9002

22. CHAETOGNATHA

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I. INTRODUCTION

The Chaetognatha are marine, highly predaceous carnivorous animals of mostly planktonic habits; their life span and anatomy appear to be devoted to the objective of providing another generation to be born as the parents of most species die soon after reproduction. The body of chaetognaths includes the head, trunk (intestine and ovaries), and tail (testes). They are protandrically hermaphrodite, male gonads maturing earlier than female gonads. Copulation occurs, and spermatozoa are reciprocally transferred to the seminal receptacle of the partner. In this process, they act as functional males, and during the extrusion of the ova into the uterus and vaginal cavity, they act as functional females. Thus in chaetognaths, the sexes are separated in time and location within the body: the trunk segment is female, the tail segment male.

II. HERMAPHRODITISM

Hermaphroditism is a mechanism to ensure fertilization, and to produce new generations in low-density populations, where meeting of partners is infrequent. This is, however, not the case with most species of chaetognaths: in population abundance in the plankton, they are only second to copepods. Hermaphroditism may nevertheless be advantageous to the scanty deep-water populations of chaetognaths. Phylogenetic studies indicate that the oldest genera and species (Alvariño, 1965a, 1968) of chaetognaths include populations of low density. This could be interpreted as a sign that original populations of chaetognaths were small, and that hermaphroditism is an atavic characteristic.

In animals that devote their life exclusively to reproduction, the entire biomass is used to meet this aim. The superb constitution of the ova will ensure the success of reproduction. Hermaphroditic chaetognaths are protandric because the formation and production of male gametes appear to consume far less energy than ovarian maturation. Once male gonads have matured, the animal restores the system and expends all energies for the maturation of the ova, and most die of exhaustion after egg-laying.

III. SEXUAL MATURATION

Segregation of male and female germinal lines in chaetognaths begins in the egg itself (see Alvariño, Volume I, pp. 592–593). Although several authors use the term 'egg' to indicate the female reproductive cell, I like to refer to it as 'ovum'; the term 'egg' will be reserved for fecundated ovum or zygote (Alvariño, 1965a).

A. Classification of Maturity Stages

Several schemes for the classification of developmental stages of chaetognaths have been published (e.g. Kramp, 1917, 1939; Russell, 1932a, b; Thomson, 1947; David, 1955). As sexual maturity is a continuous process, its division into stages is to some extent subjective. Colman (1959) divided development into six stages:

Stage 0: Testes and ovaries are not visible under × 1,000 magnification.
Stage I: Testes are visible, but no spermatogonia or spermatozoa are present in the tail coelom. Ovaries are visible, but very small.
Stage II: Testes fill the tail cavity; spermatogonia are present. Ovaries are developing, ova small.
Stage III: Testes are empty; seminal vesicles are full with sperm. Ovaries and ova are well developed.
Stage IV: Testes are empty; seminal vesicles are broken. Ova are fully mature; seminal receptacle is filled with sperm.
Stage V: Spent. Ovaries are reduced to crumbled remnants.

The genus *Eukrohnia* is the only chaetognath in which specimens at Stage V could be found. It is implied that most, if not all, specimens die after egg-laying, as mentioned above (Section II). Species, such as *Sagitta enflata* are considered to go through more than one reproductive cycle in the life span of the individual. The animal grows at each maturity cycle, and no spent or crumbled ovaries are observed, as transition to the next maturity cycle is progressive. The relative duration of the several stages of maturity, speed of transition from one stage to the next, and the relative speed of development of the testes and ovaries vary not only between species but also, to some extent, between individuals of the same species (Colman, 1959). Intermediate stages, such as I–II and II–III, are often observed.

The works of Kramp (1917) and Russell (1932a) have laid the basis for a precise classification of the maturity stages in chaetognaths. They proposed essentially similar divisions using a combination of maturity stages of sperm and ova. The divisions established were adequate for the species studied, and it was found that not all species of chaetognaths developed in the same sequence, and that the degree of protandry was different in different species. A classification base valid for all species, is difficult. The ovaries begin to develop at the same time as the testes, but mature only later. In general, spermatozoa are entirely evacuated from the tail segment before the ova reach maturity. The spermatozoa enter the seminal vesicles, and, by copulation, pass into the seminal receptacle of the partner.

The facile observation of female gonads as indicative of the maturity stage of individuals has led many authors to base maturity classification only on the development of ovaries. An account of the development of the gametes of Chaetognatha, based on a cytological study of *Sagitta enflata,* has been provided by Ghirardelli (1961a, b).

Numerous classifications of maturity stages are found in the literature, and are compiled in Alvariño (1965a). Needless to say, classification of maturity stages should include both female and male gonads and be described for each species. I have been consistently adopting a four-stage scheme of maturity, beginning from Stage I which includes the juvenile animals after the larval stage to the fully mature state (Stage IV). In general, spermatocytes first appear in Stage II, though sometimes a few may occur in Stage I itself. Spermatocytes and spermatozoa fill the testes in tail cavity during the late Stage II and in Stage III. In some species the spermatozoa are extruded before the end of Stage III, but in others they are still present in Stage IV. Stage V of Kramp (1939) and Colman (1959), with spent ovaries, has only (as explained above) been occasionally found in specimens of the genus *Eukrohnia.* Stage O of Colman (1959), juvenile, is included in Stage I.

Alvariño (1963, 1965a, 1967, 1969) has described the maturity cycles in *Sagitta enflata.* Several size-structure populations of this species consistently coexist in time and space in various regions surveyed by the author. It appears that an early life cycle of maturity includes animals mature at 8 to 9 mm, a second at 14 to 16 mm, and a third at 25 to 27 mm. A similar situation of the mixed-structure populations was observed at the southern part of Keneohe Bay, Oahu, Hawaii by Piyakarnchana (1965). The size (i.e. the length) of the animals given here for each species at each stage of maturity is the average in the main distributional region of the species. Obviously differences are found in body size for each stage of maturity: small specimens may appear at Stage IV of maturity, while some larger ones may still be at Stage I, II, or III of maturity. This is evident in specimens collected from the same plankton haul, indicating a mixture of specimens from different source locations in the distributional range of the species. Differences in size of specimens at various stages of maturity may be related to temperature (maturity being reached at smaller sizes in warm waters) or to variations in the quality and quantity of the food supply.

Young specimens of *Krohnitta subtilis* are not usually found in most 1-m net collections probably because the mesh size of nets commonly used is, 0.5 to 0.6 mm, and 0.31 at the cod-end. It is suspected that *K. subtilis* may reach a size close to that of fully mature individuals at an early stage of maturity. In this way, development of this species differs from that of other species, where both maturity and growth processes run parallel, even in species undergoing several maturity cycles. In general, specimens of *K. subtilis*, less than 10 mm long, are juveniles (neither testes nor ovaries are visible). During the last stage of maturity, the seminal vesicles are open, but not broken, and are probably filled more than once during the life cycle (Alvariño, 1967).

Tables 1–28 show the stages of maturity of several species of Chaetognatha (Alvariño, 1962, 1965a, 1967). The four stages of maturity of all species, except *Sagitta scrippsae,* described in Tables 1–28 are given in Figs. 2–4, and 6–30. Also included are illustrations of the four stages of maturity of *Eukrohnia bathyantarctica* (Fig. 1), *Krohnitta mutabbii* (Fig. 5), *Sagitta bierii* (Fig. 31), *S. elegans* (Fig. 32), *S. euneritica* (Fig. 33), *S. friderici* (Fig. 34), *S. gazellae* (Fig. 35), *S. helenae* (Fig. 36), *S. hispida* (Fig. 37), *S. marri* (Fig. 38), *S. maxima* (Fig. 39), *S. planctonis* (Fig. 40), *S. pseudoserratodentata* (Fig. 41), *S. serratodentata* (Fig. 42), *S. setosa* (Fig. 43), *S. tasmanica* (Fig. 44), and *S. tenuis* (Fig. 45).

Table 1
Maturity stages of *Eukrohnia bathypelagica* (Fig. 2)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as fine tubes; seminal vesicles beginning to appear; vas deferens well developed	Ovaries small curled tubes	13 Fig. 2A
II	Tail filled with spermatids and sperm; seminal vesicles getting filled	Ovaries curled at top, reaching up to level of top of rayed zone in the paired fins	18 Fig. 2B
III	Tail full or partially empty; seminal vesicles full or broken	Ovaries curled at top, reaching up to 2/3 from ventral ganglion, in the distance to caudal septum	20 Fig. 2C
IV	Tail empty; seminal vesicles broken	Ovaries filling body cavity, reaching up to 1/3 from ventral ganglion, in the distance from there to caudal septum	23 Fig. 2D

Table 2
Maturity stages of *Eukrohnia fowleri* (Fig. 3)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as small rods with the upper part a little enlarged, extending along half the way in region of tail segment occupied by paired fins	Ovaries short and wide	12–21 Fig. 3A
II	Tail segment filled with spermatids; seminal vesicles beginning to appear	Ovaries reaching up to level of half of extent of rayed zone in the paired fins	25–32 Fig. 3B
III	Tail segment filled with spermatids and spermatozoids; seminal vesicles full	Ovaries with the ova large; seminal receptacle well apparent	34 Fig. 3C
IV	Tail segment partially discharged; seminal vesicles bursting	Ovaries with ova fully developed; seminal receptacle filled with sperm	> 35 Fig. 3D

Table 3
Maturity stages of *Eukrohnia hamata* (Fig. 4)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as fine tubes; seminal vesicles not present	Ovaries as fine tubes	Up to 18 Fig. 4A
II	Tail segment filled with sperm; seminal vesicles incipient to full	Ovaries longer than in previous stage	23 Fig. 4B
III	Tail segment partially discharged; seminal vesicles broken	Ovaries increasing in length; ova developing	25 Fig. 4C
IV	Tail segment discharged; region of seminal vesicles covered by a thickening of epidermis	Ovaries reaching up to 2/3 of distance from ventral ganglion; ova fully developed	40 Fig. 4D

Table 4
Maturity stages of *Krohnitta pacifica* (Fig. 6)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes are fine tubes; caudal segment empty; no seminal vesicles visible	Ovaries reaching up to midlength of the extent of fins on trunk	4 Fig. 6A
II	Testes filling tail cavity; spermatids well visible; seminal vesicles beginning to appear	Ovaries reaching up to a level close to anterior end of the paired fins	5 Fig. 6B
III	Spermatozoids are well visible, filling tail cavity; seminal vesicles getting filled with sperm	Ovaries reaching up to midlength from ventral ganglion to anterior end of the paired fins	6–7 Fig. 6C
IV	Tail segment empty; seminal vesicles filled with sperm or broken	Ovaries reaching to region of ventral ganglion; filled with large ova arranged in one line	6–8 Fig. 6D

Table 5
Maturity stages of *Krohnitta subtilis* (Fig. 7)

Stage	Male gonads	Female gonads	Size (mm)
I	Tail segment getting filled with spermatids; seminal vesicles beginning to develop	Ovaries reaching up to 1/5 the length of the extent of the paired fins on trunk; ova small	Up to 10 Fig. 7A
II	Spermatozoids well visible in tail cavity; seminal vesicles beginning to get filled; cross-fertilization appears to take place during this stage; pouring of the sperm into seminal receptacle of another specimen's ovary	Ovaries reaching up to 1/2 the length of the extent of the paired fins on trunk	11–12 Fig. 7B
III	Tail segment empty; seminal vesicles appearing in a regenerative process	Ovaries reaching up to 2/3 the length of the extent of the paired fins on trunk	11–12 Fig. 7C
IV	Tail segment empty, and seminal vesicles appear either as in previous stage or tail filled with sperm and vesicles getting filled with male cells	Ovaries reaching up to anterior end of the paired fins	12–16 Fig. 7D

Table 6

Maturity stages of *Pterosagitta draco* (Fig. 8)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as fine tubes; tail segment empty; no seminal vesicles present	Ovaries as fine tubes reaching less than ¼ of length to neck	5–6 Fig. 8A
II	Tail segment filled with sperm; seminal vesicles filling or full	Ovaries reaching up to 2/3 of level from neck region	7 Fig. 8B
III	Tail segment empty; seminal vesicles empty	Ovaries reaching up to level of ventral ganglion	8 Fig. 8C
IV	Tail segment empty; seminal vesicles disappear	Ovaries filling body cavity, reaching up to neck region	9–10 Fig. 8D

Table 7

Maturity stages of *Sagitta bedfordii* (Fig. 9)

Stage	Male gonads	Female gonads	Size (mm)
III	Tail filled with sperm; seminal vesicles beginning to be filled	Ovaries reaching up to level of posterior end of anterior fins	2.8–3.0 Fig. 9C
IV	Tail totally or partially depleted of sperm; seminal vesicles bursting or full	Ovaries reaching up to level of region of ventral ganglion	3.5–4.0 Fig. 9D

Table 8

Maturity stages of *Sagitta bedoti* (Fig. 10)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as fine tubes; seminal vesicles not present yet	Ovaries reaching up to near anterior end of posterior fins	9 Fig. 10A
II	Testes well visible, filling tail cavity; seminal vesicles beginning to appear	Ovaries reaching up to level of anterior end of posterior fins	11 Fig. 10B
III	Tail filled with spermatids and spermatozoids; seminal vesicles conspicuous, beginning to be filled with sperm	Ovaries reaching to level of posterior quarter of anterior fins	13–14 Fig. 10C
IV	Tail cavity beginning to empty sexual cells; seminal vesicles full or bursting	Ovaries reaching up to a level near region of ventral ganglion	14–15 Fig. 10D

Table 9

Maturity stages of *Sagitta bipunctata* (Fig. 11)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes beginning to appear; seminal vesicles incipient	Ovaries are thin tubes, reaching up to the first quarter of the length of posterior fins along trunk	9 Fig. 11A
II	Testes filling the tail cavity; seminal vesicles well visible	Ovaries reach up to level of anterior end of posterior fins	11 Fig. 11B
III	Tail segment filled with spermatids; seminal vesicles are getting filled with sperm	Ovaries reach up to posterior end of posterior fins	13 Fig. 11C
IV	Tail segment filled or emptying the sexual products into the seminal vesicles which appear turgid and filled with sperm	Ovaries reach up to anterior third of anterior fins; ova round	14 Fig. 11D

Table 10

Maturity stages of *Sagitta bruuni* (Fig. 12)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as short, thin tubes; no seminal vesicles visible	Ovaries thin tubes, reaching up to level of midlength of the extent of posterior fins on trunk	8–10 Fig. 12A
II	Testes filling tail cavity; spermatids well visible; seminal vesicles beginning to appear	Ovaries reaching up to level of anterior end of posterior fins	10–11 Fig. 12B
III	Tail cavity filled with spermatids and sperm; seminal vesicles beginning to be filled with sexual cells	Ovaries reaching up to posterior part of anterior fins	12 Fig. 12C
IV	Tail filled with sperm; seminal vesicles full	Ovaries reaching up to anterior quarter of anterior fins	14–15 Fig. 12D

Table 11

Maturity stages of *Sagitta decipiens* (Fig. 13)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as fine tubes; seminal vesicles beginning to appear	Ovaries beginning to appear as small tubes	10 Fig. 13A
II	Testes filling tail cavity; seminal vesicles increasing in development	Ovaries reaching up to anterior end of posterior fins	12 Fig. 13B
III	Spermatids and spermatozoids filling tail cavity; seminal vesicles getting filled	Ovaries reaching up to posterior end of anterior fins	13–14 Fig. 13C
IV	Tail segment totally or partially empty; seminal vesicles full, bursting or discharged	Ovaries reaching level of anterior quarter of anterior fins	14–16 Fig. 13D

Table 12
Maturity stages of *Sagitta enflata* (Figs. 14 and 15)

Stage	Male gonads	Female gonads	Size[1]
I	No testes or vesicles visible	Ovaries reaching to 1/4 or 1/2 of length of posterior fins along trunk	Fig. 14A Fig. 15A
II	Testes well visible; seminal vesicles beginning to appear	Ovaries reaching to about midlength of the extent of posterior fins on trunk or near anterior end of posterior fins	Fig. 14B Fig. 15B
III	Testes filled with sperm; seminal vesicles beginning to be filled	Ovaries reaching to near anterior end of posterior fins or posterior end of anterior fins	Fig. 14C Fig. 15C
IV	Seminal vesicles full, bursting or already empty	Ovaries reaching to anterior end of posterior fins, or in the last cycle up to anterior fins; ova thus in small or in large number, respectively	Fig. 14D, G,H Fig. 15D

[1] Sizes are not given owing to the more or less continuous degree of variation.

Table 13
Maturity stages of *Sagitta ferox* (Fig. 16)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes beginning to appear; no trace of seminal vesicles beginning to appear	Ovaries as fine tubes, reaching up to near anterior end of posterior fins	9 Fig. 16A
II	Tail filled with spermatids and sperm; seminal vesicles developing	Ovaries reaching up to midlength of anterior fins	12 Fig. 16B
III	Tail beginning to discharge sperm; seminal vesicles beginning to be filled	Ovaries reaching up to midway from neck to ventral ganglion	16 Fig. 16C
IV	Tail totally or partially empty; seminal vesicles full or discharged	Ovaries reaching up to neck region, filling body cavity; ova large, in two or three rows	17–18 Fig. 16D

Table 14
Maturity stages of *Sagitta hexaptera* (Fig. 17)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes beginning to appear; seminal vesicles incipient	Ovaries like thin tubes, extending up to midlength of the extent of posterior fins on trunk	22 Fig. 17A
II	Testes filling the tail cavity; seminal vesicles developing	Ovaries reaching up to level of posterior end of anterior fins	27–30 Fig. 17B
III	Tail empty or partially emtpy; seminal vesicles full or broken	Ovaries reaching up close to level of posterior end of ventral ganglion	34 Fig. 17C
IV	Tail empty; seminal vesicles broken	Ovaries filled with large ova, reaching up to level of ventral ganglion	38–40 Fig. 17D

Table 15
Maturity stages of *Sagitta lyra* (Fig. 18)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as fine tubes; seminal vesicles not present	Ovaries reaching up to ⅓ of the extent of posterior fins on trunk	17–22 Fig. 18A
II	Tail filled with spermatids; seminal vesicles beginning to appear	Ovaries reaching up to ¾ of length of posterior fins on trunk, or to anterior end of posterior fins	22–25 Fig. 18B
III	Tail segment filled with sperm, or emptying; seminal vesicles full	Ovaries reaching up to level of posterior third of anterior fins	27 Fig. 18C
IV	Tail segment empty; seminal vesicles empty	Ovaries reaching up to level of anterior end of anterior fins	30–38 Fig. 18D

Table 16
Maturity stages of *Sagitta macrocephala* (Fig. 19)

Stage	Male gonads	Female gonads	Size (mm)
I	No traces of testes or fine tubes apparent	No trace of ovaries, but when 14 mm long, ovaries reach up to 1/3 of extent of posterior fins on trunk	8–14 Fig. 19A
II	Testes as small rods at upper part of tail segment; seminal vesicles beginning to appear	Ovaries reaching up to level of midlength of extent of posterior fins on trunk	17 Fig. 19B
III	Testes filling tail cavity; seminal vesicles oval in shape, getting filled with sperm	Ovaries reaching up to a level close to posterior end of anterior fins	20–21 Fig. 19C
IV	Tail segment empty of sexual cells; seminal vesicles discharged	Ovaries reaching up to level of ventral ganglion; ova small and in four rows	22 Fig. 19D

Table 17
Maturity stages of *Sagitta minima* (Fig. 20)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes not yet visible or beginning to appear; seminal vesicles absent	Ovaries short, with small oocytes	4 Fig. 20A
II	Testes filling tail cavity; seminal vesicles beginning to develop	Ovaries reaching up to posterior third of length of posterior fins on trunk; oocytes of several orders visible	6–5 Fig. 20B
III	Spermatids and spermatozoids filling tail cavity; seminal vesicles beginning to be filled	Ovaries reaching up to midlength of extent of posterior fins on trunk; ova large	6–7 Fig. 20C
IV	Tail segment filled as in previous stage, partially or totally empty and seminal vesicles full	Ovaries reaching up to a level anterior to midlength of posterior fins on trunk; only three large ova per ovary found at this stage because one already released, as in the previous stage where four ova per ovary mostly seen	9–10 Fig. 20D

Table 18
Maturity stages of *Sagitta nagae* (Fig. 21)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as fine tubes; no seminal vesicles visible	Ovaries reaching up to level of half of anterior third of the extent of posterior fins on trunk	11–12 Fig. 21A
II	Testes filling tail cavity; seminal vesicles beginning to develop	Ovaries reaching up to posterior part of anterior fins	15 Fig. 21B
III	Tail cavity filled with spermatids and sperm; seminal vesicles beginning to be filled	Ovaries extending up to posterior fourth of anterior fins	19–20 Fig. 21C
IV	Tail cavity filled with sperm being released to seminal vesicles which are full	Ovaries reaching up to midlength of anterior fins	25 Fig. 21D

Table 19
Maturity stages of *Sagitta neglecta* (Fig. 22)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes appearing as thin tubes; seminal vesicles incipient	Ovaries as thin tubes reaching up to anterior third of extent of posterior fins on trunk	5 Fig. 22A
II	Testes filling tail cavity; spermatids well visible, seminal vesicles developing	Ovaries reaching up to level of midlength of anterior fins	6 Fig. 22B
III	Tail filled with sperm; seminal vesicles getting filled with spermatozoids	Ovaries reaching up to a level near anterior end of anterior fins	7 Fig. 22C
IV	Tail totally or partially empty; seminal vesicles full, bursting or broken	Ovaries reaching up to midway from neck to ventral ganglion, filling trunk cavity; ova large, round, and in one row	8 Fig. 22D

Table 20
Maturity stages of *Sagitta oceania* (Fig. 23)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as thin tubes or partially filling tail cavity	Ovaries reaching up to anterior end of posterior fins or to posterior end of anterior fins	4.4–8.0 Fig. 23A
II	Spermatids and sperm filling tail cavity; seminal vesicles beginning to be filled	Ovaries reaching to posterior part of anterior fins	4.9–5.0 Fig. 23B
III	Tail filled with sperm; seminal vesicles full	Ovaries reaching up to anterior end of anterior fins	5.0–5.5 Fig. 23C
IV	Tail partially or totally empty; seminal vesicles discharged	Ovaries reaching up to a level anterior to anterior end of ventral ganglion	5.5–6.5 Fig. 23D

Table 21
Maturity stages of *Sagitta pacifica* (Fig. 24)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as fine tubes; seminal vesicles beginning to appear	Ovaries as fine tubes, reaching up to level of anterior end of posterior fins	7 Fig. 24A
II	Testes filling tail cavity; seminal vesicles conspicuous	Ovaries reaching up to posterior end of anterior fins	9–10 Fig. 24B
III	Tail filled with spermatogonia and spermatozoids; seminal vesicles turgid, filled with sperm	Ovaries reaching up to anterior quarter of anterior fins	10–11 Fig. 24C
IV	Tail partially or totally empty; seminal vesicles full or empty	Ovaries with large ova, filling body cavity and reaching up to level of ventral ganglion or close to neck	12–14 Fig. 24D

Table 22
Maturity stages of *Sagitta pulchra* (Fig. 25)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes visible; seminal vesicles beginning to appear	Ovaries like thin tubes reaching up to a level close to anterior end of posterior fins	18 Fig. 25A
II	Tail filled with spermatogonia; seminal vesicles developing	Ovaries reaching up to posterior end of anterior fins	20–22 Fig. 25B
III	Tail filled with sperm; seminal vesicles beginning to get filled	Ovaries reaching up to level of midlength of anterior fins	23 Fig. 25C
IV	Tail empty; seminal vesicles full	Ovaries reaching up to level of ventral ganglion	23–24 Fig. 25D

Table 23
Maturity stages of *Sagitta regularis* (Fig. 26)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes beginning to appear as small thread-like tubes; no seminal vesicles visible	Ovaries as thin tubes, reaching up to anterior end of posterior fins	3.0–3.7 Fig. 26A
II	Testes filling tail cavity; seminal vesicles beginning to appear	Ovaries reaching up to posterior part of anterior fins	4 Fig. 26B
III	The tail cavity completely filled with spermatids and spermatozoids; seminal vesicles getting filled with sperm	Ovaries reaching up to midlength of anterior fins	5 Fig. 26C
IV	Tail segment almost empty; seminal vesicles swollen and filled with sperm	Ovaries reaching further or up to level of ventral ganglion; ova large, oval and elongated along the longitudinal axis and distributed in one row	6 Fig. 26D

Table 24
Maturity stages of *Sagitta robusta* (Fig. 27)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as fine tubes; seminal vesicles incipient	Ovaries reaching up to level of anterior end of posterior fins	6–8 Fig. 27A
II	Testes filling tail cavity; spermatids well visible and spermatozoids beginning to appear; seminal vesicles conspicuous	Ovaries reaching up to anterior part of anterior end of anterior fins	10 Fig. 27B
III	Tail filled with sperm; seminal vesicles filled with sperm	Ovaries reaching up to midway of distance from neck to ventral ganglion	11–12 Fig. 27C
IV	Tail partially or totally empty; seminal vesicles filled with sperm	Ovaries reaching up to anterior septum at neck, filling trunk cavity	12 Fig. 27D

Table 25
Maturity stages of *Sagitta scrippsae*

Stage	Male gonads	Female gonads	Size (mm)
I	Testes present	Ovaries beginning to appear	7–30
II	Tail segment filled with sperm; seminal vesicles beginning to appear	Ovaries reach up to the anterior end of posterior fins in the most advanced phase of this stage	31–38
III	Transfer of sperm from the tail segment to the seminal vesicles	Ovaries reach to the middle of anterior fins	39–49
IV	Tail empty; seminal vesicles ready to burst, or broken and discharged	Ovaries reach near the neck region; seminal receptacles filled with spermatozoa; ova polygonal in shape, distributed in five or six stacked rows	50–60

Table 26
Maturity stages of *Sagitta septata* (Fig. 28)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as fine tubes; seminal vesicles incipient	Ovaries reaching up to level of anterior end of posterior fins	4.5–5.0 Fig. 28A
II	Testes filling tail cavity; spermatids and sperm visible; seminal vesicles developing	Ovaries reaching up to level of posterior end of anterior fins	5.5 Fig. 28B
III	Tail cavity partially emptied of sperm; seminal vesicles full or bursting	Ovaries reaching up to level of ventral ganglion	5.5–6.0 Fig. 28C
IV	Tail cavity empty; seminal vesicles empty	Ovaries reaching up to neck; ova in one line with 20–30 ova per ovary	6 Fig. 28D

Table 27
Maturity stages of *Sagitta tokiokai* (Fig. 29)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as fine tubes, or beginning to fill tail cavity; seminal vesicles beginning to appear	Ovaries reaching up to level of anterior end of posterior fins	13 Fig. 29A
II	Testes filling tail cavity; spermatids and bunches of sperm can be seen; seminal vesicles developing	Ovaries extending up to posterior third of anterior fins	15 Fig. 29B
III	Tail cavity filled with sperm; seminal vesicles filled with sexual cells	Ovaries reaching close to level of ventral ganglion	18 Fig. 29C
IV	Sperm still in tail cavity; seminal vesicles full	Ovaries reaching up to anterior septum, filling trunk cavity; ova in three or four rows	19–22 Fig. 29D

Table 28
Maturity stages of *Sagitta zetesios* (Fig. 30)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes beginning to appear; no seminal vesicles apparent	Ovaries beginning to appear as thin tubes, extending to about half the extent of posterior fins on trunk	20 Fig. 30A
II	Testes filling the tail cavity; spermatogonia clearly visible; seminal vesicles beginning to appear	Ovaries as fine tubes reaching up to a level anterior to anterior end of anterior fins	29 Fig. 30B
III	Tail filled with spermatogonia and sperm; seminal vesicles oval, beginning to be filled	Ovaries as thin tubes reaching up to level of middle of anterior third of anterior fins	32–34 Fig. 30C
IV	Seminal vesicles filled or broken; an oval groove indicating place once occupied by vesicles	Ovaries reaching up to midway between neck and ventral ganglion	39–43 Fig. 30D

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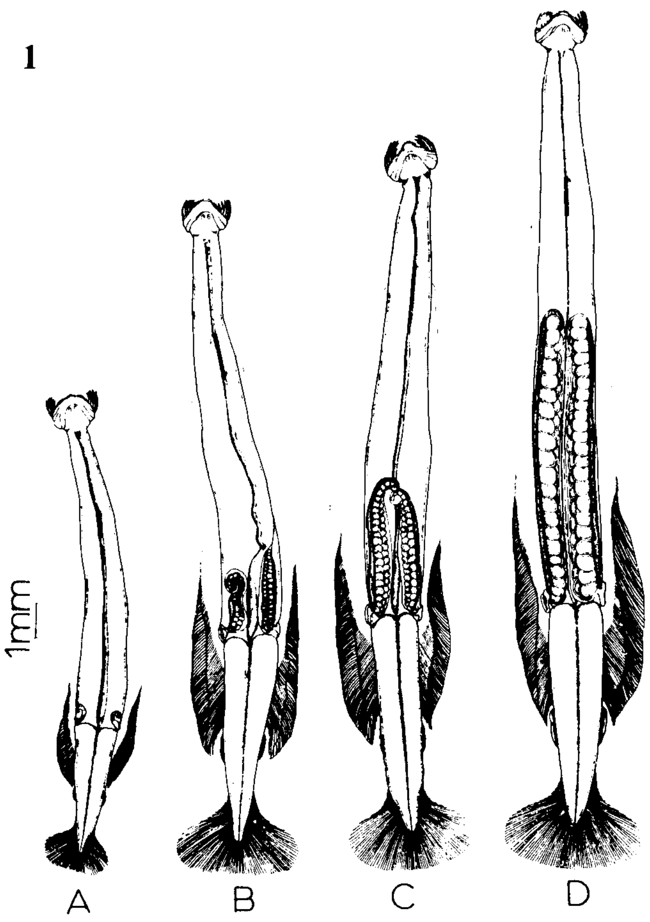

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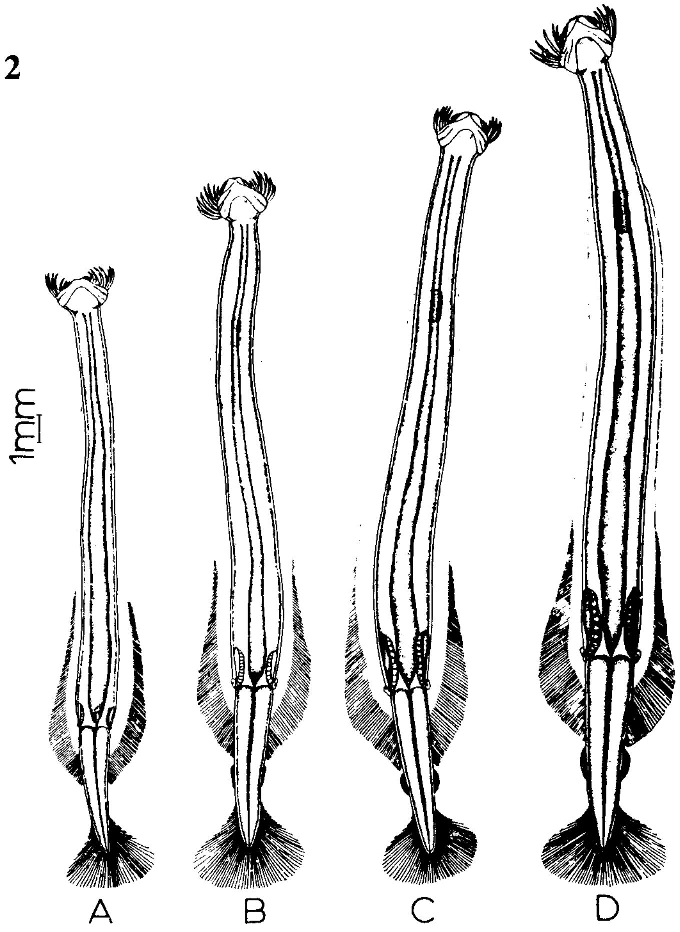

Fig. 1. Four stages of maturity of *Eukrohnia bathyantarctica*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967, 1969.)

Fig. 2. Four stages of maturity of *Eukrohnia bathypelagica*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967, 1969.)

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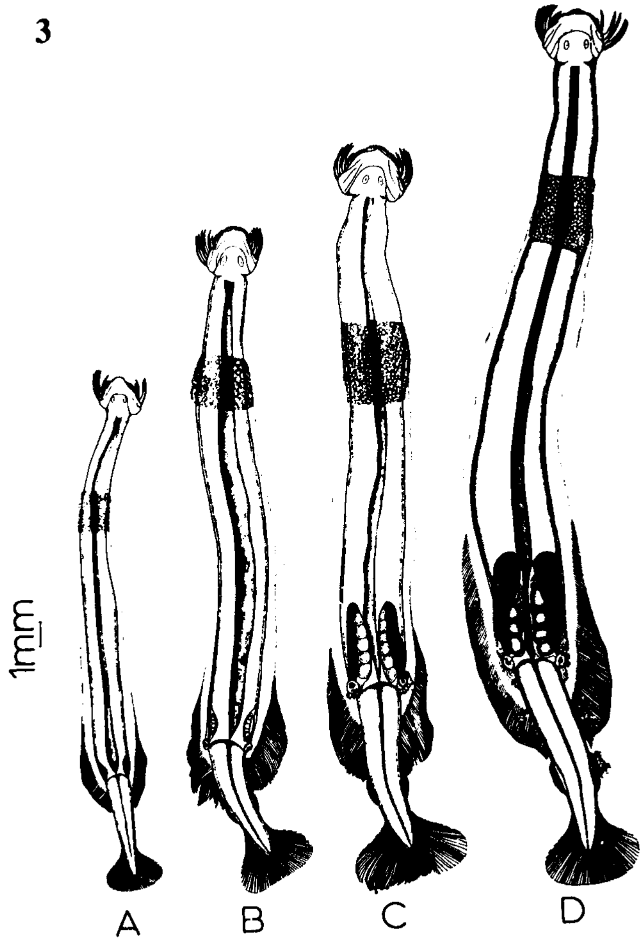

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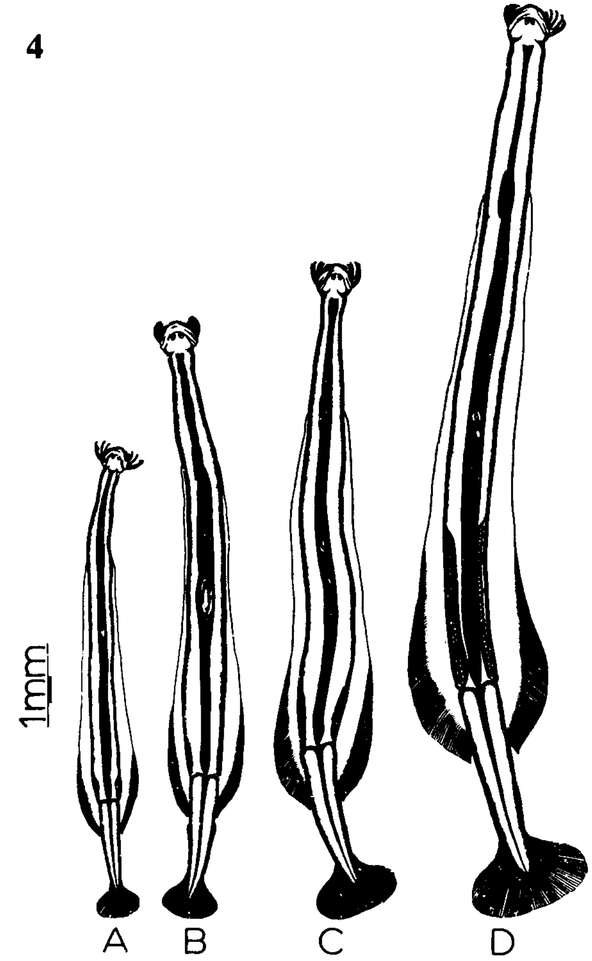

Fig. 3. Four stages of maturity of *Eukrohnia fowleri*. **A**: Stage I; **B**: Stage II; **C**: Stage III; **D**: Stage IV. (From Alvariño, 1967, 1969.)

Fig. 4. Four stages of maturity of *Eukrohnia hamata*. **A**: Stage I; **B**: Stage II; **C**: Stage III; **D**: Stage IV. (From Alvariño, 1967, 1969.)

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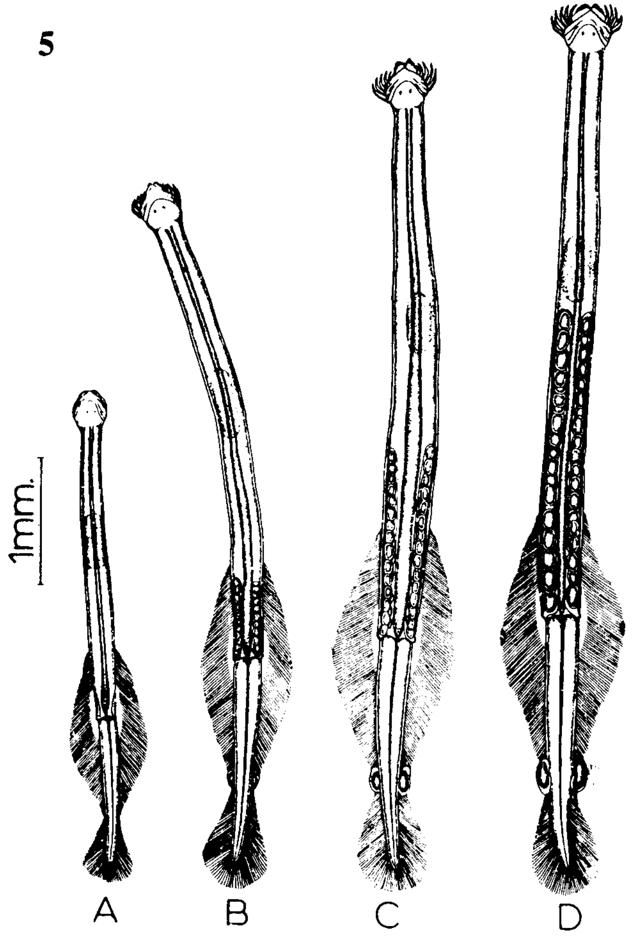

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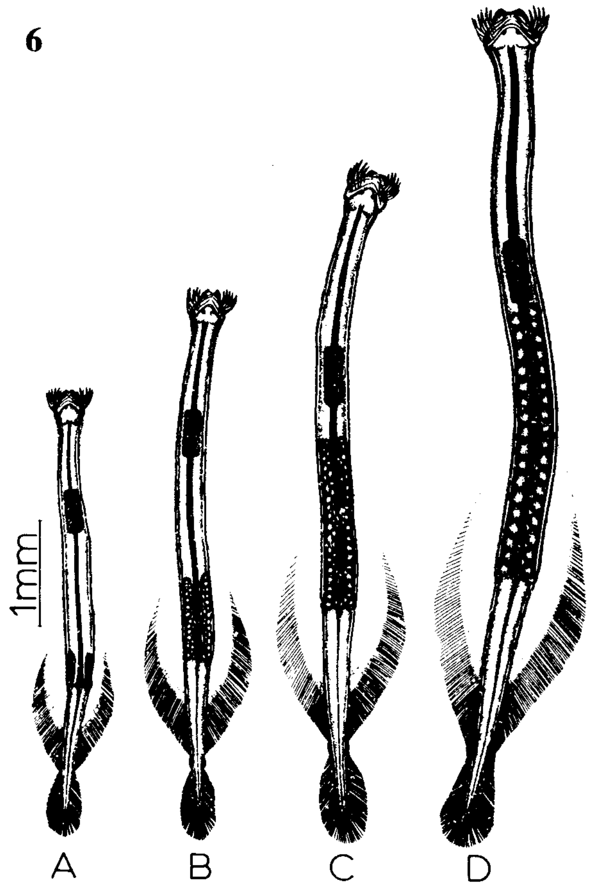
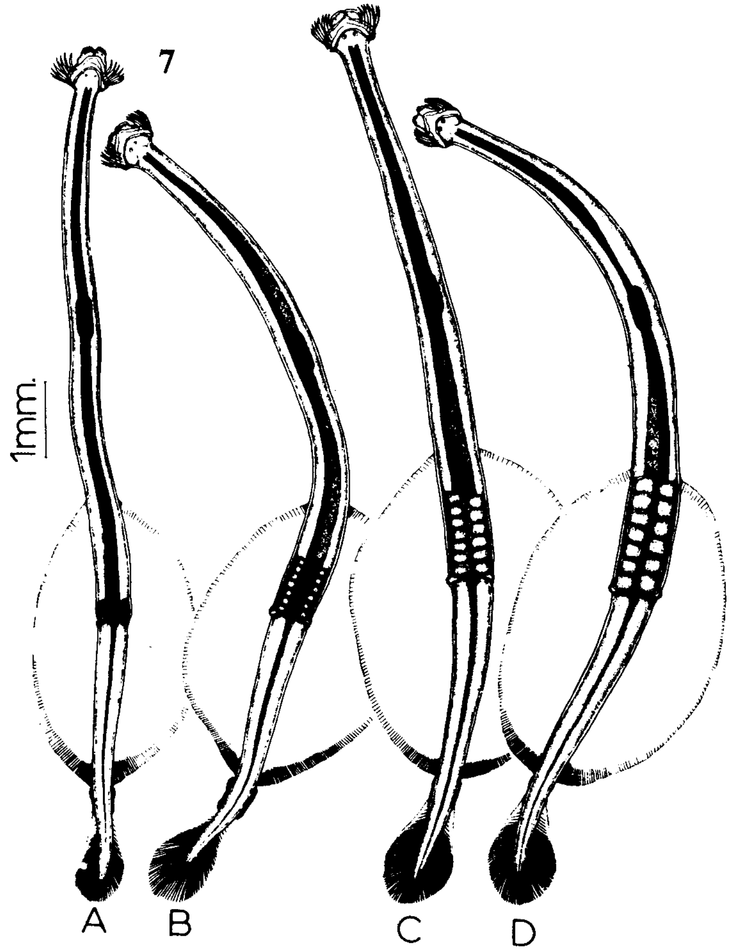


Fig. 5. Four stages of maturity of *Krohnitta mutabbii*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1969.)

Fig. 6. Four stages of maturity of *Krohnitta pacifica*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1963, 1967.)



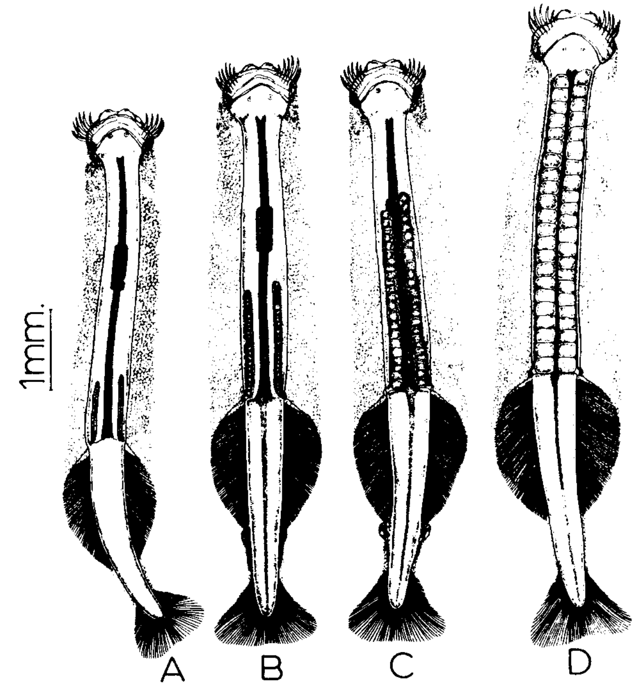


Fig. 7. Four stages of maturity of *Krohnitta subtilis*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1963, 1967, 1969.)

Fig. 8. Four stages of maturity of *Pterosagitta draco*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967, 1969.)

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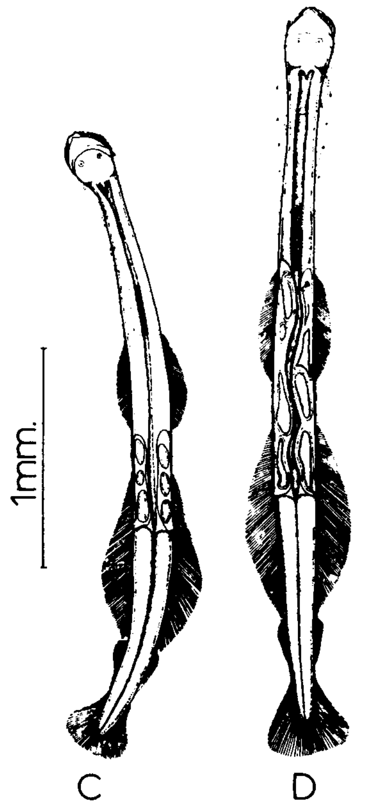

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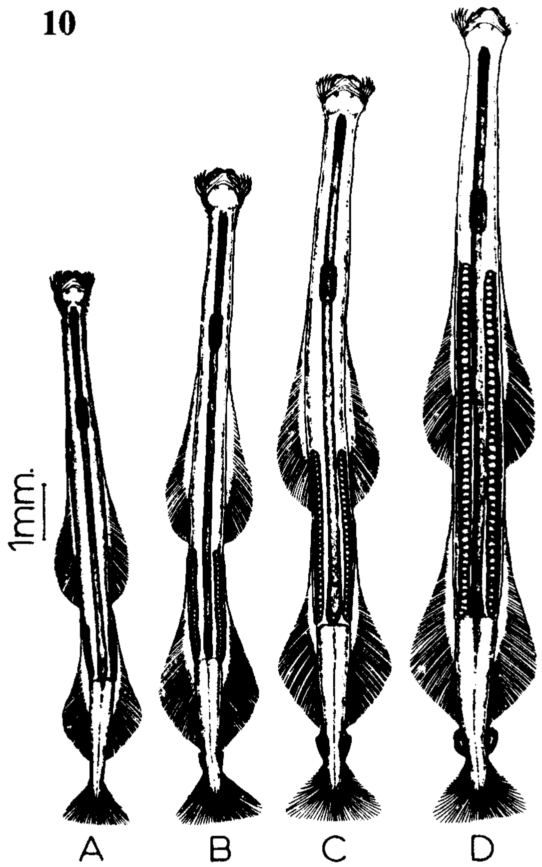
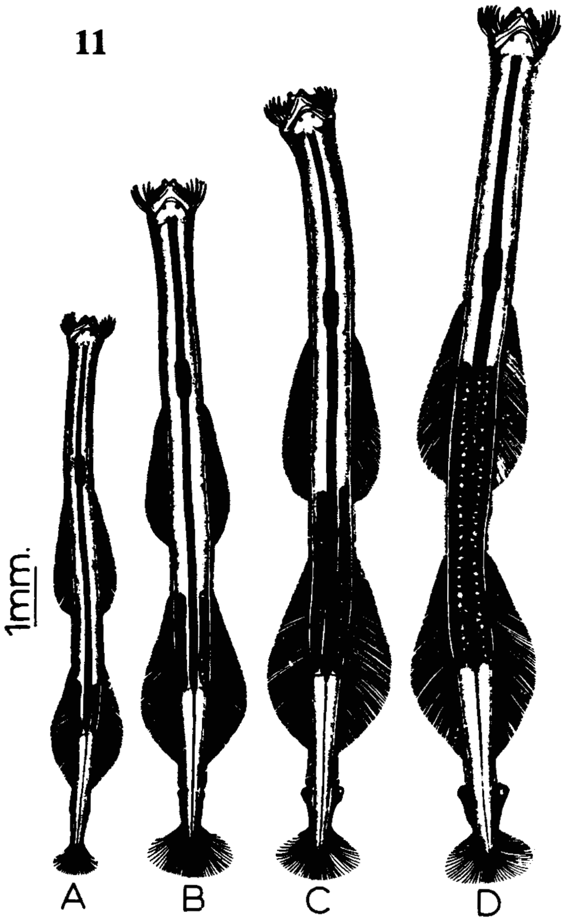


Fig. 9. Two stages in development of *Sagitta bedfordii.* **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967.)

Fig. 10. Four stages of maturity of *Sagitta bedoti.* **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967.)

11



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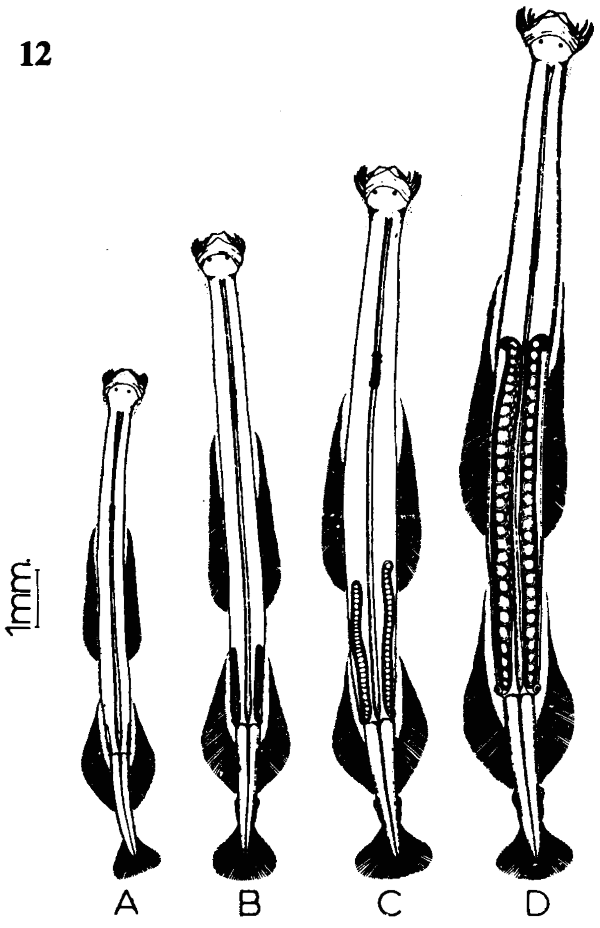
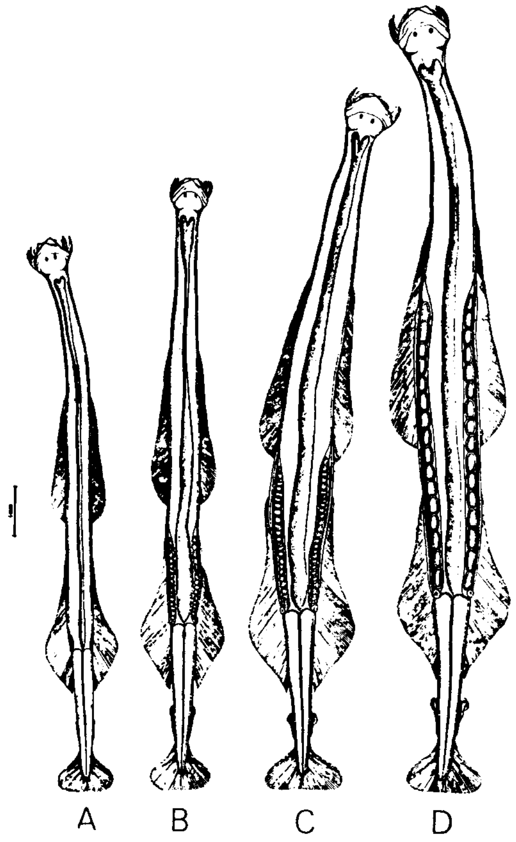


Fig. 11. Four stages of maturity of *Sagitta bipunctata*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967, 1969.)

Fig. 12. Four stages of maturity of *Sagitta bruuni*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967.)

13



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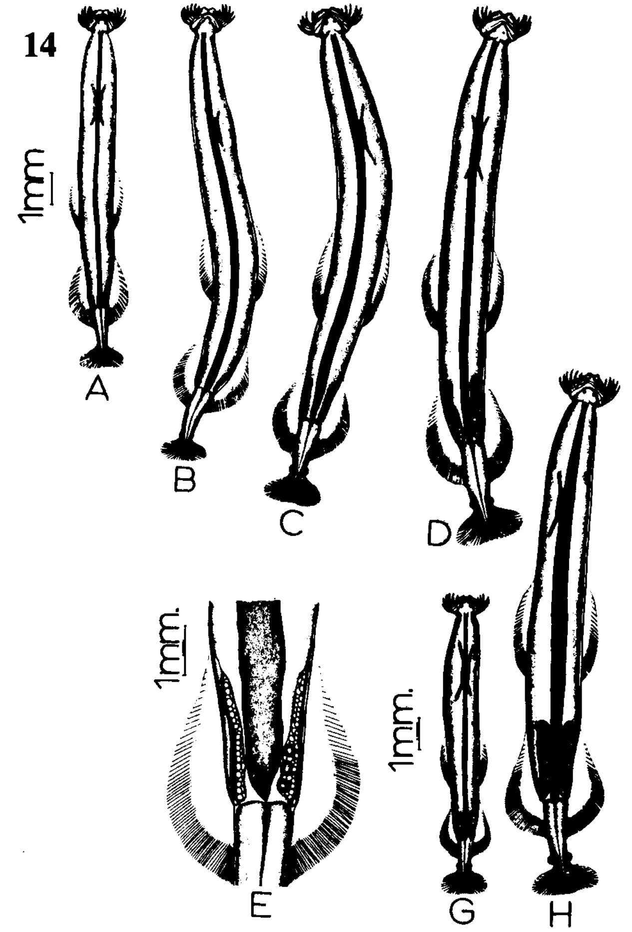
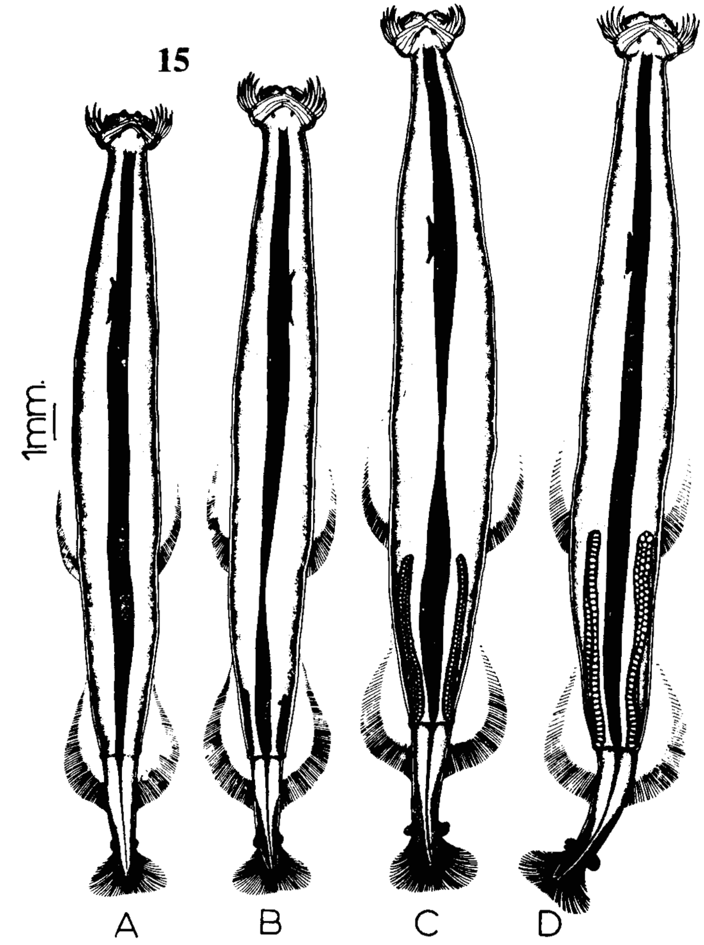


Fig. 13. Four stages of maturity of *Sagitta decipiens*. **A**: Stage I; **B**: Stage II; **C**: Stage III; **D**: Stage IV. (From Alvariño, 1963, 1967, 1969.)

Fig. 14. Four stages of maturity of *Sagitta enflata*. **A**: Stage I second cycle; **B**: Stage II second cycle; **C**: Stage III second cycle; **D and H**: Stage IV second cycle; **E**: Detail of ovaries in the developing period of second cycle, **G**: Stage IV first maturity cycle. (From Alvariño, 1963, 1967, 1969.)

15



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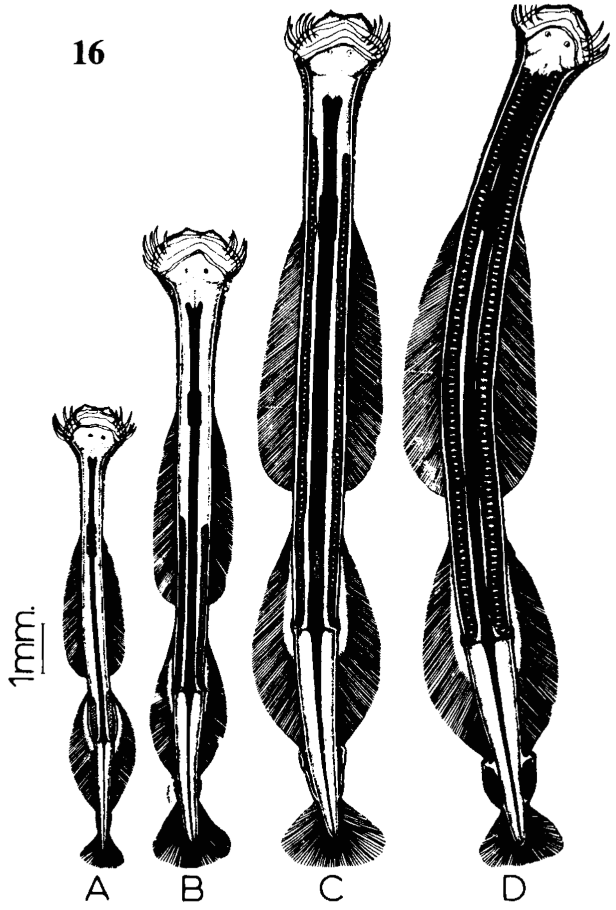
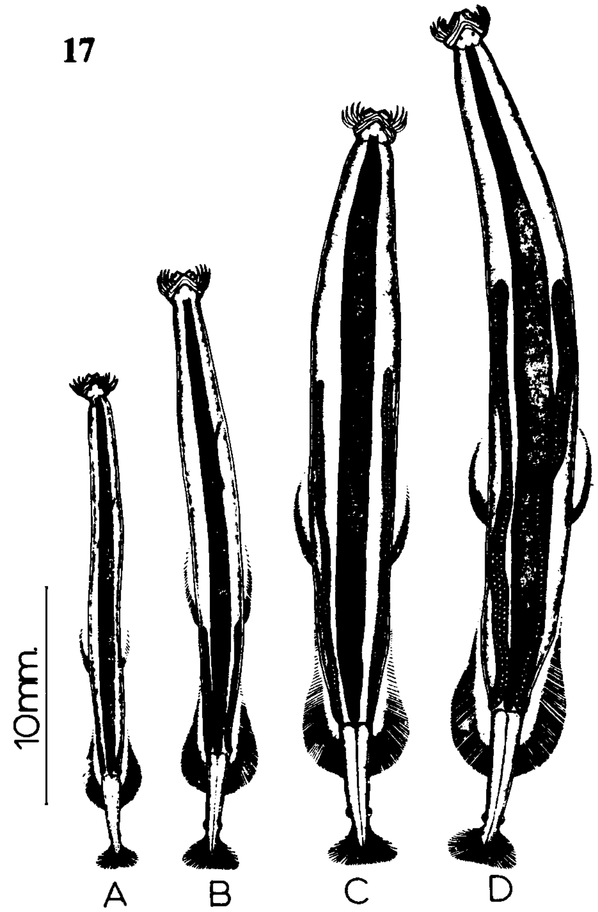


Fig. 15. Four stages of maturity of *S. enflata*, last cycle. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1963, 1967, 1969.)

Fig. 16. Four stages of maturity of *Sagitta ferox*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967, 1969.)

17



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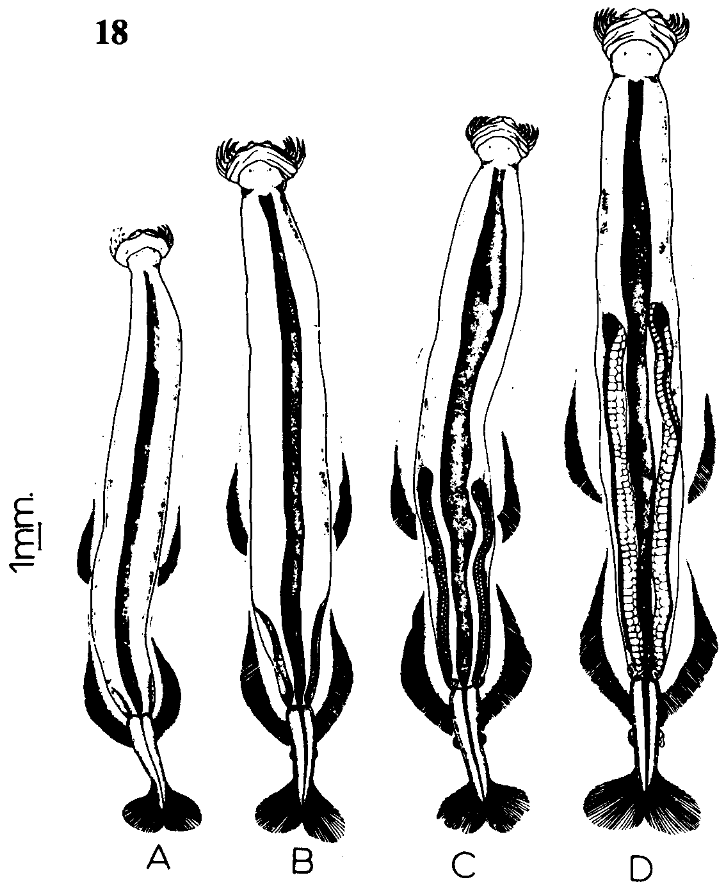
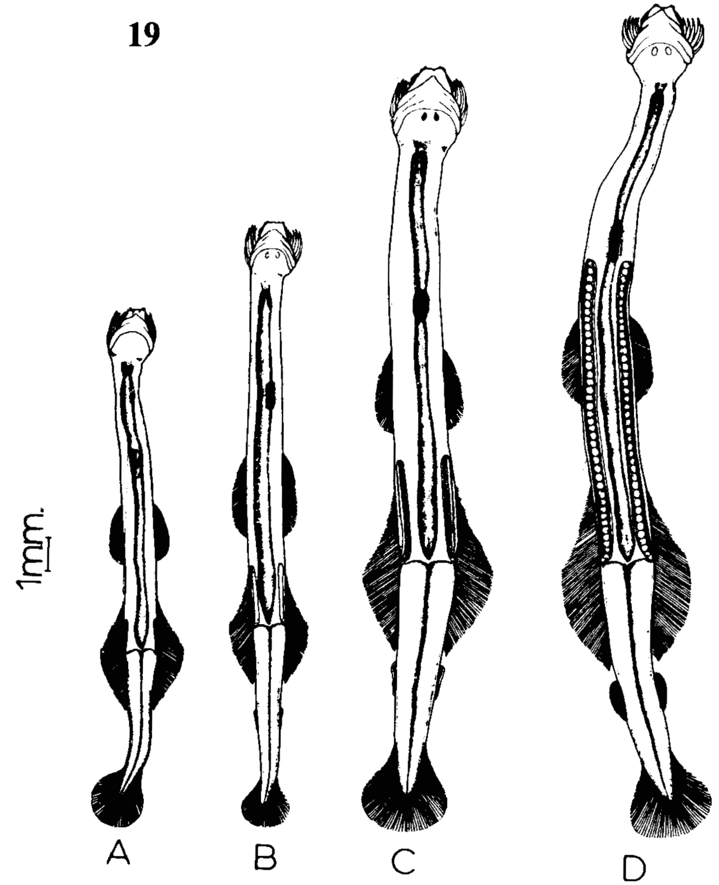


Fig. 17. Four stages of maturity of *Sagitta hexaptera*. **A**: Stage I; **B**: Stage II; **C**: Stage III; **D**: Stage IV. (From Alvariño, 1963, 1967, 1969.)

Fig. 18. Four stages of maturity of *Sagitta lyra*. **A**: Stage I; **B**: Stage II; **C**: Stage III; **D**: Stage IV. (From Alvariño, 1967, 1969.)

19



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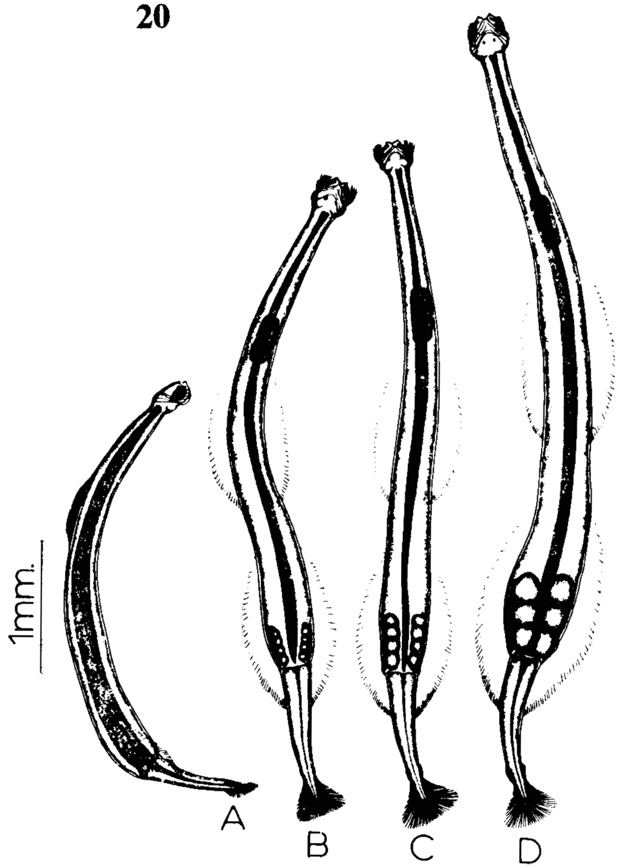
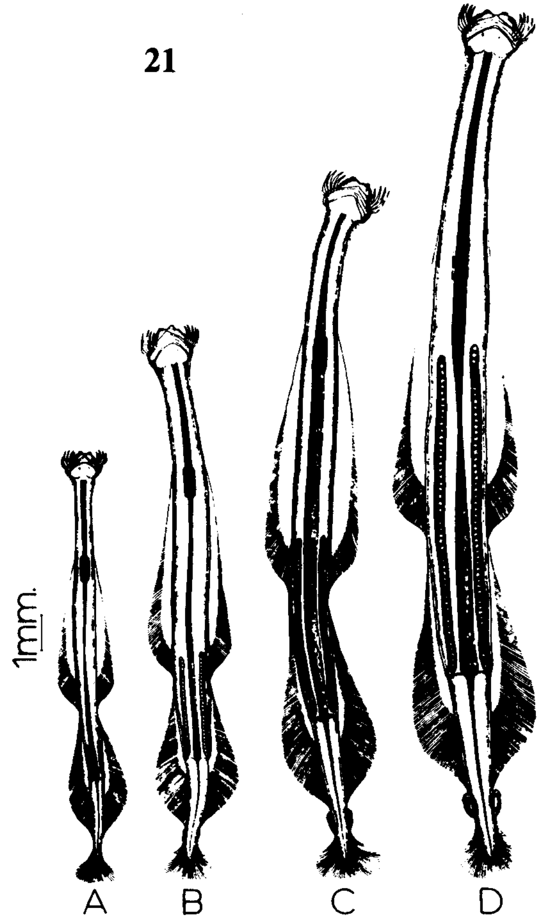


Fig. 19. Four stages of maturity of *Sagitta macrocephala*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967, 1969.)

Fig. 20. Four stages of maturity of *Sagitta minima*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1963, 1967, 1969.)

21



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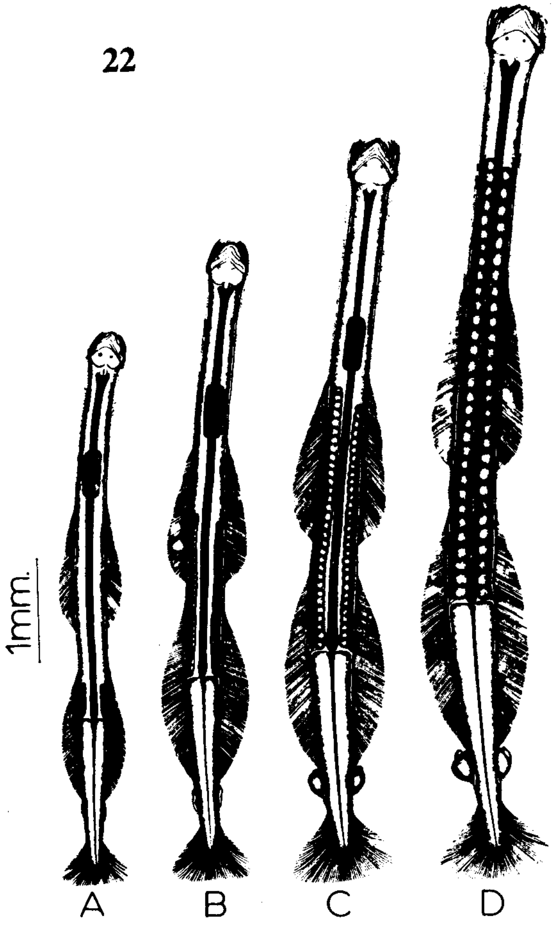
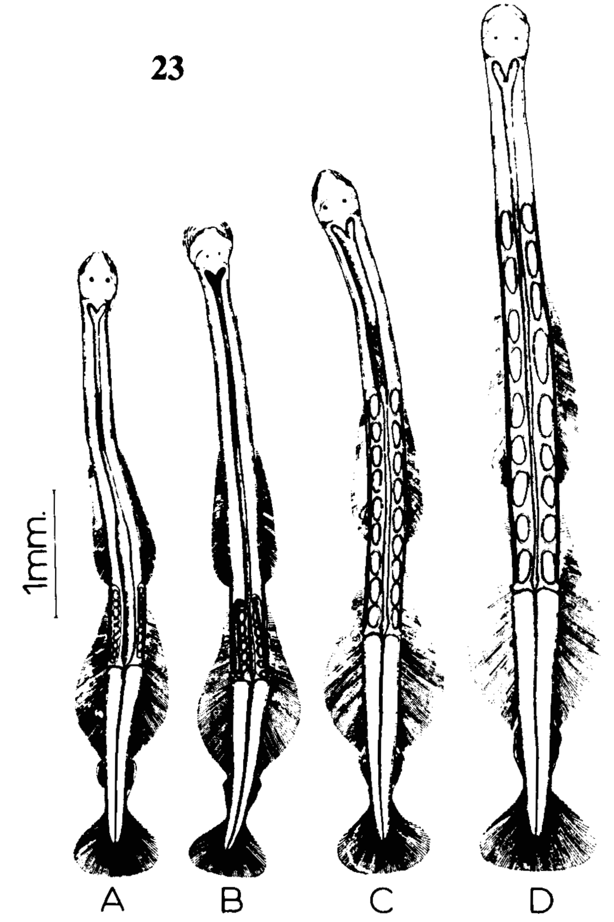


Fig. 21. Four stages of maturity of *Sagitta nagae*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967.)

Fig. 22. Four stages of maturity of *Sagitta neglecta*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1963, 1967.)

23



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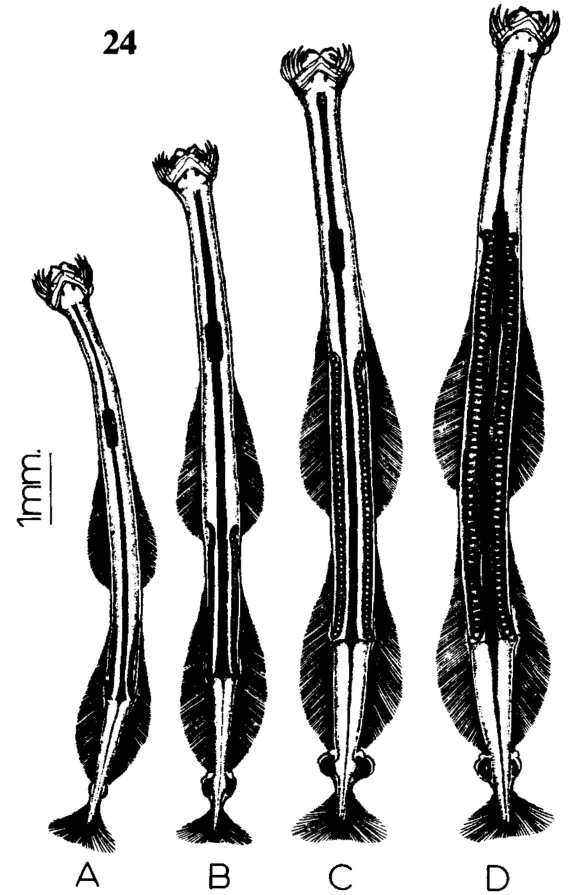
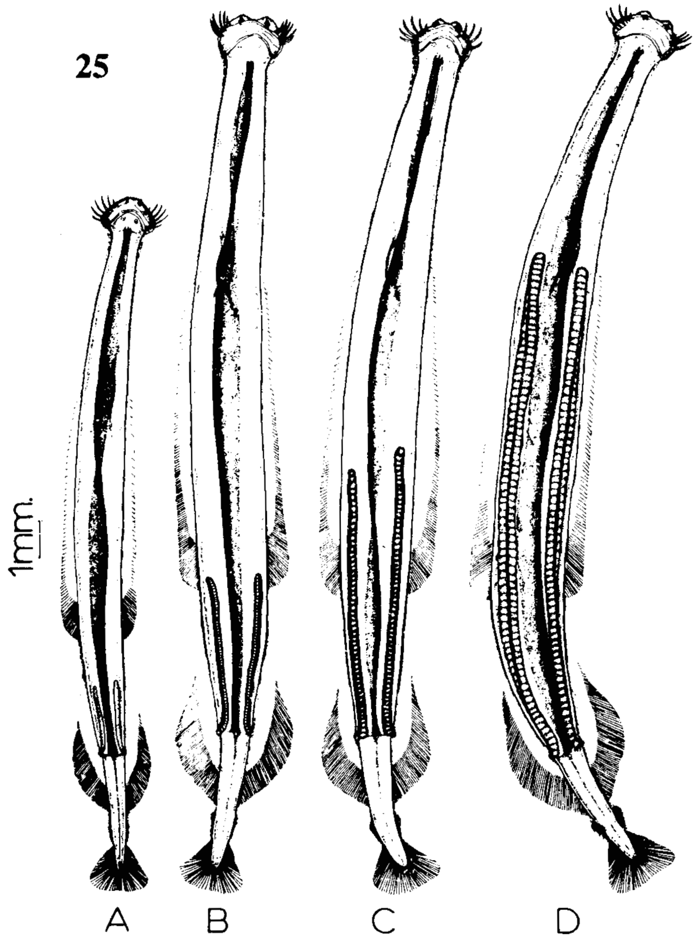


Fig. 23. Four stages of maturity of *Sagitta oceania.* **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967)

Fig. 24. Four stages of maturity of *Sagitta pacifica.* **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1963, 1967.)

25



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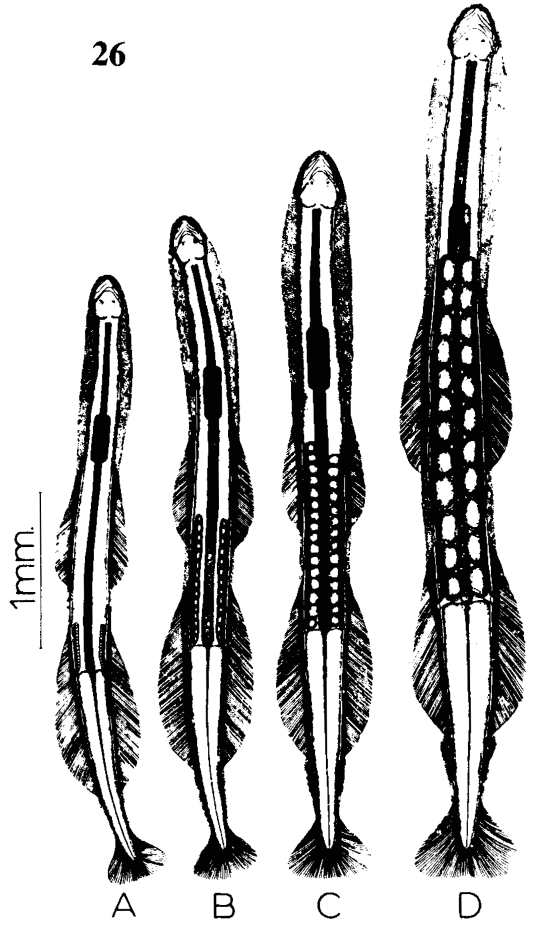
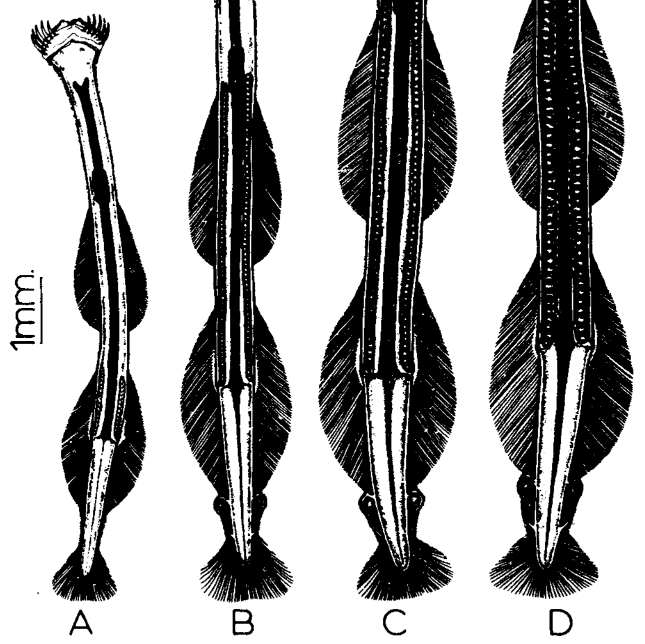


Fig. 25. Four stages of maturity of *Sagitta pulchra*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967.)

Fig. 26. Four stages of maturity of *Sagitta regularis*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1963, 1967.)

27



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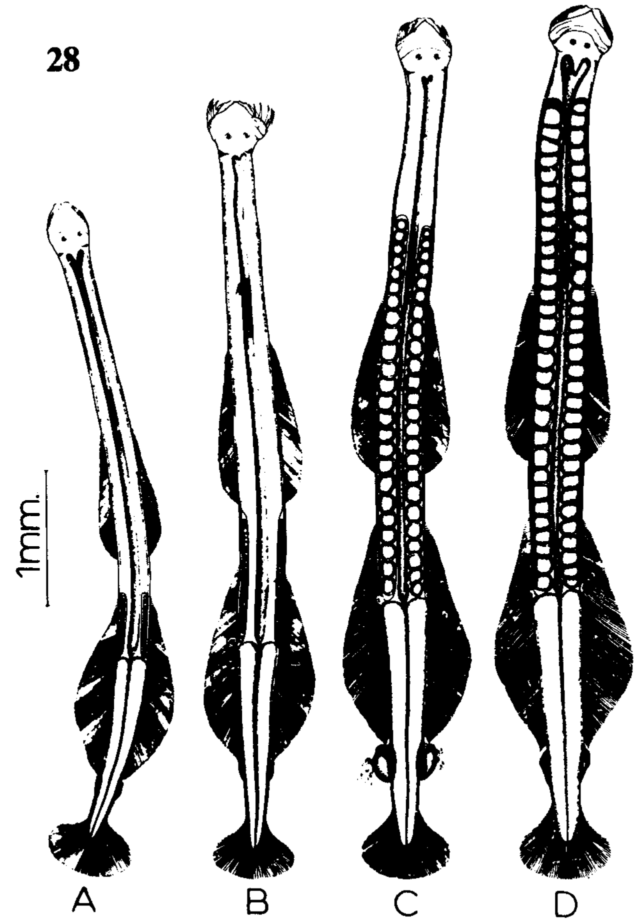
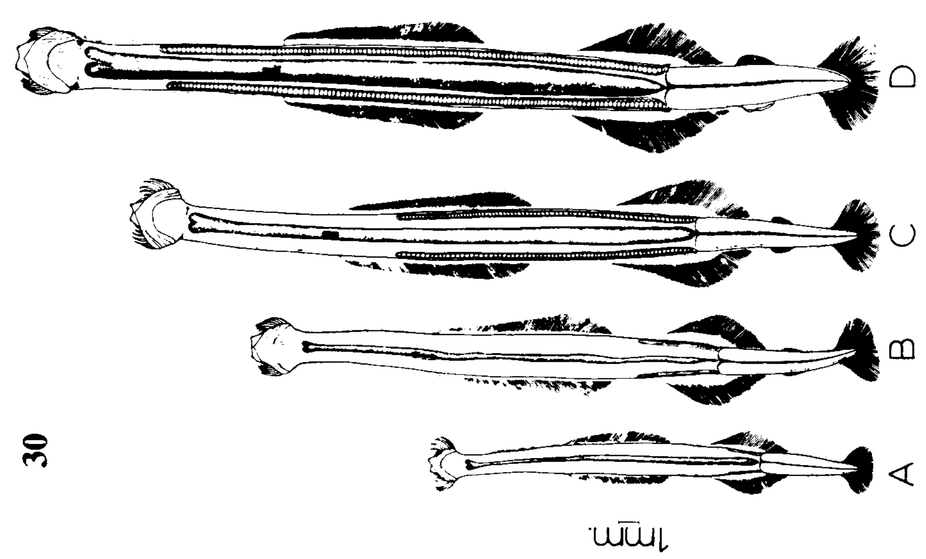


Fig. 27. Four stages of maturity of *Sagitta robusta*. **A**: Stage I; **B**: Stage II; **C**: Stage III; **D**: Stage IV. (From Alvariño, 1967.)

Fig. 28. Four stages of maturity of *Sagitta septata*. **A**: Stage I; **B**: Stage II; **C**: Stage III; **D**: Stage IV. (From Alvariño, 1967.)



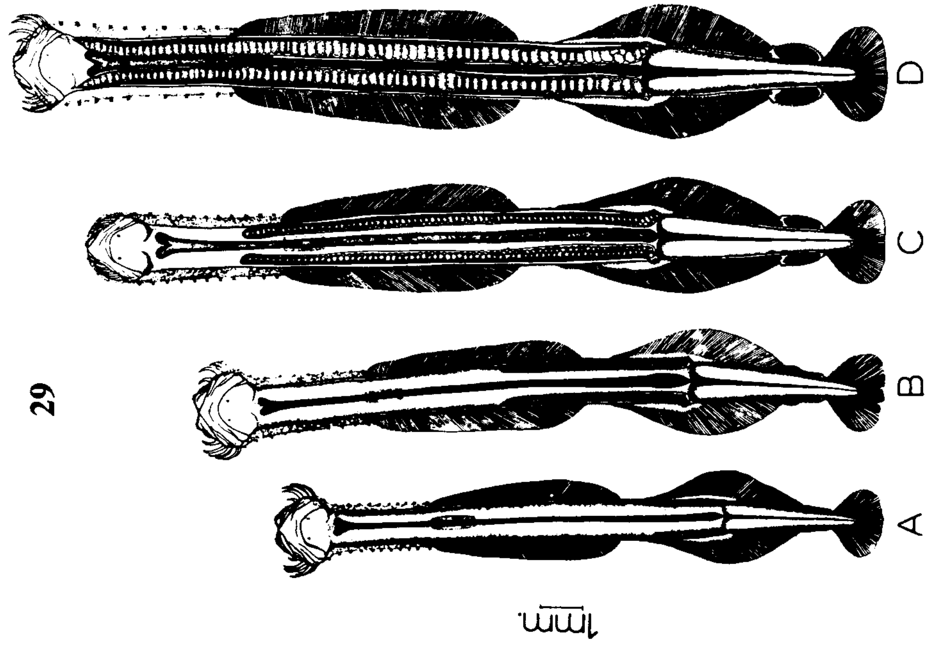
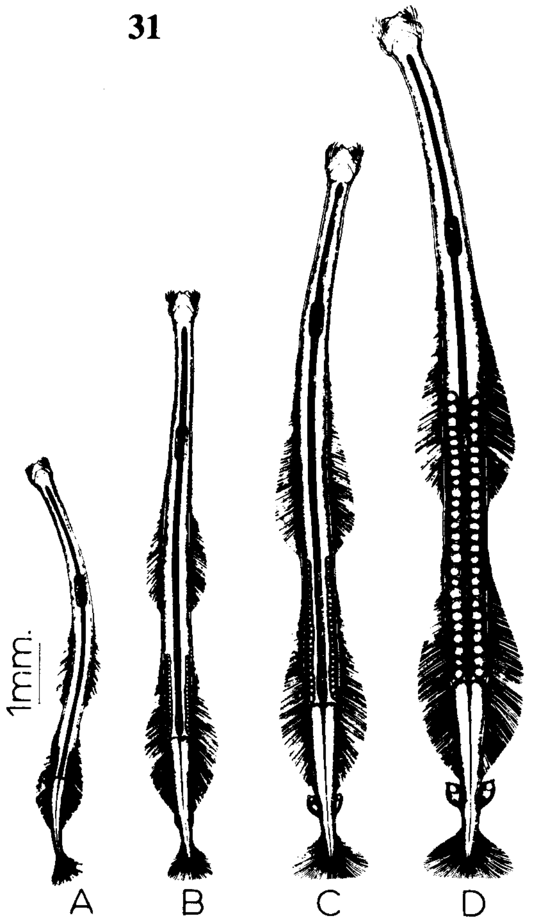


Fig. 29. Four stages of maturity of *Sagitta tokiokai*. **A**: Stage I; **B**: Stage II; **C**: Stage III; **D**: Stage IV. (From Alvariño, 1967.)

Fig. 30. Four stages of maturity of *Sagitta zetesios*. **A**: Stage I; **B**: Stage II; **C**: Stage III; **D**: Stage IV. (From Alvariño, 1967, 1969.)

31



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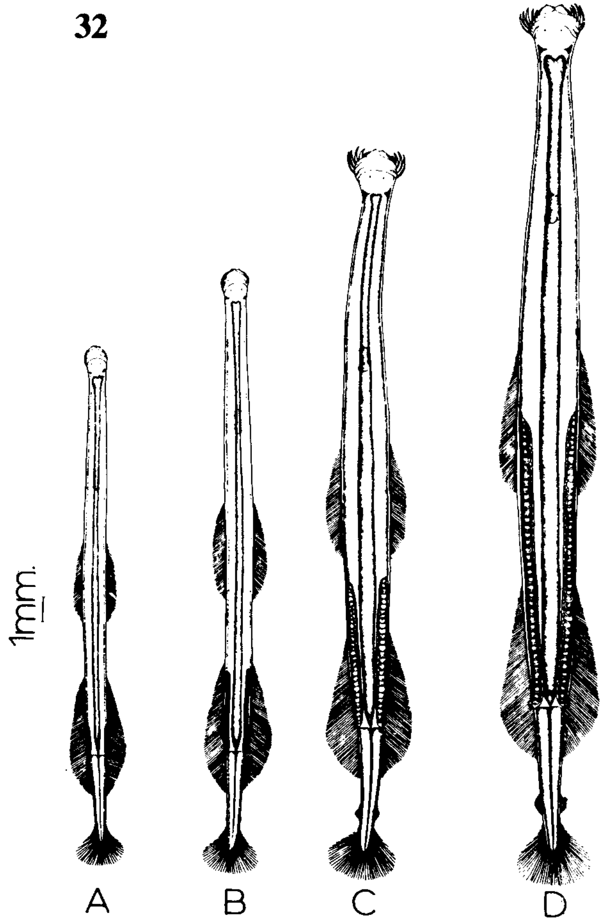
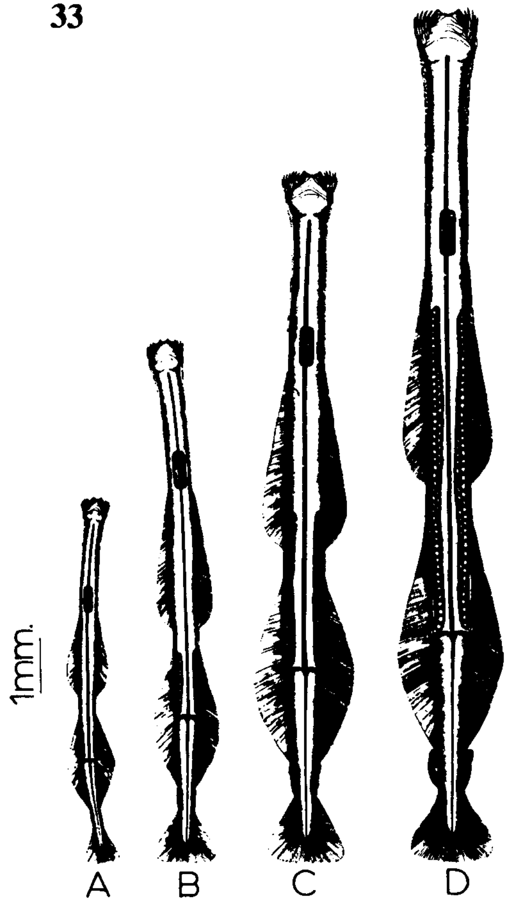


Fig. 31. Four stages of maturity of *Sagitta bierii*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1963.)

Fig. 32. Four stages of maturity of *Sagitta elegans*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1969.)

33



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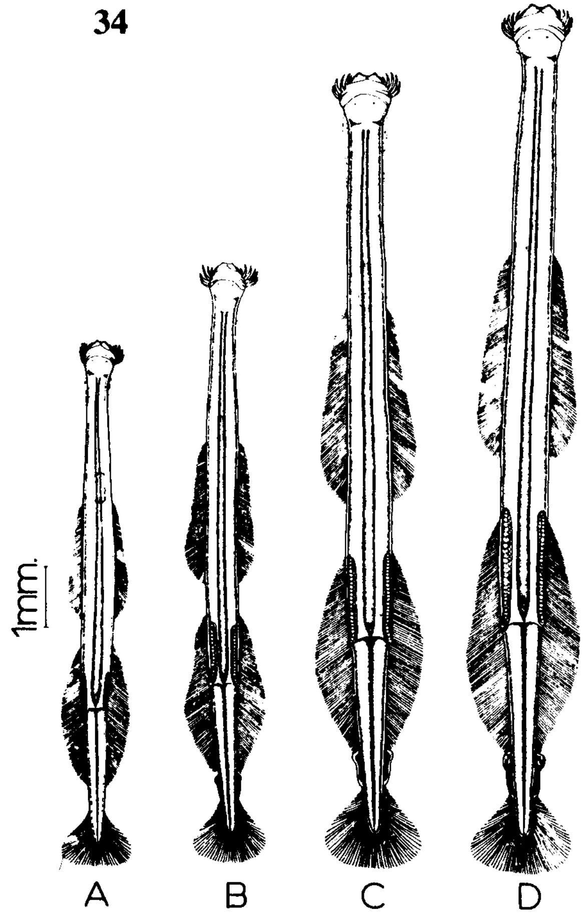
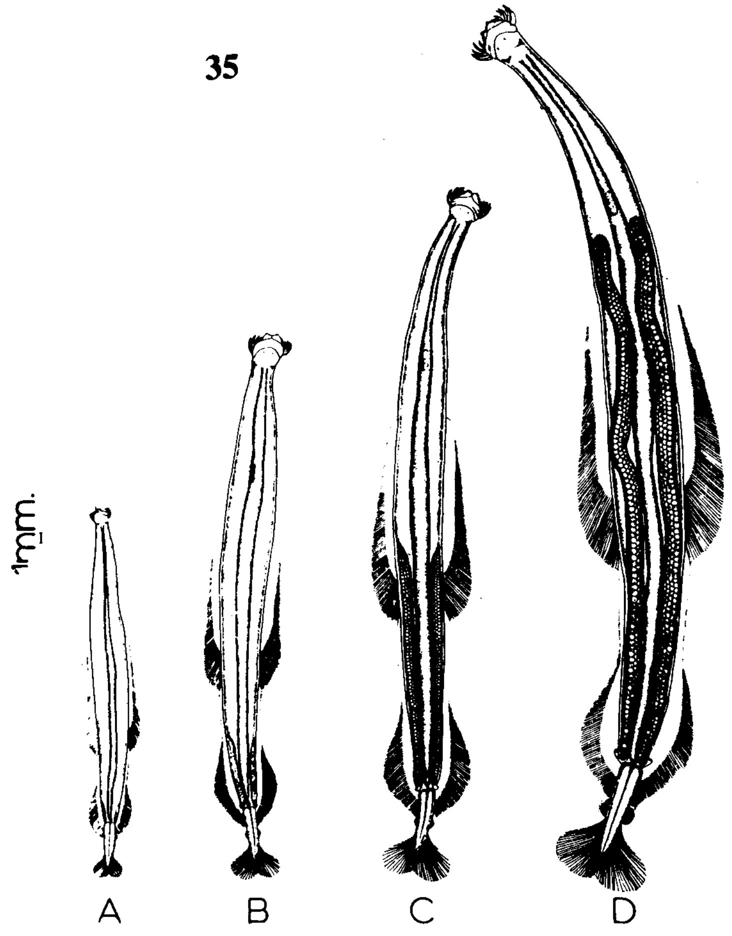


Fig. 33. Four stages of maturity of *Sagitta euneritica*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1963.)

Fig. 34. Four stages of maturity of *Sagitta friderici*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1969.)

35



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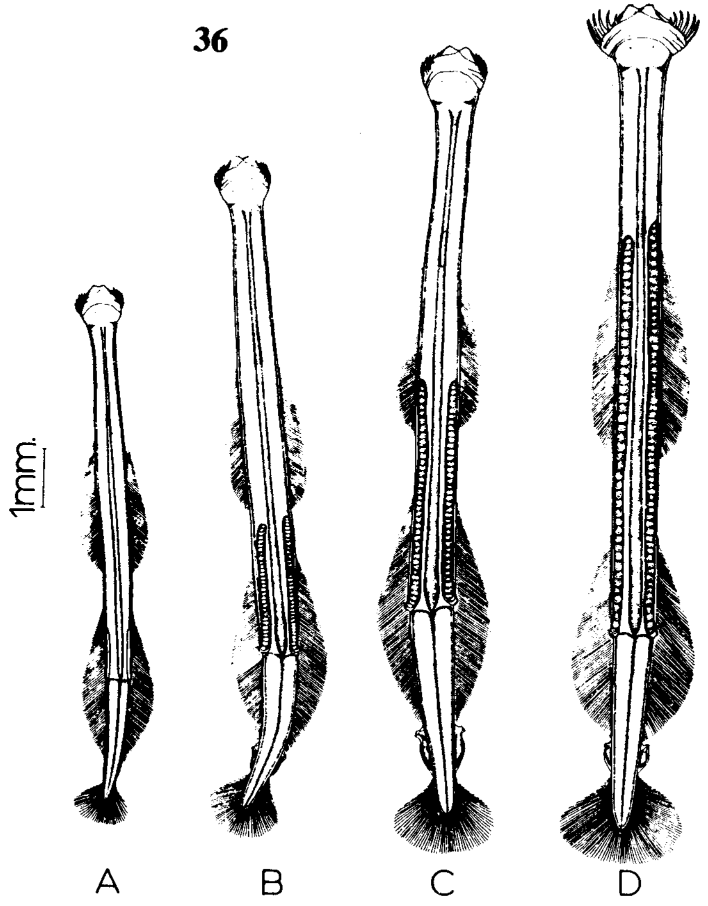
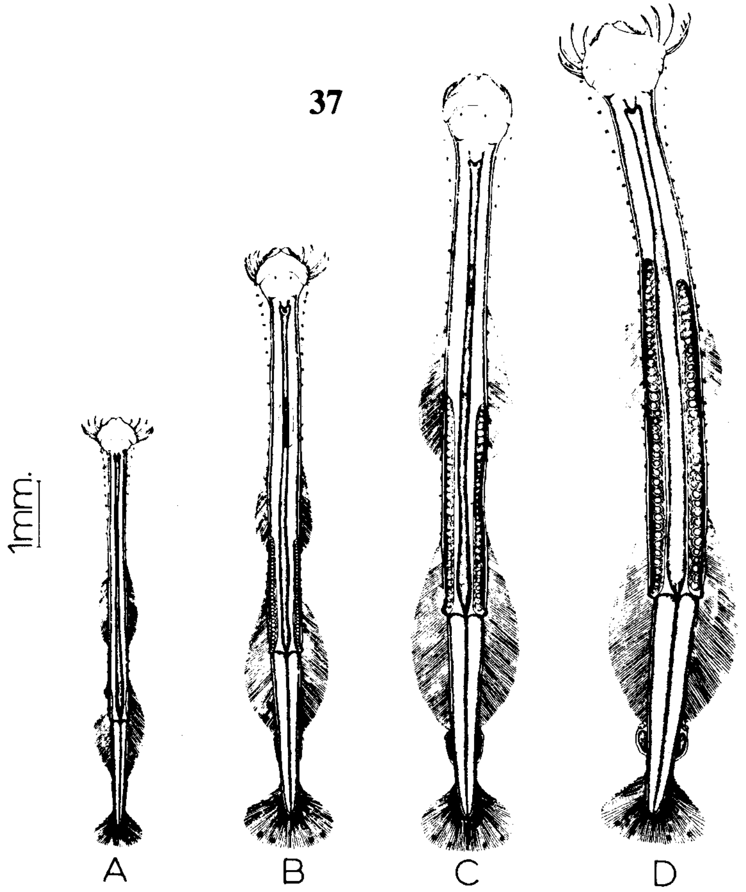


Fig. 35. Four stages of maturity of *Sagitta gazellae*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1969.)

Fig. 36. Four stages of maturity of *Sagitta helenae*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1969.)

37



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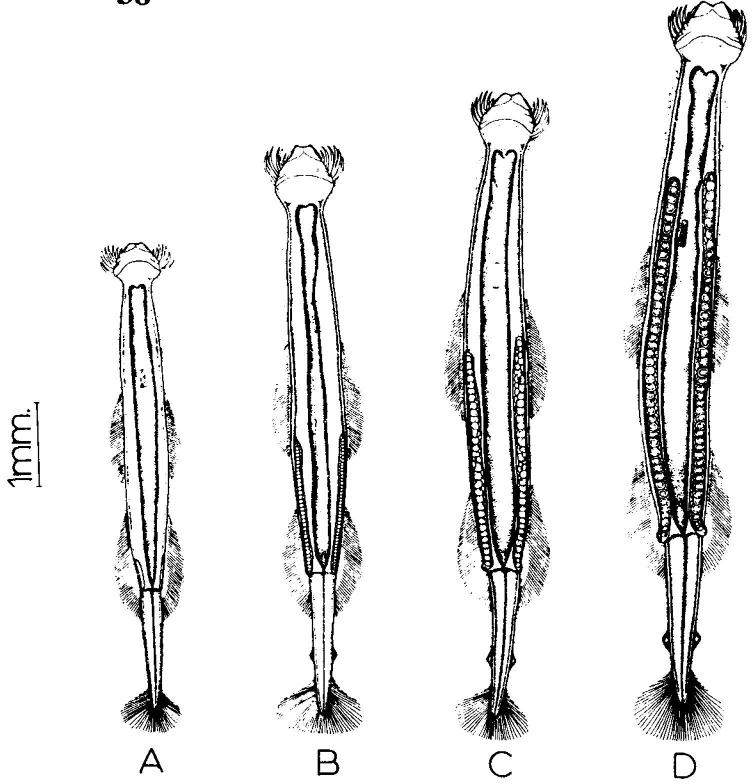
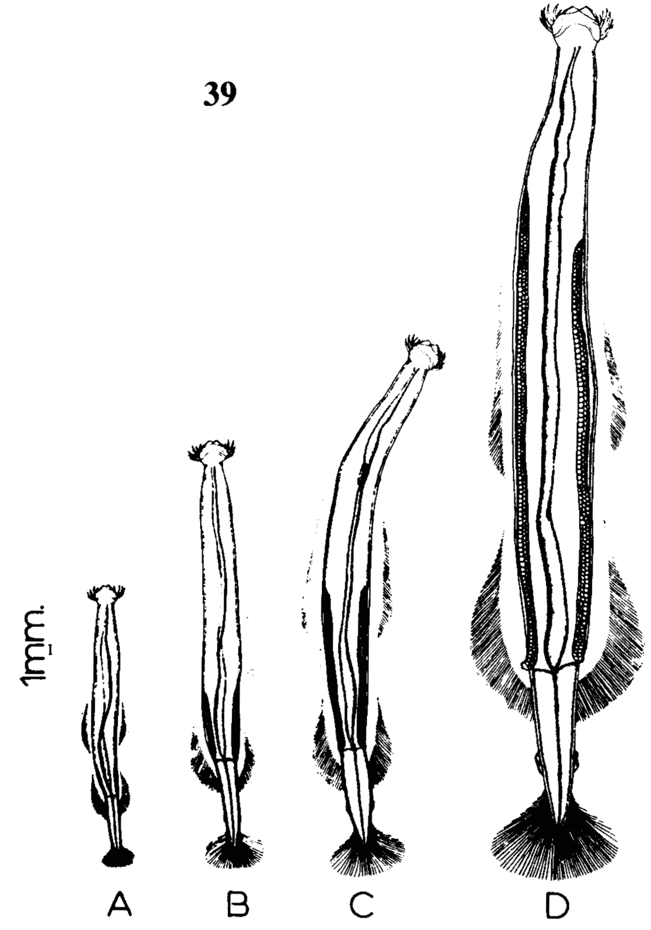


Fig. 37. Four stages of maturity of *Sagitta hispida*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1969.)

Fig. 38. Four stages of maturity of *Sagitta marri*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1969.)

39



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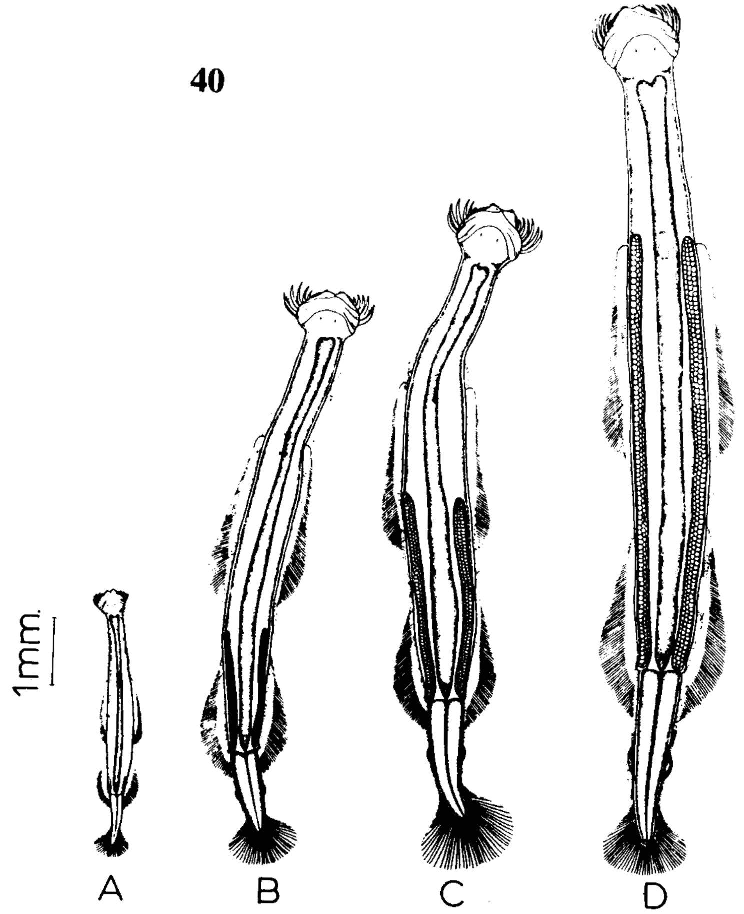
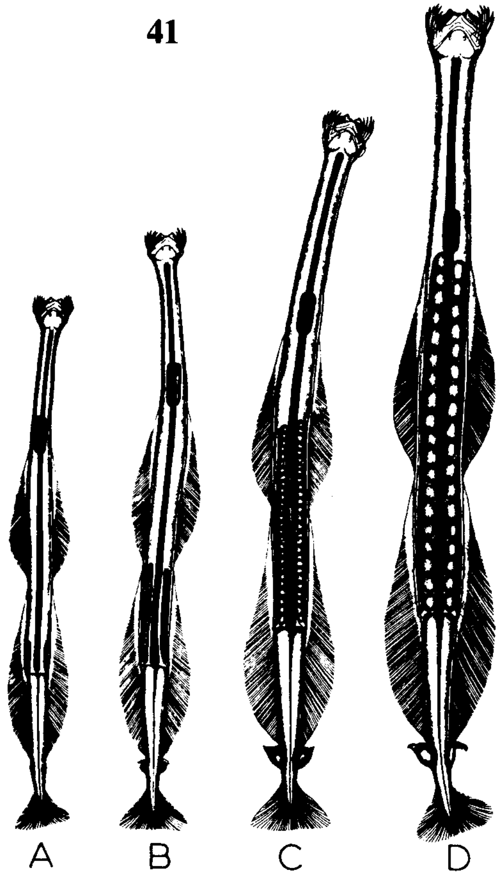


Fig. 39. Four stages of maturity of *Sagitta maxima*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1969.)

Fig. 40. Four stages of maturity of *Sagitta planctonis*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1969.)

41



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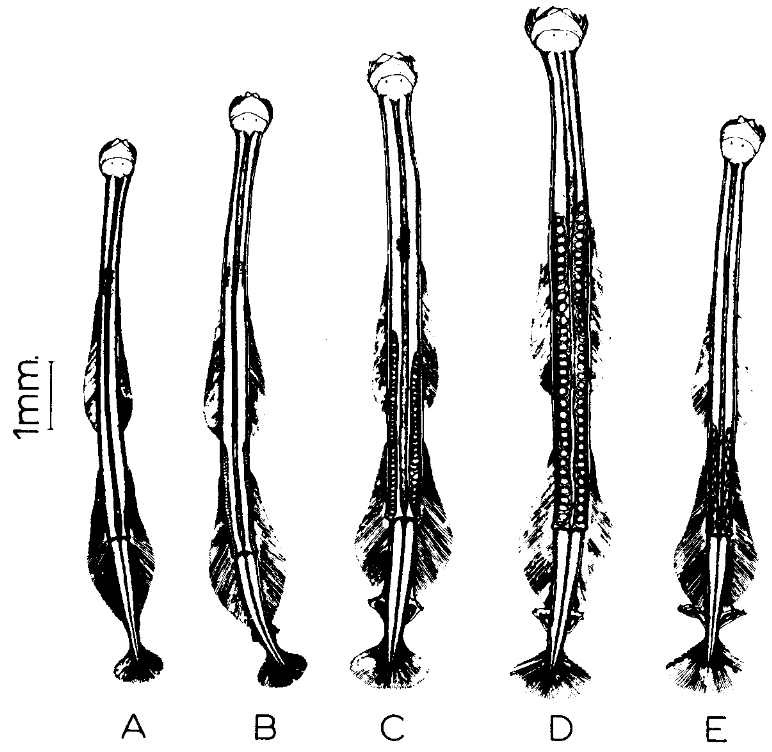
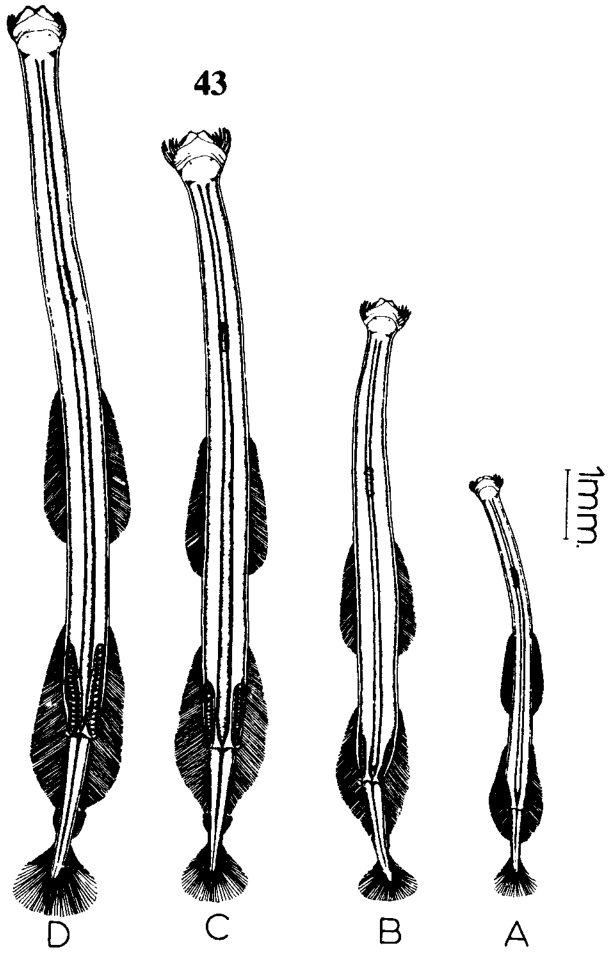


Fig. 41. Four stages of maturity of *Sagitta pseudoserratodentata*. **A**: Stage I; **B**: Stage II; **C**: Stage III; **D**: Stage IV. (From Alvariño, 1963.)

Fig. 42. Stages of maturity of *Sagitta serratodentata*. **A**: Stage I; **B**: Stage II; **C**: Stage III; **D**: Stage IV; **E**: spent. (From Alvariño, 1969.)

43



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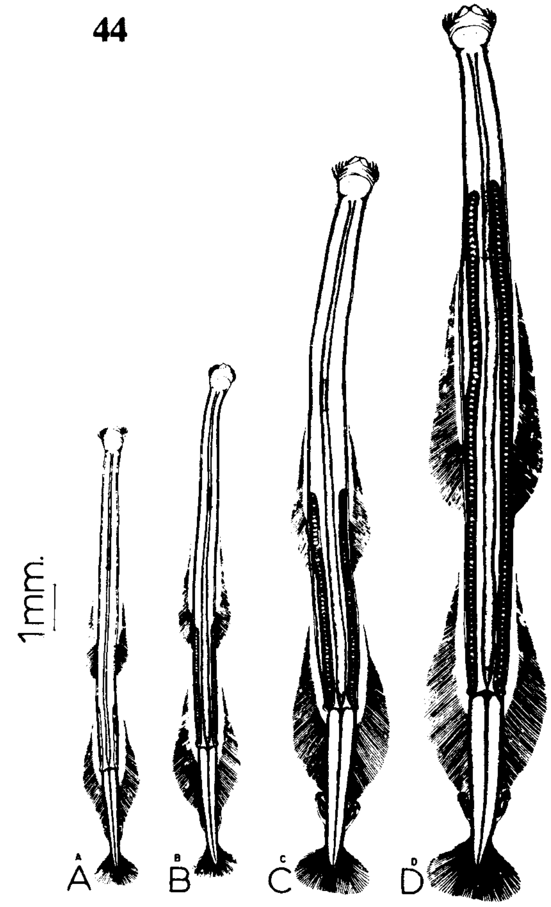

Fig. 43. Stages of maturity of *Sagitta setosa*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1969.)

Fig. 44. Four stages of maturity of *Sagitta tasmanica*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1969.)

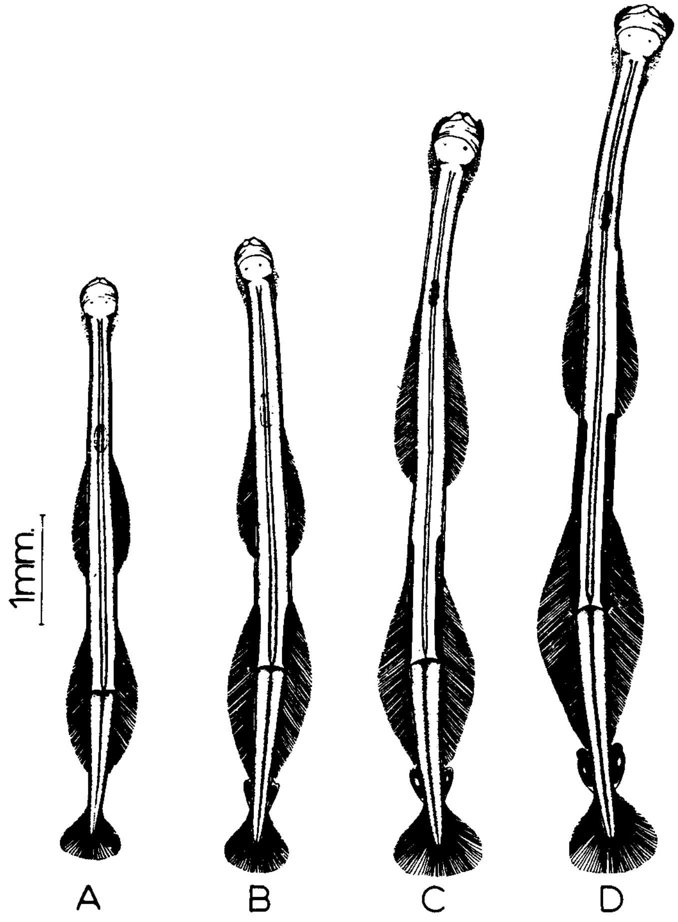

Fig. 45. Four stages of maturity of *Sagitta tenuis*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1969.)

B. Factors Influencing Sexual Maturity in *Sagitta scrippsae*

Sagitta scrippsae inhabits the Transition region of the North Pacific, extending into the California Current and Alaska Gyre. The population structure of *S. scrippsae* has been analysed during the monthly cruises of 1954, 1956 and 1958, and from seasonal day/night stratified collections of 1969 (see Alvariño, 1983). Four maturity stages are considered (Table 25). There are, however, exceptions to the above: specimens 50–60 mm long could appear at Stage III and specimens 31–40 mm long may reach the fully mature Stage IV. Stage I includes three size groups (up to 10 mm, 11 to 20 mm, 21 to 30 mm). Stages II, III, and IV each correspond to the next 10 mm increase in size, from 31 mm to 60 mm. Judging from the nature of the ovary, there appears to be only one 'female' maturity cycle in this species. Protandry is strong: late Stage II specimens, 39–40 mm long, may have mature seminal vesicles, but the ovaries are not mature until the animal is more than 50 mm long.

There is some evidence the testes of this species might go through several cycles of maturity in the life span of the individual, producing sperm, releasing them by copula into the seminal receptacle of another *S. scrippsae,* and starting a new cycle of sperm production to enable the animal to copulate again with another specimen.

The breeding season of chaetognaths can be determined by counting the number of individuals at Stage I, juveniles and larvae, and by comparing the percentage of mature adults to the percentage of young ones. The total number of ova produced by each individual ranges from 700 to 1,000 in *Sagitta scrippsae.* The average number of ova in mature specimens can be used to determine egg production at optimum conditions for reproduction, growth, and survival of the populations, in the species domain. There is a need for caution in that the California region is the margin of the distributional range of *S. scrippsae.*

It is obvious that the population structure of *Sagitta scrippsae* will change progressively with the southern drift of the California Current. In the northern-most part of the region, close to the main distributional area of *S. scrippsae,* the whole population structure may be represented, but the number of mature individuals will be decreasing progressively southward, until the only ones present are at Stage I. It is possible that some population replacement may occur locally. The fact that in most of the California region only Stage I specimens were observed in abundance, indicates that the conditions here may not be suitable for survival of the species, and that specimens may experience an arrest in their normal development. In the region surveyed off California, two phenomena were superimposed during the spring–summer period: the major spawning in the population and the maximum flow of the California Current which conveys the population of *S. scrippsae* southward into the California region (Alvariño, 1983).

Adults of *Sagitta scrippsae* are present all year round in the Transition region of the North Pacific (domain of the species, and area where massive reproduction takes place). In fact, in the Transition region the complete structure of the population of *S. scrippsae* is present, from newly hatched individuals (Alvariño, 1962, 1964, 1965a, b) to fully mature ones, while in the California waters young and large mature specimens were only occasionally observed, mainly at the northern part of the region (Alvariño, 1983).

The population of *Sagitta scrippsae,* observed off California during the four seasons of 1969 (Alvariño, 1983), included some young (10–20 mm), which indicates some breeding had occurred mainly during the spring and summer months. Stage I appeared all year round, and constituted 90 per cent of the population; other stages made up the rest. Some individuals, 35, 40, 41, and 45 mm long, were obtained off California in May with precociously mature female gonads (Stage IV). This may be because these individuals received optimal conditions of food and other factors, which together with high temperature permitted precocious development of their gonads. Or, it could be, as observed by Reeve (1970) in laboratory studies on *S. hispida,* simply the mistaken result of shrinkage in body length due to starvation. There seems to be a marked relation between oxygen consumption and temperature in the ecology of *Sagitta scrippsae*. Consumption of oxygen is generally relatively high in northern species (Sparck, 1936). With increase in temperature and the rise in metabolism, the need for food and oxygen reaches such a degree that the animal is likely to risk starvation.

Temperature and salinity conditions encountered by *Sagitta scrippsae* off California are similar to those found in the distributional domain of the species, as the population sinks with the waters flowing from the north. The conditions off California should be adequate for breeding and survival of the species. However, breeding took place only at random south of San Francisco. Perhaps some chemical in the waters, or the kind of food available, or both may stop the maturity process, and reduce the chances of survival of the newborn. Disappearance of fully mature animals from the California region may be due to their inability to survive under conditions adverse to the species. The result of the decimation of the population is that large mature individuals will be in small numbers, with little chances to be represented in the plankton collections.

Growth, maturity of the gonads, and production of oocytes and eggs might be related to characteristics of the food supply. *Sagitta scrippsae* devour every type of zooplankton, including fish larvae. However, both the amount and quality of available food might be critical factors. *Sagitta scrippsae,* like all chaetognaths, is incapable of storing food.

Sameoto (1973) stated that food was not a limiting factor in determination of growth and maturity of *Sagitta elegans* in Bedford Basin, Nova Scotia, and that growth and maturity were determined by the water temperature. It is generally accepted that growth rate is retarded by lack of food or unfavourable conditions in the natural habitat (Russell, 1932a), and that growth rate and maturity of the gonads are accelerated with increasing temperature. Some specimens of *Sagitta scrippsae* studied here were sexually retarded, e.g. 40 to 45 mm specimens, normally corresponding to Stage III, appeared to be at Stage I or II. Such differences in maturity of the gonads might be dependent on food and other environmental conditions that affect the physiology of the animals. Temperature may be relevant, when other factors remain constant, such as food or other undetermined environmental conditions. In this study, even though temperature encountered in the waters inhabited by the species off California was similar to or even higher than that in the range for the species in the main distributional region, gonad development did not appear directly related to this variable. Growth and sexual maturity should not have been retarded, only increased by such temperatures. However, a failure of gonad development was observed.

C. Parasitic Arrest of Gonad Development

A variety of parasites (e.g. cercaria: Hutton, 1954; nematodes: Russell, 1932a, b) have been found within the trunk cavity of chaetognaths, at times pushing the ovaries away, and Alvariño (1965a) asserts that this would adversely affect reproduction.

In *Sagitta scrippsae,* parasitized by nematodes and trematodes in the trunk cavity, the ovaries showed retarded development. Individuals, more than 40 mm long were only at Stage I of maturity. Parasitic retardation of ovarian development seen in *S. scrippsae* may be related to the paucity of nutrients in the host caused by the parasites. It may be hypothesized, from this cue, that lack of adequate food could be the factor responsible for gonad arrest normally seen in *S. scrippsae* population of the California region.

D. Adaptive Significance of Large Size and Long Life

Marine zooplankters of high latitudes develop more slowly, reach large size, and live longer than related species in warm regions. This is an adaptation of the organisms (Digby, 1954) to low temperatures. Large size and associated low growth and low metabolism may confer advantages on animals enduring periodic food shortages (McLaren, 1966).

Sagitta elegans matures in two years in the Arctic and North Canada, and in one year or less in warmer regions. The newborn, 2 mm in length, appear in the plankton during the seasonal plankton boom, when nauplii of small copepods are abundant (Dunbar, 1962). Three generations of *S. elegans* may be found in the arctic region: newborn and young, one-year-olds (adolescents), and mature two-year-olds.

The complete cycle of development of *Sagitta hispida,* 'from egg to egg', was obtained by Reeve (1970) in the laboratory. Eggs obtained from mature animals, were maintained at 22° to 24°C and 30‰ salinity, and about 3,000 larvae were produced. These larvae developed into juvenile adults in a few days.

E. Annual Cycle and Production

Sagitta crassa, from Japan Inland Sea, produces at least three generations a year: a spring–summer population born in spring and laying eggs in summer, a summer–autumn population with a three-and-a-half-month life span, and an autumn–winter population with a five-month life span (Murakami, 1959). The author thinks that a fourth generation, born in summer and laying eggs in winter, may also be present. Seasonal variations observed in abundance of larvae, adults, and breeding individuals appear to confirm the presence of such a fourth generation. The strongest and the most abundant spring–summer generation develop during the warm period, when food is abundant and the metabolism rapid; the animals reach maturity at a small size, lay eggs, and die. During cold periods, it takes longer for *S. crassa* to reach maturity as the animals grow slowly due to the low rate of metabolism. Factors, such as awailability of food, hormones or other active substances, and temperature, accelerate metabolism *vis-à-vis* sexual maturity.

While studying Chaetognatha populations in the ocean, polymodal curves could be observed: populations structures show a mixture of specimens or populations from different sources and environments converging in the region. Many authors have indicated great variations in size of specimens at the stages of maturity, without realizing that the population they were observing was a mixture of individuals of different environmental origins.

Sagitta hispida, abundant in Biscayne Bay, Florida, was studied in some detail by Reeve (1966). There is a large fluctuation in *S. hispida* population in that region, ranging from 2 per m^3 to about 80 m^3, with at least two peaks of abundance from April to June and October to November. It appears that from approximately May to September, the population remains almost static in size. The high temperature of the summer arrests the development of *S. hispida,* and the population merely survives. *S. hispida* studied experimentally in the laboratory by Reeve (1970), reached maturity in 33 days. Small larvae fed on copepod nauplii, veligers, polychaete larvae, and tintinnids. Larval stage was 0.9 to 4.0 mm long (10 to 15 days old), juvenile stage was 4.0 mm to 6.5 mm (four to eight days old), and adults ranged from 6.5 mm to more than 8.00 mm, when mature eggs were laid.

Sagitta elegans, from Bedford Basin, Nova Scotia, appears to produce two generations a year, one in the spring and another in the fall. The specimens in the population of Bedford Basin reached a maximum length of 27 mm and those of St. Margaret's Bay 32 mm (Sameoto, 1971, 1973). It appears that the fall generation of *S. elegans* constitutes 86 per cent of the total for the year, and the spring generation 14 per cent. Egg-laying begins late in May and increases subsequently as more and more copepods become available in the plankton. The decline in numbers of copepods is the result of increased predation by the newly hatched *S. elegans* larvae. In the Plymouth region (Great Britain), *S. elegans* presented a seasonal size difference: 19.5 to 20.0 mm in May, 13.4 to 14.5 mm in June, 13 mm in July, 10.0 to 10.5 mm in September, 12.0 to 12.5 mm in February, and 16 mm in April–May (Russell, 1932a). Those laying eggs in February were born under higher temperature conditions than those laying eggs in September. Consequently, those developing under high temperature reached maturity early in life and at small size. It is probably also that size attained is conditioned by the food supply. Clarke *et al.* (1943) observed that the *S. elegans* population in the Georges Bank region ranged from 16 to 30 mm. Temperature in the U.S. North Atlantic is similar to that off Plymouth (England). The difference in size of the specimens here is explained by the flow of *S. elegans* from the northern population into the Banks via the Labrador current. Therefore, in the U.S. North Atlantic, there is mixture of indigenous population of *S. elegans* and that from the Canadian waters (Alvariño, 1965a). No such mixing of the populations takes place in the British waters.

Russell (1933b) indicates that *Sagitta elegans* in the English Channel shows two periods of maximum abundance: February and July–September, or March and August–September. *Sagitta setosa* also presented two periods of maximum abundance: April and August–November, or March and August–November. *S. elegans* and *S. setosa* populations reached a maximum in spring and summer, and a minimum during the winter months (Russell, 1932a, b; 1933a, b).

IV. ECOLOGICAL ASPECTS OF REPRODUCTIVE CYCLES

Much work on reproductive cycles of marine invertebrates has been directed towards elucidation of the exogenous proximate factors synchronizing the cycles. However, it should be remembered that the timing of the various models of reproduction is a response to selection pressure, a reflection of environmental conditions favourable for a successful reproduction.

The breeding cycles are so regulated and synchronized with the environment that the larvae hatch at a time when temperature, salinity, and food conditions are favourable. In temperate seas most species breed in spring and summer, when the necessary planktonic food for the larvae is available. Demonstration by Barnes (1957) that diatom blooms induce barnacles to release their larvae is a good example for this kind of close adaptative synchrony.

Conditions in polar seas (Thorson, 1946, 1950) are decidedly unfavourable for planktonic larvae. Low temperature slows down development and reduces the period during which phytoplankton and other foods are available. Most polar species apparently respond to these circumstances by brooding their young (e.g. *Eukrohnia*), and thus avoid unfavourable food conditions during the critical period of larva hatching. In the tropics, where food and other conditions are almost uniformly favourable throughout the year, breeding is more or less continuous (Thorson, 1950). There is scanty knowledge of the ultimate causes of breeding cycles in marine animals. At present, human activities are drastically changing many areas of the world, including the sea, and it is important to ascertain the environmental factors critical to the success of reproduction in the different marine animals.

A. Temperature

Temperature changes in the sea may influence the reproductive activity of marine animals. Sea temperatures often vary rhythmically through the year, not as drastically as on land. Changes in sea temperature might therefore provide marine animals with reliable clues to seasonal changes, and may serve to synchronize their reproduction. Many reviews on the subject are available (Gunter, 1957; Kinne, 1963, 1970). Each species may have a critical breeding temperature (Orton, 1920) which should occur before reproductive activities develop. Species mature at different temperature ranges within their distributional region, and the above statement should apply to the various populations corresponding to the species. How precisely temperature influences various aspects of reproduction, such as gametogenesis, spawning, and breeding, is not known. Receptors in the animals initiate these events, but they have not been identified. Temperature changes influence both feeding activity and general metabolic processes, and consequently influence reproduction by affecting the utilization of nutrients available.

B. Day Length

Day length (amount of light) could be a factor in synchronizing biological events, because it is constant for the same latitude and time of the year. The farther the localities from the equator, the greater the seasonal difference in day length; and in consequence this would be a clue to the animal to determine the season. In the equatorial region, day length is homogeneous through the year, and reproduction is continuous, not restricted to a season or period. However, gametogenesis is generally triggered by hormones, the production of which is influenced by extrinsic factors. It is well known that, under light control, animals produce hormonal substances that trigger the reproductive process (Wells, 1960; see also Brahmachary, Volume IV, Part A, p. 336). In this connection, there is need to consider, in Chaetognatha, the size of the eyes and the thickness and extension of the pigment in them (directly related to the amount of light in the habitat). Deep-water chaetognaths have large ommatidia and only a small amount of pigment, which will permit the bright reception of light. When breeding takes place in the dark, higher temperature is required than when some illumination is provided each day, suggesting that light has some stimulatory influence upon gametogenesis (Barnes, 1963).

C. Salinity

Fluctuations in salinity are not likely to affect reproduction in chaetognaths. This is because salinity changes are not sharp in most regions, except in shallow waters, estuaries and coastal lagoons. Prolonged changes in salinity only occur during rains, flooding of rivers, strong evaporation during dry seasons, and strong tides. Along the coast of India (Cochin backwater), chaetognaths reproduce ten times more frequently than normal during the post-monsoon period in the boundary area between backwaters and coastal waters, an enriched region providing adequate setting for successful reproduction (Nair, 1974). However, in this case, the factor responsible for the productivity may not be salinity, but food concentration.

D. Food

Abundance of food may be important in the regulation of gametogenesis. Seasonal plankton blooms might regulate gametogenesis by making available adequate supplies of food at certain times. This may be the case in temperate regions, particularly the polar seas, where plant production occurs mainly in summer. At least the spring and summer breeding periods of temperate and polar species are correlated to the increase in plant production (Pearse, 1966).

Prolonged starvation, started early in the season, prevents gametogenesis and fertilization in cirripedes (Barnes and Barnes, 1967). Chaetognatha do not store food, as already mentioned (Section III B) and, therefore, are in need of continuous food supply for survival. Gametogenesis seems to be sensitive to levels of reserve nutrients, which, in turn, are dependent upon seasonal fluctuations in quantity and quality of food supplies. In chaetognaths developing at locations of low food supply close to starvation levels, the development of gonads and maturity is arrested; ova may be reabsorbed and only a few elongated thin ova are present in the ovaries.

Chemicals related to changes in quality of nutrient supplies, such as trace metabolites in the food, might serve as synchronizers of reproduction. The chemical composition of many planktonic organisms varies seasonally (Wort, 1955; Jensen, 1969; Rao, 1969) and qualitative nutrient changes may be detected by feeding animals. These changes would serve as proximate exogenous regulators of reproduction. *Sagitta scrippsae* inhabiting the North Pacific Transition region do not reproduce off California (Section III B) due probably to lack of a certain substance in the food supply necessary to trigger maturity (Alvariño, 1962, 1983, and other personal data).

V. CHEMICAL SIGNALS AND MALE RECOGNITION

Metabolites may leak (Giese and Pearse, 1973) from plants and animals to be detected by other animals as exogenous clues, and influence the reproductive activities of other members of the same species or other animals (pheromones). Chemical releases during spawning often stimulate other members of the same or other species, leading to synchronous epidemic spawning (Lucas, 1961; Alvariño, 1989; Hardege *et al.*, 1991).

Chemical signals play an important role in inter- and intraspecific communication. Aquatic animals depend on chemical and mechanical receptors more than on the visual sensory equipment (Mackie and Grant, 1974). Many volatile and odoriferous sex attractants and other pheromones have been isolated in arthropods (see e.g. Hinsch, this volume). In marine animals pheromones have been identified, but, in general, these water-soluble signals are only in trace amounts, and the isolation of pure pheromone is a difficult task. The nuptial-dance-coordinating sex pheromone of some epitokous heteronereid polychaetes is 5-methyl-3-heptanone (see Hardege *et al.*, 1991), a pheromone also found in insects. Chemical interactions in animals of different species deal with chemicals secreted by one species that affect the population of another species (Mackie and Grant, 1974).

Chemical information may be basic in survival of the species. Organisms are dependent on chemicals in their activities of feeding, reproduction, and protection. Living organisms, through metabolic processes, release substances to the environment, chemicals which might serve as clues for predators and partners. Receptor mechanisms in chaetognaths are the corona ciliata and sensory epidermal tufts, and the substances released are specific. Communication for reproduction is necessary in aquatic organisms, which could be specific chemical signals triggering the mating process. The dissemination of the signal and the distance reached have not been determined.

The chemoreceptor cells in the nervous system are directly associated with the secondary neurones, acting as conduction pathways to the central nervous system. The Chaetognatha have a fairly well-developed nervous system, with the unique corona ciliata, a chemoreceptor.

'Female-substances' may induce the passage of sperm into the seminal receptacle annex to the oviduct. In chaetognaths, the ova seem to activate sperm maturation in the seminal receptacles, and the sperm deposited therein, in turn, seem to activate oocyte development. I have never seen chaetognaths with full mature ovaries and no sperm in the seminal receptacle: the absence of sperm in the seminal receptacle may, in fact, arrest the development of the female gonads. This observation also illustrates that mating is an indispensable prerequisite for successful reproduction in chaetognaths: sperm directly from the seminal vesicle are not adequately mature to fertilize the ovum. It is not clear whether a process of sperm capacitation is involved here. More work is needed in this area.

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