50	4.8	3
9	15	2000	60	4.2	4
10	15	2000	62.5	5.3	5
11	15	2000	100	6	1
12	10	1000	100	5.5	2
13	10	1000	250	5.5	3
14	10	1000	250	6	6
15	10	1000	350	7.2	2
16	10	1000	350	9	4
17	10	1000	450	7.6	5

Table 28.- Daily average consumption of prey for *Sagitta elegans*

8.0.

Discussion.

8.1.

Zooplankton composition and abundance.

The zooplankton composition and abundance was, in general, mirrored in the gut content of the sagittas. Copepods were most abundant in the majority of the samples and were also usually the dominant food items found in the stomachs of the predators. These findings in general agree with the results of other workers (see review of Feigenbaum and Maris, 1984). However comments are necessary as to clarify some of the results obtained in this study.

Results in this work agree to a great extent with those from Williamson (1952, 1956a) regarding the composition and abundance of the zooplankters. *Temora* and *Acartia* dominated the copepod population and the zooplankton samples as a whole at certain times of the year. Lee (1971), however, found *Pseudocalanus* as consistently more abundant than the species mentioned above. The artifact seem to be related to the mesh size of the nets as Lee (1971) used a smaller mesh net (240 μ). This allowed the net to catch not only the adults and later copepodites but also the early stages. Williamson (pers. Comm.) commented that these different findings might also be explained by long term shifts in the plankton composition.

8.2.

Food items.

Pseudocalanus was consistently one of the most important prey

items for *S. elegans* and also contributed substantially to the diet of *S. setosa*. This was observed even at times when this copepod was not as abundant as other copepod species in the plankton samples (usually *Acartia* and *Temora*). Rakusa-Suszczewski (1969) working in the British Isles reported that "*Pseudocalanus elongatus* was the most frequent species in the gut content of *P. (Parasagitta) elegans*, with *Calanus finmarchicus* also appearing". Ohman (1986), reported that *Pseudocalanus* could comprise 61% in April and 67% in June as prey for *S. elegans*.

It also should be noted that in this work no distinction was made whether the prey eaten was a copepodite stage or an adult. This is of particular importance because the number of generations produced annually for *P. elongatus* is not known in the Irish sea, although it is well known that *Pseudocalanus* in other areas has between five and nine generations yearly. Marshall (1949), in Loch Striven, Scotland, found that during the season with high egg production (late February to about August) six generations can be produced. Digby (1950), in the Plymouth area, found this season of high productivity lasted from February to the end of October with a total of nine generations. Evans (1977) in Northumberland, England, reported seven generations a year produced between April and October. (For the number of generations produced annually in other areas see Corkett and McLaren, 1978). It is not possible to determine the number of generations produced in the Irish Sea from this work or the work of Lee (1971), but he suggested that the breeding pattern was similar to that recorded at Plymouth. This relatively high number of generations would support the findings of Lee (1971) for the abundance of this species and also would

explain the high predation rate by *Sagitta*. (For the generations produced yearly of other copepod species in the Irish sea, See Lee, 1971).

Øresland (1987), found *Calanus* and *Temora* as important food items of *S. elegans* in Gullmarsfjorden, Sweden. However, he pooled all the other copepods which did not belong to the species mentioned above. He also commented that these copepods were preyed upon only by chaetognaths near 20mm length (maximum length attained by the chaetognaths in that area was 37mm). Rakusa-Suszczewski (1969), working around the British Isles, also found these copepods to make important contributions to the diet of *S. elegans*. In the present work, however, *Calanus* was unimportant as prey species except at station 2 (west of the Isle of Man) and two factors are thought to have contributed to this result. 1) *Calanus* was more abundant at this station and 2) the sagittas attained larger sizes. (see Table 24 for composition and abundance of the zooplankton and also Figs. 18a and 19a for maximum size attained by the predators). The chaetognaths examined by Øresland (1987) and Rakusa-Suszczewski (1969) attained larger sizes than those from the Irish sea, as the size of mature animals is temperature dependant (see discussion for populations above), and this allowed them to prey on larger items. Sullivan (1980) pointed out that "there is no question that small prey provided the most important items in the nutrition of the 0-17mm chaetognaths, since these were the only items consumed".

More difficult to explain is the low percentages for *Temora* and *Acartia* as food content, particularly when these copepods were highly abundant in the field. However, in the case of *Temora* it was

observed that this copepod tended to aggregate, forming compact conglomerates (see below). Williamson (pers. comm.) observed this swarming behaviour in natural conditions. This behaviour may discourage relatively "small" predators like sagittas, whilst the opposite may be true for larger predators such as adult herrings. Rice (1963), working with specimens from near the Isle of Man, reported that *Temora* was certainly the most abundant prey species in the herrings he examined. Hardy (1924) reported similar conclusions and also showed that *Sagitta* made up a significant part of the diet of the North Sea herring. Reeve (1964b, 1980) and Feigenbaum and Reeve (1977) found in laboratory conditions that chaetognaths showed some evidence of feeding inhibition at food levels above critical densities. Pearre (1980a), who studied the relationship of several species of chaetognaths and the size of their prey, found that the best correlation is between body width of prey and chaetognath head width. *Pseudocalanus* and *Temora* attain more or less the same cephalotorax length, but while *Pseudocalanus* is nearly cylindrical, the body of *Temora* is rather wider and deeper. This means that for a given size of predator only a certain range in size of *Temora* as prey would be eaten, whilst in *Pseudocalanus* this range would be greater. (Measurements of width body in adult females for *Pseudocalanus* and *Temora* are approximately 0.35mm and 0.50mm respectively, pers. obs.).

Regarding *Acartia*, when carrying out the gut content analysis, it was observed (when identification to this extent was possible) a relatively higher feeding rate on the male copepods or copepodite stages and clearly lower feeding rate on the females. This result from the field lead to experiments with these three different

"kinds" of *Acartia* and similar results were found (see Table 27). This low predation on adult females of *Acartia* is probably related to the relatively larger size of the species, the spiny processes of the antennae or the possible differential swimming behaviour within the species regarding females and males or copepodites, or a combination of these factors. Feigenbaum and Reeve (1977) found that the swimming speed and movement pattern of the prey can (by means of random encounters) affect the probability of being eaten. Feigenbaum and Maris (1984) pointed out that "selection by species or type of prey may be more an artifact of the strength and clarity of the prey signal or the prey's ability to avoid capture than an indication of preference on the part of the predator". Sullivan (1980) working with *S. elegans* and *Eukrohnia hamata* found that for a similar size of both species the latter consumed more *Oncaea* than *S. elegans*, this could be an example of the statement given by Feigenbaum and Maris (1984) above.

During the feeding experiments it was observed, that when catching the copepod species as food for the chaetognaths, the following order of "easyness" for pipetting them was evident : *Centropages* > *Oithona* > *Pseudocalanus* > *Temora* > and *Calanus* and *Acartia* were the most difficult to catch. It can be argued that catching a copepod by means of a pipette is not the same situation as a *Sagitta* catching a prey, particularly because most sagittas are ambush hunters (Feigenbaum and Maris, 1984). However, it also suggest that different species have different thresholds in the water perturbation of the micro-environment, and therefore gives indication of the degree of facility to be caught by a predator. Gauld (1966) reported

that calanoid copepods are known to sense small changes in hydrostatic pressure and make large leaps or jerks to avoid contact or capture.

Oithona also contributed substantially to the diet of the chaetognaths with a higher predation rate by *S. setosa*. The high percentage of this copepod in the gut content of the predators does not agree with the usually low percentages of *Oithona* in the plankton samples. However, this copepod species has a rather small and slender body, which probably allowed it to escape through the net, as the mesh size used in this work was probably too wide to retain all the specimens. Lee (1971) reported that *Oithona similis* was the most abundant copepod in the Irish sea and that " Its numbers averaged double those of any other species". Thus, although the plankton samples analyzed did not denote the actual abundance in the field, this copepod species was probably very abundant, which was strongly suggested by the gut content analysis of the sagittas.

Appendicularians were in a similar situation to *Oithona*, probably being underestimated in their abundance in the field . They were also found to contribute substantially to the diet of *Sagitta*, particularly *S. setosa*.

It is well documented in the literature that larger chaetognaths feed upon larger prey (Reeve, 1966; Rakusa-Suszczewski, 1969 and revision of Feigenbaum and Maris, 1984). This was clearly shown in both species of *Sagitta* from this area. Thus, the larger species *S. elegans*, preyed upon larger food items such as *Pseudocalanus* and *Acartia*, and *S. setosa*, which is the smaller species, had as

main prey *Oithona* and appendicularia. Nevertheless, *S. elegans* frequently did take small prey, and in fact both species of *Sagitta* overlapped in their diet. *S. setosa* and *S. elegans* also included in their diet small organisms such as tintinnids and dinoflagellates, but this only was observed to occur when the size of the chaetognaths was as small as 2 to 5mm.

Cirriped larvae were also substantially preyed upon by *S. elegans*. These larvae reach their maximum abundance in March and April, and at this time of the year *S. setosa* was not found in the study area (see Tables 10,16 and 17). However, in April 1986, feeding upon this organism was very low, and the reason was that the population of *S. elegans* was made up mainly of small specimens (see Fig. 4c). However, in March next year when cirripeds were already abundant and large sagittas dominated the population, predation upon the barnacle larvae was heavy, and in fact they were the main prey eaten (Fig. 11a). Next month (April), even when cirripeds were still abundant in the plankton samples (table 17), as in the preceding year, spawning of *S. elegans* had occurred and the predation rate on those organisms decreased sharply. Many chaetognaths are mainly ambush predators (Feigenbaum and Maris, 1984), and they do not pursue escaped prey (Parry, 1944; Nagasawa and Marumo, 1972). Thus they depend on the prey's movement in order to catch them (see Feigenbaum and Maris, 1984). It is clear, however, that abundance of the prey (as in the case of the cirriped larvae) is not the only limitant for the predator to catch the prey. Instead this is a clear example of feeding according to size of both predator and prey,

rather than abundance of the prey.

Probably due to their economical importance in terms of fisheries, fish eggs and larvae have frequently been reported to be preyed upon by chaetognaths (Lebour, 1922, 1923; Bigelow, 1924; Khulman, 1977; Alvariño, 1985). Although Khulman (1977) found a certain degree of predation on fish larvae in laboratory conditions, it was much lower than for copepods. He also reported no predation on fish eggs. Tungate (1975), arrived at the conclusion that the mortality rate of plaice larvae due to predation by *Sagitta* was insignificant due to the relatively large size of this fish larvae. Reeve (1966) found that chaetognaths would not attack eggs of the brine shrimp *Artemia*.

In this work similar results were found and only one fish egg was recorded from a *sagitta* stomach during the whole study period. Eggs of crustaceans as food were more frequent, probably as the result of sagittas feeding on females bearing eggs in various stages of development. As mentioned before (see discussion on populations: vertical migration), crustacean eggs are rich in oil or oil derivatives which have a long digestion time. This could be the reason for finding them, even when the rest of the copepod could have even been defecated.

Fish larvae were relatively abundant within the spawning season of the herring, which lasts from September to usually November (Bowers, 1952, Bowers and Williamson, 1950). In this work larvae

of herring with yolk sacs (about 5mm to 9mm length) were found as late as January 1987, while in February 1986 only larvae larger than 16mm were found (unpublished records). Although they were at times relatively abundant they were usually predated in very low percentages. There are several possible explanations for those this results:

- 1) The relatively low abundance of fish larvae as compared to other plankters (e.g. copepods).
- 2) Immobility of the herring larvae during the time they have food reserves (yolk-sac larvae).
- 3) Herring larvae without yolk sacs have a greatly increased swimming capacity which probably allows them to escape from predators.
- 4) Herring larvae are visual feeders and the same visual mechanism that permits them to catch prey is likely to work for avoiding predation.

Point 1 is self-explanatory and only the other points will be discussed in greater detail. Regarding the second and third points, chaetognaths are known to feed on mobile prey (Feigenbaum and Reeve, 1977; Horridge and Boulton, 1967), and fish larvae at yolk sac stage are practically quiescent. Hunter(1981) reported that "only yolk-sac larvae are vulnerable to attacks by other plankters as *Euphausia* and *Labidocera* (copepod), because old larvae easily avoided sagittas".

Cushing and Harris (1973) concluded that due to the chaetognath's abundance they are responsible for only about 1% of the predation on fish larvae. Bowers and Williamson (1950) found that yolk-sac larvae would not feed when about less than about 6mm length, but feeding activity would gradually increase with decreasing yolk (Bowers, pers. comm). It is well documented in the literature that the feeding activity of fish larvae becomes well established only when the organs of the animals are functional, e.g. fins, gills, pigmented eyes (Ahlstrom and Ball, 1954). The yolk sac in herring disappears at about 10mm and at this size the larvae are already efficient swimmers, able to avoid plankton nets (see review by Clutter and Anraku, 1976).

On point 4, the literature is replete with reports establishing that herring larvae are visual feeders (Blaxter, 1965, 1966, 1968; Blaxter and Jones, 1967, Bainbridge and Forsyth, 1971; Noskov, et al, 1979), and vision which is utilized for prey detection is also applicable for avoiding predation, (cf. Blaxter, 1986).

Intrageneric predation, which for convenience in this work will be referred to as "cannibalism", was also observed. This behaviour in chaetognaths has long been known (Scott, 1893), and the literature is packed with many more recent reports (Mironov, 1960; Stone, 1969; Alvarino, 1975; Nagasawa and Marumo, 1976a; Pearre, 1981, 1982; Øresland, 1987). Feigenbaum and Maris (1984) mentioned that "true cannibalism may be an adaptive behaviour when food is limited, particularly if it is behaviourally related to reproduction

in mature individuals". Pearre (1982), found that predation on other chaetognaths increases with the abundance of the predator species and that large headed animals are the primary predators of smaller ones. In this work similar results were found and cannibalism was observed only when food was scarce (February, 1986; January, 1987). Øresland (1987), found a higher occurrence of cannibalism in *S. setosa* than in *S. elegans*. He assumed an intermediate digestion time of 250min at 14 °C in October when the feeding rate was 0.07 (Khulman, 1977, reported a a digestion time of between 200 and 300 min. at 15 °C), and calculated that if only half of the population were cannibals the *S. setosa* population would be reduced by 50% in 4 days. He commented on the possibility that cannibalism could be in part responsible for the sharp decrease of this species in autumn as recorded in his previous reports (Øresland, 1983, 1985). In the present work cannibalism was observed to have a higher occurrence in *S. elegans* than in *S. setosa*. The different results from those of Øresland above is probably related to density (org/m³) of both species in the area studied at the time when food availability was low; *S. setosa* in February 1986 and January, 1987, was low in abundance (see tables 9 and 15). Pearre (1982) predicted that " if chaetognath prey are selected randomly, constantly or with a linearly size-dependant bias the proportion of chaetognaths in the diet should increase as some exponential function of predator size and as the logarithm of the abundance", which means that a certain degree of crowding is needed for the cannibalism to occur.

8.3.

Digestion time.

It is generally agreed that digestion time is temperature dependant, i.e. the higher the temperature the shorter the digestion time. However, Canino (1981) (cited in Feigenbaum and Maris, 1984) compared digestion times for *S. tenuis* at 21 °C and 25 °C and did not find them significantly different. Also, it has to be taken into account that most of the experimental reports have been carried out with copepods as prey, possibly because copepods are the most common prey found when making gut content analysis from nature (Khulman, 1977; Nagasawa, 1984, 1985; Øresland, 1987; see also review by Feigenbaum and Maris, 1984). Furthermore, digestion times vary even within the same type of food organism, e.g. copepods. Nagasawa (1985) found that *Sagitta crassa* had different digestion times when fed with three species of copepods, namely *Oithona aruensis*, *Acartia clausi* and *Tigriopus japonicus*, digestion time increasing in that order. Nagasawa (1985) attributed these differences to the thickness of the exoskeleton of the prey, particularly for *T. japonicus*. At the present there are no digestion times available for small "soft" prey, such as rotifers, which can be a times important in the diet of the chaetognaths (Pearre, 1981), nor for other organisms such as tintinnids, dinoflagellates or appendicularians. Also in most of the literature (see review by Feigenbaum and Maris, 1984), digestion time estimates have been calculated assuming that predators have consumed only one prey at a time. This is an obvious error in assessing the feeding rates of the animals in natural conditions. Reeve (1980) and Canino (1981) pointed out that multiple prey will usually increase digestion time

and will make it even more variable. In this respect it has to be noted that multiple prey does not necessarily refer to the same type of prey, e.g. two *Pseudocalanus*. In nature it often means two distinct kinds of prey, e.g. one *Acartia* one *Oithona*, or any other possible combination. In this same context, Reeve *et al* (1975) demonstrated photographically that multiple prey are wrapped in a peritrophic membrane and are defecated as one single faecal pellet. Even if some of the prey are poorly digested, and it should be remembered that digestion time was defined as the time from the ingestion of the prey until its defecation (Feigenbaum and Maris, 1984). Digestion time also varies according to the degree of pigmentation of the prey, and Khulman (1977) reported longer digestion times for heavily pigmented ones. All these factors together undoubtedly affect the feeding rates of the chaetognaths, which is used in assessing the predation impact of these animals.

8.4.

Food Containing Ratio.

The food containing ratio in planktonic chaetognaths has been found to be higher at night and near the surface (Rakusa-Suszczewski, 1969; Nagasawa and Marumo, 1972; Pearre, 1973, 1974; Sullivan, 1980; Harris *et al*, 1982; Szyper, 1978; Øresland, 1987; this work; see also review by Feigenbaum and Maris, 1984). Pearre (1973) stated that "light inhibits feeding and that the state of satiation of the animals influences its depth control mechanism (see below). Pearre (1973) also reported a smaller difference of the FCR between day and night samples in December than in July. He explained this difference in his results as due to the greater light intensity in July (illumination in July was twice as high as in December), which

inhibited feeding, or possibly due to the longer days which provided more time for digesting the prey captured at night.

Although attempts have been made to correlate feeding in nature with prey availability, they have been unsuccessful (Feigenbaum and Maris, 1984), and two possible reasons have been offered for these findings:

- 1) Chaetognaths do not necessarily feed at the depth they were caught (Pearre, 1973).
- 2) The difficulty of estimating, with a net tow, the actual availability of prey on a scale relevant to the predator (Sullivan, 1980).

Pearre (1973) in his study of the vertical migration of *Sagitta elegans* proposed that this species migrated in darkness or low light intensities to upper waters for hunting, and that after satiation they swam downwards, resulting in the removal of the feeders from the surface waters. He also mentioned that "in seasons and latitudes such that the dark period was longer than the digestive period some of the early feeders might return to the surface to hunt a second time". Thus although prey availability is higher during summer the feeding period is shorter because days at that season are longer; in winter, however, the scarcity of available food is partly outweighed by predators having longer hunting time. Sullivan (1980) could not find a relationship between feeding rate and prey density for *S. elegans*. She, however, reported this relation to exist for *Eukronhia hamata* in the upper layers where a high abundance of prey was recorded. In this work the feeding rates did not show a regular pattern in relation to the abundance of plankton.

8.5.

Feeding experiments.

Results on prey selection agree to a great extent with the gut content analyses from the field, and all prey offered were eaten in high percentages. They also showed that *Temora* was the prey least consumed and, as mentioned in the discussion above this could be due to the swarming behaviour of the species. It also should be noted that, although most of the experiments were carried out with small prey, and consequently the body-width of the prey was narrower, the predator size was also small.

In the laboratory, *Centropages* together with *Oithona* were the prey most eaten. In the field *Oithona* was well represented in the gut content analyses, while *Centropages* was less consistent. The reason appears to be related to the more irregular abundance of this calanoid copepod. As for *Oithona*, the results from the laboratory suggest that the species was probably underestimated in the field samples, as digestion time (gut clearance) depends also to a certain extent on the nature of the prey. Nagasawa (1985) showed that digestion time for *Oithona* was shorter than for two other copepod species with thicker exoskeletons (*Acartia* and *Tigriopus*). Appendicularians were also eaten to a certain extent. Unfortunately not many experiments were made because the animals are damaged very easily with the handling of the samples. This handling could also have stressed them to the extent of affecting their motility while the experiments were in progress. Feigenbaum and Reeve

(1977) and Feigenbaum and Maris (1984) reported that chaetognaths fed only on motile prey. Khulman (1977), when examining the predation on fish eggs and larvae, arrived at the conclusion that fish fry contributed only very low percentages to the diet of *S. elegans* due to their immobility.

Concerning the daily feeding experiments, it is noticeable that high concentrations of prey are required to induce chaetognaths to feed. Feigenbaum and Maris (1984) reported that " the critical densities (for the sagittas to feed) lie far above the range of densities in nature ". Reeve (1980) found that chaetognaths appear to attain satiation and maximum ingestion rates even at modest prey densities in nature. Results from the present work show that predation increases with increasing prey concentration (see experiments 1 to 11). However, when prey concentration was sharply increased (experiments 12 to 17), the predation rate became irregular. Reeve (1964, 1980) reported similar results and mentioned that above a certain prey density (he called this "critical density") the predators attained satiation and showed evidence of feeding inhibition. He concluded that chaetognaths are not superfluous feeders, and he found the critical density to be about 60,000 organisms per m³ for *S. elegans*.

In this study the critical density was found to be at about 100 organism per liter (100,000 per m³). However, Reeve (1980) reported a higher digestion time for older predators and his specimens were up to 16mm length, while in this work specimens

rarely attained 15 mm. Reeve (1980) also noted a possible lower threshold and cited that "below 10,000 food items/m³ chaetognaths were unable to obtain 1% of their specific daily ration". No lower threshold was found in this study as the minimum concentration of prey offered was 10 organisms per liter (10,000 per m³).

It is to be noted that the numbers of prey eaten per day in laboratory conditions are higher than those reported from the gut content analyses from nature. At present the maximum reported feeding rate of *S. elegans* under experimental conditions is 4 prey per day (Reeve, 1980, see also review by Feigenbaum and Maris, 1984). However, unpublished reports from Sullivan (cited in Reeve, 1980), found that *S. elegans* would consume at least 8 prey per day in large enclosures (CEPEX) with a plankton concentration of about 10,000 org/m³.

9.0.

Conclusions.

9.1.

Plankton.

1.- Plankton density (org./m³) was found to be low from winter to early spring. Summer was the season with higher plankton production, gradually decreasing to late autumn.

2.- Copepods were usually the most abundant planktonic organisms throughout the year.

9.2.

Populations of the chaetognaths.

Sagitta elegans.

3.- *Sagitta elegans* overwintered mainly as stage II.

4.- The length of the species ranged from 1.2mm to 23mm length.

5.- The spawning of the species started in spring (April-May) and continued until about the end of the summer.

6.- The animals die after spawning and spawners (stage III) were usually not recorded by September.

7.- *S. elegans* was found to be more abundant in summer than at any other time of the year.

8.- The species shows a typical vertical migration: i.e. specimens are more or less evenly distributed in the water column at night but they are scarce near the surface by day. Newly hatched specimens showed minimal migratory behaviour.

9.- It is proposed that : *S. elegans* migrate downwards mainly to avoid predation by visual hunters. Undigested food increases visibility as does the development of gonads in older specimens. Large specimens are the strongest migrators. Small specimens possibly do not migrate because of inefficient swimming or due to the high cost of energy in terms of metabolism.

10.- *S. elegans* has a one year life-cycle in the Irish Sea.

Sagitta setosa.

11.- *Sagitta setosa* overwintered mainly as gonadic stage I, with an important percentage of stage II which varies from year to year.

12.- The size of the species ranged from 2.0 to 16.8 mm length.

13.- The spawning of the species probably starts in early summer and continues until the end of the autumn.

14.- The animals die after spawning and large animals in stage III are not caught by the end of the winter.

15.- Although the data from this work are not fully conclusive, it is proposed that this species also has a one year life-cycle. The findings of Pierce (1941) of two generations produced annually by the animals in the Irish Sea, are not accepted.

9.3.

Feeding.

16.- Copepods were the main prey eaten by the sagittas.

17.- Other plankters such as cirriped larvae, appendicularians and dinoflagellates or tintinnids also contributed substantially to the diet of both species.

18.- Predation of fish eggs and larvae was found to be negligible.

19.- *Sagitta elegans* fed on larger plankters than *Sagitta setosa*. However, feeding of both species overlapped to a great extent.

20.- *Pseudocalanus* was the main prey eaten by *S. elegans*, while for *S. setosa* the main items found were *Oithona* and appendicularians.

21.- Both species included in their diet small items such as tintinnids and dinoflagellates, but these prey were usually eaten only by the smaller predators.

22.- The presence of diatoms (*Coscinodiscus*) in the gut of *S. setosa* is thought to be accidental.

23.- Both species showed a higher predation rate at night, particularly near the surface. Samples from near bottom also evidenced feeding, but it was usually lower.

24.- Larger predators had a higher Food Containing Ratio than smaller predators.

25.- Most of the animals were usually found with a single prey specimen in the gut, however, multiple prey was also found. The highest number of prey in a single predator was 9 (*Stenosomella*) in *S. setosa*.

26.- The Feeding Rate for *S. elegans* was found to lie between 0.75 to 3.55 prey consumed per day. *S. setosa* had a Feeding Rate of 1.38 to 5.35 prey per day.

27.- Assuming a feeding rate average of 2 prey per day for *S. elegans* and a maximum abundance of 40 org./m³, the predation impact of the species is minimal. Although *S. setosa*, has higher feeding rates, its impact is even less, as the species was recorded in the area only for about 6 months of the year and its abundance was lower. In some years, however, *S. setosa* can reach much greater concentrations than those recorded in the present work.

28.- At station 2, the food Containing Ratio was usually higher from the samples collected at midwater.

29.- "Cannibalism " was found to occur at winter in both species. *S. elegans* was more cannibalistic than *S. setosa*.

9.4.

Feeding experiments .

30.- Feeding experiments showed a high predation for most of the items offered (*Centropages*, *Pseudocalanus*, *Oithona*, male or copepodite stages of *Acartia*). The lowest predation was found for *Temora*.

31.- It was found that *S. elegans* increased predation with increasing prey concentration. However, when food density reached 100 org./Litre (critical density), the predation rate became irregular.

32.- The prey consumption in laboratory conditions ranged from 1.3 to 9 prey per day.

10.0.

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