Sagitta friderici Ritter-Záhony (Chaetognatha) from South Atlantic waters: abundance, population structure, and life cycle

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The life cycle of *Sagitta friderici*, a neritic species from Pacific, Atlantic, and Mediterranean waters, has been poorly studied. Aiming at increasing our knowledge of this species in the Argentine Sea, the size structure, dry weight, distribution of maturity stages (ovarian, testicular, and seminal vesicles development), and life-cycle duration were studied from samples obtained at a permanent station (EPEA STATION, 38°28′S 57°41′W) from 9 March 2000 to 10 April 2001. The almost permanent presence of juveniles and the extended period during which mature adults (stage III) were detected suggest that reproduction occurs continuously with two main peaks, the main one in the summer (December–February) and a lesser one in the fall (April–May). Significant ($p < 0.05$) inverse correlations between water temperature and the mean size of stages 0 (juveniles), I, and II were found in this data set. Owing to the influence of temperature, those individuals that develop during the warm season and mature in the fall attain smaller sizes (7.6–12.4 mm) than those that develop during the coldest period of the year and mature in the spring (10.0–15.2 mm). The life-cycle duration is approximately 15 months, and the growth rate ca. 0.03 mm d^{-1}. The weight increase as a function of individual size was similar in the fall and in the spring (Fisher Test, $p > 0.05$).

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Introduction

Among marine zooplankters, Chaetognaths are active predators that have an extensive distribution in the oceans of the world. Out of more than 100 identified species (Bieri, 1991; Casanova, 1999) the duration and type of life cycle are known from less than 10%. In species such as *Sagitta elegans* and *Sagitta setosa*, different life-cycle durations have been reported (one or more generations per year) either within the same or in different geographic areas (for example, Bainbridge, 1963; Khan and Williamson, 1970;

Jakobsen, 1971; Weinstein, 1972; Sweatt, 1980; Øresland, 1983, 1985; Conway and Williams, 1986; Båmstedt, 1988; Terazaki, 1998).

Sagitta friderici is a characteristic species of the coastal waters of the Pacific and Atlantic Oceans as well as the Mediterranean Sea (Pierrot-Bults and Nair, 1991). In the eastern Atlantic, the species has been reported from approximately 50°N down to the Cape of Good Hope (Heydorn, 1959; Pierrot-Bults and Nair, 1991), whereas on the western side of the ocean its more scattered distribution extends from 30°N to 49°S (McLelland, 1980, 1984;

Mazzoni, 1990). In spite of its broad distribution, the life cycle of this species has only been studied from the coastal waters of Morocco, Senegal (Furnestin, 1957) and Alexandria (Halim and Guerguess, 1973). In the Southwestern Atlantic, studies on this species were focused on spatial distribution patterns (Mazzoni, 1990), feeding (Vega-Pérez and Liang, 1992), and seasonal variation of gonad development and size structure in a neritic population off Mar del Plata harbour (Ramírez and Viñas, 1982). This last study was carried out on samples restricted to the upper 6−7 m of the water column, thus losing all information about the fraction of the population located at deeper depths. Since *S. friderici* is frequent on the Argentine continental shelf, the present study was aimed at analysing the variations in the distribution of maturity stages, sizes, and population biomass throughout 14 months in the coastal waters of the Province of Buenos Aires, Argentina.

Materials and methods

Eighteen plankton samples were collected from a permanent station located in coastal waters of the Province of Buenos Aires (EPEA STATION, 38°28′S 57°41′W, 48 m deep), once a month (or twice on some occasions) from 9 March 2000 through 10 April 2001. A mini bongo net, 20 cm diameter mouth part with 200-μm mesh, was vertically hauled from the bottom to the surface during daytime. The samples were fixed with 2% buffered formaldehyde. A mechanical flowmeter (Hydrobios) was used for measuring the filtered volume. Conductivity, temperature, and depth were measured *in situ* with a CTD system (Seabird SBE-19). CTD temperature and salinity data were calibrated using a thermometer and a salinometer on discrete water samples.

The specimens present in each sample were identified, counted, and assigned to the maturity stages proposed here (Figure 1a and b): 0 (juvenile) − anterior and posterior fins developed, no ovaries or testes; I − ovaries undergoing development containing small oocytes, testes-like fine tubes. Some loose spermatocytes in the basal part of the tail. Seminal vesicles absent; II − larger ovaries, oocytes of various sizes. Spermatocytes occupying the coelom of the tail. Seminal vesicles undergoing development, but not yet having begun to fill; III − ovaries fully developed with scarce or no small oocytes. Tail segment filled, partially filled, or empty of spermatids. Seminal vesicles with different degrees of filling or broken by the expulsion of the sperm.

The following measurements were taken on each specimen (Figure 1a):

Size (TL): total length from the extreme of the head to the end of the tail (except the caudal fin).
Trunk length (TrL): from the base of the head to the tail septum.
Length of tail segment (CS): from the tail septum to the extreme of the tail (except the caudal fin).

Ovary length (OL): from its anterior extreme to the gonopore.
Oocyte diameter (oD): mean diameter of two oocytes.
Number of oocytes: per mature ovary (only stage III specimens).

For all maturity stages, the correlations between mean size and water temperature were explored for the whole data set by means of the Pearson correlation coefficient at 5% significance level (Sokal and Rolf, 1995).

The growth of TrL, CS, and OL as a function of TL was analysed through a test of the slope. In each case we tested the null hypothesis ($b = 1$ or isometric growth) against the alternative one ($b \neq 1$ or allometric growth). The slopes were estimated by Ricker's method (Sokal and Rolf, 1995).

To determine the relationship between TL and dry weight (DW) we selected well-preserved specimens without parasites or food remnants. The size interval considered was 0.4 mm. The 170 specimens of *S. friderici* collected in April were measured (3.2−8.8 mm) and grouped into 14 size intervals, and the 194 specimens collected in August (3.2−15.2 mm) formed 28 size intervals. The number of specimens per size interval varied between 2 and 30, depending on the size considered. Each specimen was washed in distilled water, placed in aluminium-foil containers (previously tared), and oven-dried at 60°C (Lovegrove, 1966) until constant weight. Dry specimens were kept in a desiccator until they cooled down, and then weighed on a 1-μg precision microanalytic balance (Sartorius MP1000) using a minimum amount of material of 40 μg.

For the two groups of specimens collected in April and in August, simple linear regression models were applied to the mean size (TL) of each size interval, as the fixed variable, and to the corresponding dry weight (DW), as the aleatory variable. Both variables were log-transformed. The slopes obtained were then compared by means of Fisher's test of parallelism, assumption required to perform covariance analysis (ANCOVA) (Sokal and Rolf, 1995). The biomass (mg DW m^{-3}) of *S. friderici* during the study period was estimated from the TL−DW relationship obtained.

Results

During the study period, temperatures at 10 m ranged from 10.1°C to 21.1°C, whereas salinities varied between 33.1 and 34.2. *S. friderici* was the only Chaetognath species present in the samples during the whole study period. The total density of *S. friderici* showed two peaks, one in the fall−winter period and a greater one in the summer (Figure 2).

The distribution of maturity stages during the whole study period is summarized in Figure 3. Juveniles (stage 0) were present year round, but they dominate during the summer months. Intermediate stages (I and II, with reproductive organs in different degrees of development) were also found during the whole year. Adults (stage III) were present from April through November, reached their highest
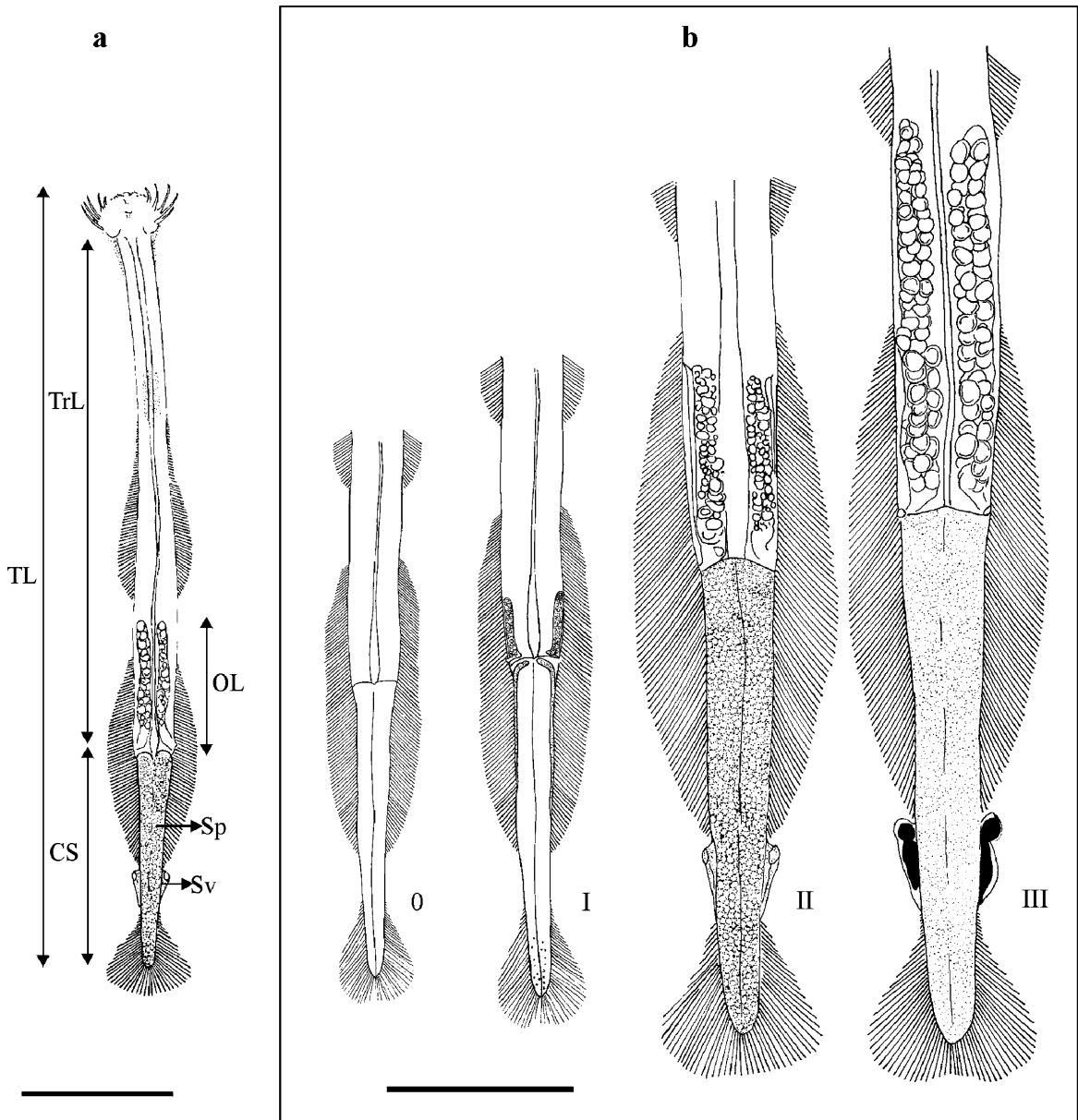
Figure 1. *Sagitta friderici*. (a) Ventral aspect showing measurements. (b) Rear part of specimens displaying differences among maturity stages: 0 (juvenile), I, II, III. LT (total length or size), BL (body length), CS (length of the tail segment), OL (ovary length), Sp (spermatocytes), Sv (seminal vesicles). Scale = 1 mm.

representation in April and August, experienced a marked decrease in November, and finally disappeared during the summer. The largest specimens, collected in October, had empty seminal vesicles and ovaries in different degrees of contraction. Larval stages (anterior fin poorly developed, ventral ganglion about 30% of the total length) (Figure 4) were present on most sampling occasions, but they were best represented during the summer (December−February).

As a whole, the size of the specimens varied between 2.4 and 15.1 mm. The size ranges corresponding to each matu-

rity stage are summarized in Table 1. The maximum sizes attained by the more mature specimens (stage III) varied from 14.1 to 15.1 mm. The relationships TL−TrL, TL−CS, TL−OL in all four maturity stages suggest that the growth of the different body regions can be either allometric or iso-metric, except for TL−OL, which is always allometric (Table 1).

In the more mature specimens, the length of the ovary represented 18.4−19.5% of the size of the animal, and it contained from 36 to 54 oocytes measuring a maximum of
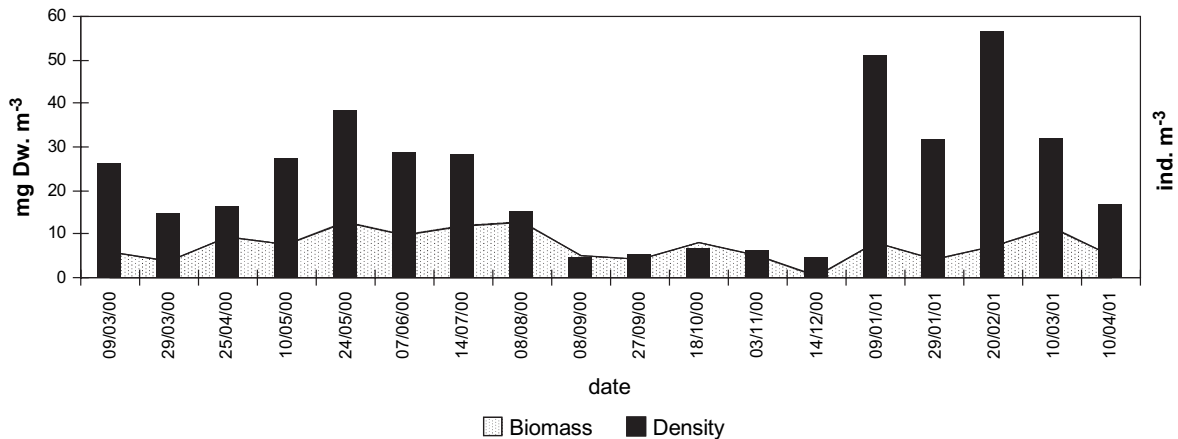
Figure 2. Distribution of densities (ind. m^{-3}) and biomasses (mg DW m^{-3}) of *Sagitta friderici* from March 2000 through April 2001.

0.14–0.18 mm in diameter. In 1.8% of the specimens with fully developed ovaries the lengths of the right and left ovaries differed within the same specimen (2.6–15.9%). The relationship between CS and TL (CS 100 LT^{-1}) varied between 32.4% and 24.9% in specimens measuring 2.9–15.1 mm.

All stages showed an inverse correlation between mean size and temperature, which was significant in all cases ($p < 0.05$) except stage III. For the juvenile stage this correlation had an $r^2 = 0.68748$ ($p < 0.001$, n = 18); for stage I it was $r^2 = 0.48434$ ($p = 0.0019$, n = 17); and for stage II it was $r^2 = 0.79224$ ($p < 0.001$, n = 17).

In April, the relationship between size and dry weight was log DW = 3.11 log TL − 1.02 ($R^2 = 0.96167$, n = 14), whereas in August it was log DW = 2.88 log TL − 0.83 ($R^2 = 0.97727$, n = 27) ($p < 0.0001$). Since the lines obtained for both months had similar slopes (F = 1.316, p = 0.2587), a common slope (b = 2.93) can be used. This indicates that in both months DW increases as a function of TL in a similar way. Covariance analysis failed to show significant differences between months (F = 0.083, p = 0.7749), thus implying that for a given TL the same DW will be obtained.

The biomass values obtained from the former formula followed the pattern of abundance (Figure 2). The highest biomass values, however, were recorded in the fall–winter period, with lesser peaks from January to March (summer months).

Discussion

Since the samples analysed were obtained by hauls over the whole water column, we consider that a representative number of specimens of the different maturity stages found in this population must have been captured. However, it is possible that some of the smallest individuals (<3.8 mm TL and 0.2 mm wide) may have escaped the 200-μm mesh net.

The presence of specimens showing empty seminal vesicles and ovaries in different degrees of contraction would suggest that oocytes are not released at the same time, but that oviposition probably takes place during a longer period, as reported for *S. hispida* (Reeve, 1970), *S. crassa* (Murakami, 1959; Nagasawa, 1984), and *S. setosa* (Dallot, 1968). An extended oviposition period associated with the presence of mature specimens during several months of the year would explain the almost continuous presence and importance of larvae (Figure 4).

The year round presence of juveniles and the extended period with mature adults suggest that reproduction occurs continuously, with two reproductive peaks; a lesser one during the fall (April–May) and a greater one during the summer months. This is in agreement with the observation by Ramírez and Viñas (1982) for the population off Mar del Plata. The summer peak probably results from the reproduction of the adults of October, which had larger sizes, developed ovaries and empty seminal vesicles. The disappearance of mature stages during the summer months would indicate that they die once they reproduce. Similar conclusions were posed by Furnestin (1957).

This supports the idea of the existence of continuous reproduction in *S. friderici* in waters of the Southwestern Atlantic. Furnestin (1957) concludes that in the Southeastern Atlantic this species reproduces constantly, with reproductive peaks during the summer. Alvariño (1990) reports the same reproductive pattern for populations of the Iberian Atlantic. In coastal waters off Alexandria, Halim and Guerguess (1973) found reproductive peaks in the spring and in the fall.

Since juveniles are incorporated to the population year round, the range of size groups in the population is so great that it is impossible to identify or follow the progress of any particular brood. Nevertheless, growth rate can be estimated from the maximum size attained in each station and sampling date. In Figure 3 we visualize that starting from
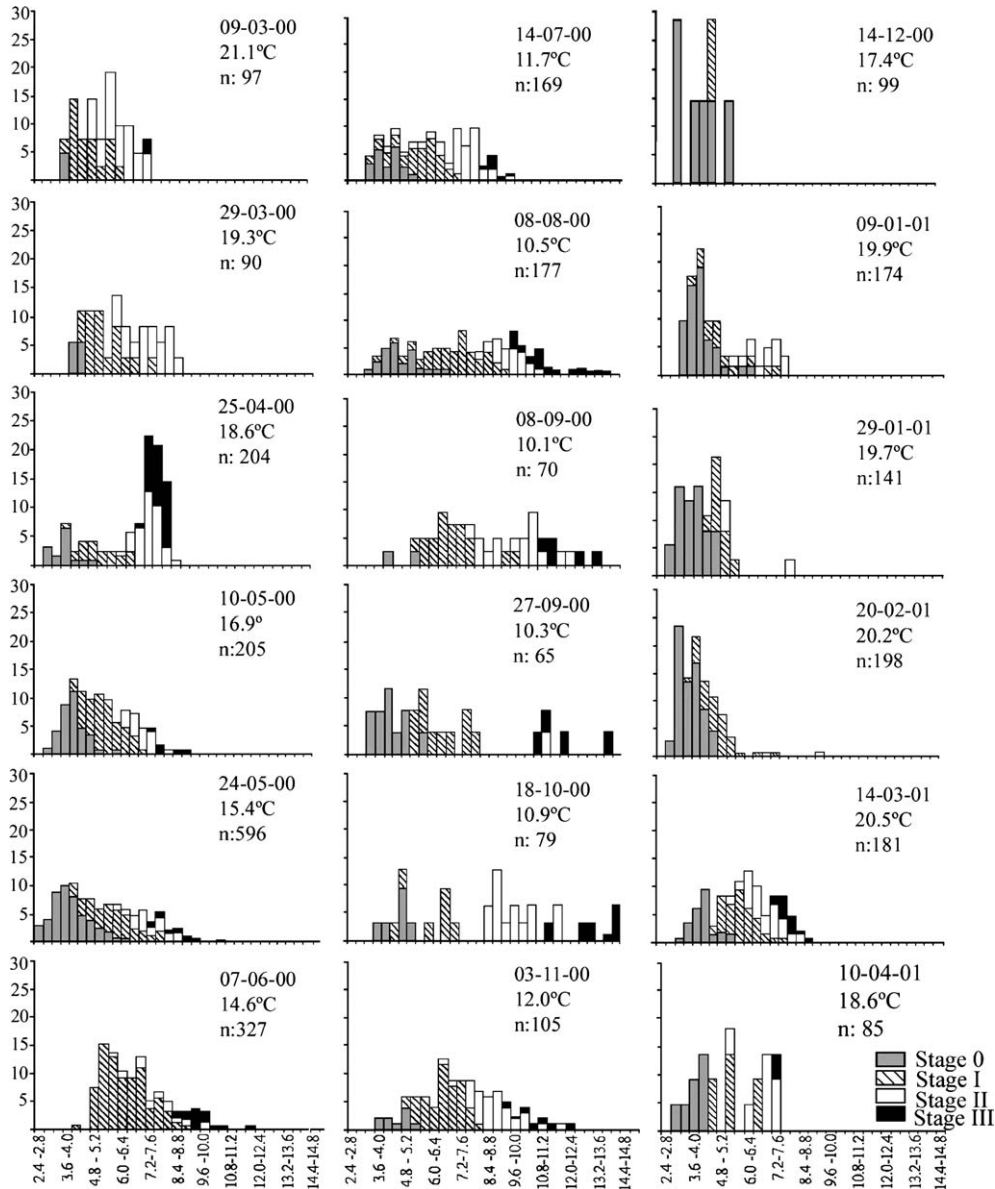
Figure 3. Distribution of the different maturity stages of *Sagitta friderici* from March 2000 through April 2001. Each graph shows date, water temperature (T°C) at 10 m of depth and number of sampled specimens (n).

a maximum size of 7.6 mm in April 2000, length gradually increases to finally reach 15.1 mm in October 2000. This 7.5-mm increase took 249 d; therefore, the average daily increase can be estimated in 0.03 mm d^{-1}. Considering that the smallest juveniles ranged from 2.8 to 3.2 mm, it would take them a little more than 13 months to reach 15.1 mm. Moreover, if we add the time required to attain 2.8 mm starting from the moment of eclosion, this period will extend to approximately 15 months. Thus the life cycle of *S. friderici* in Argentine waters is longer than in the population studied by Furnestin (1957). This difference

may be attributed to the influence of water temperature, which in our study varied between 10.1°C and 21.1°C, whereas in the Moroccan Atlantic it ranged from 16°C to 22.5°C. Reeve and Walter (1972) also report that the time to reach maturation for a population of *S. hispida* varies between 18 and 50 d when raised at 17−31°C.

The maximum sizes attained by *S. friderici* varied from 14.2 to 15.1 mm (stage III) and correspond to specimens having at least one seminal vesicle empty. The differences in the size attained by the same maturity stage at different times of the year were correlated with temperature. In
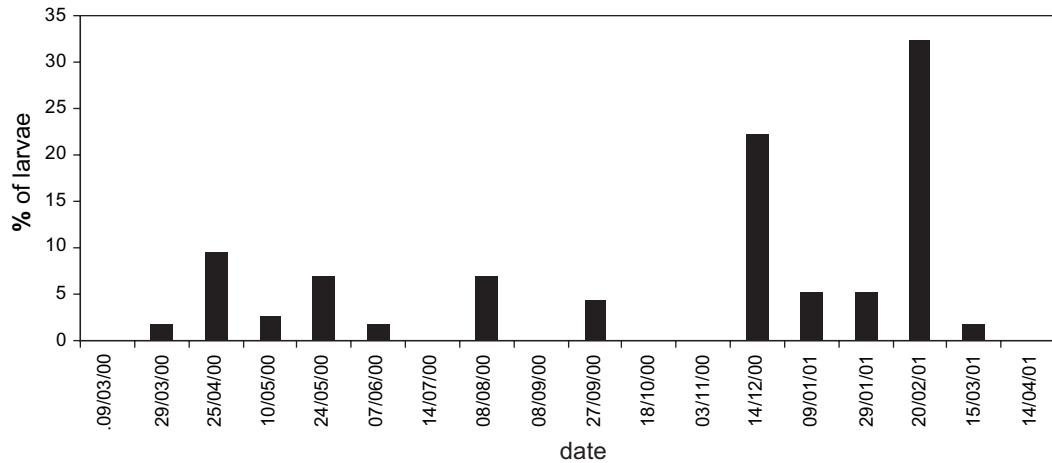
Figure 4. Larval distribution from March 2000 through April 2001.

general, the smallest sizes of stage III (7.7 mm) corresponded to specimens whose development occurred at higher temperatures (21.1−18.6°C). On the other hand, the largest sizes (15.1 mm) corresponded to specimens that developed at lower temperatures (16.7−10.5°C). Similar results on the influence of temperature were reported by Reeve and Walter (1972) for *S. hispida* raised under laboratory conditions, where the largest sizes corresponded to specimens raised at lower temperatures.

Temperature may also explain the differences in maximum size found by other authors for different populations of *S. friderici*. The specimens studied by Mazzoni (1990) measure up to 18−19 mm, the Moroccan ones reach 13 mm (Furnestin, 1957), and the Mediterranean material is smaller than 10.5 mm (Halim and Guerguess, 1973). The latter authors also state that the high constant temperatures of the Mediterranean Sea prevent these specimens from attaining larger sizes. The Moroccan specimens were collected in an area where the mean annual temperature is 18.02°C, whereas those studied by Mazzoni (1990) came from the colder waters (below 10.5°C) of the Southern Atlantic (45°S). Furnestin (1957) also found differences between the maximum sizes attained by populations of

S. friderici from the Alboran Sea (9 mm) and the coastal waters of Israel (10 mm).

The relationships between TL and CS, TrL and OL reveal the existence of allometric growth in younger stages, whereas for stage III it becomes isometric, except for OL. Allometric growth is mainly evidenced by CS, which in young specimens represents 32.4% of TL and 24.9% in adults.

The ovary length of the more mature specimens was greater in our specimens (9−13.3%) than in those examined by Furnestin (1957). This difference may be related to the greater growth attained in colder waters. The higher number of oocytes (36−54) and their size (0.14−0.18 mm) also correspond to larger ovaries. On the other hand, a reduction in the number of oocytes determined by the presence of specimens with shorter ovaries was negligible in our case because of the low proportion of such specimens in the population. Out of the 50 analysed specimens in this condition (right and left ovaries of different length), parasites were found only in two cases in the side corresponding to the smallest ovary. Neither parasites nor signs of damage were detected in the remaining specimens; therefore, in our case, ovary length differences do not seem to be related to parasitism (Pearre, 1976) but to factors that were not assessed.

Biomass was estimated from the TL−DW relationship. In general, published data on this relationship are scarce for Chaetognaths, but those contemplating differences between fixed and fresh animals of the same species are even rarer. Stuart and Verheye (1991) report a TL−DW relationship of $DW = 0.00021 \, LT^{2.870}$ for fresh specimens of *S. friderici*. In the present study the relationship determined on fixed *S. friderici* was $DW = 0.121695 \, LT^{2.930}$. Since the shrinkage process is unknown in this species, the curve determined by Stuart and Verheye (1991) cannot be compared with ours. Provided comparable temperature ranges (10.1−21.1°C), the TL−DW relationship for fixed material

Table 1. Maturity stages of *Sagitta friderici*. Size intervals and relationships among the measurements of the different body regions. Test of hypothesis for the slope (Ricker's method) (*p < 0.05): b (slope), TL (size or total length), TrL (trunk length), CS (length of the tail segment).

	Stage 0	Stage I	Stage II	Stage III
Size interval (mm)	2.4−7.6	3.2−10	4.2−12.3	7.6−15.1
TL−TrL (b_1)	1.13*	1.07*	1.07*	0.98
TL−CS (b_2)	0.83*	1.04	1.05	1.07
TL−OL (b_3)	−	1.75*	2.57*	1.69*

would allow estimation of the total biomass either of broad ecological studies (difficult to replicate) or of specimens collected in campaigns carried out in poorly studied areas.

The biomass values calculated using the above-mentioned equation (Figure 2) show discrepancies with respect to density. The high density values and low biomasses recorded from January through April may be ascribed to the dominance of stages 0 and I, whereas the high biomass and lower density found in August correspond to the presence of stages II and III of larger size and more developed ovaries.

Acknowledgements

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