12. CHAETOGNATHA

ANGELES ALVARIÑO
7535 Cabrillo Avenue, La Jolla, California 92037, U.S.A.

I. INTRODUCTION

Analyses of the anatomy of the gonads and of changes in their functional features (see Alvariño, Volumes I and II) serve as useful tools to establish the behavioural and physiological aspects of reproduction in chaetognaths. The entire phylum is hermaphroditic. Hermaphroditism is an important character making special demands on the process of sperm transfer and the physiology of reproduction and development.

II. FERTILIZATION

The mature spermatozoa pass from the testes down the vas deferens to the seminal vesicles, and are transferred from the seminal vesicles to the seminal receptacle of another individual during copulation. It was once thought that the sperm were extruded to the water and that they reached the ovary by currents developed by ciliary movement at the opening of the oviducts. This possibility is excluded because there are no ciliary epithelia at the female genital openings in chaetognaths. It was then considered that the transport of the semen was accomplished by approximation of the opening of the seminal vesicles to the openings of the female ducts, and in that way the tail of one specimen would be under the trunk of the other and vice versa.

The chaetognaths do not normally shed spermatozoa freely into the water. There is copulation with transfer of sperm which are stored in the seminal receptacle, a tube attached to and along the length of the ovary (Fig. 1,c; see also Alvariño, Volume II). In the seminal receptacle, the sperm develop to a new stage of maturity. In many animals, series of steps or stages are observed in maturation of the sperm, i.e. from the stage it is formed to the stage it is ready to fecundate the ovum. The series of changes undergone by the sperm is not morphological, but involves their chemistry and cytology. It is considered that the ova, due to the proximity of the sperm, may obtain some organic substances and ions that are related to the activity

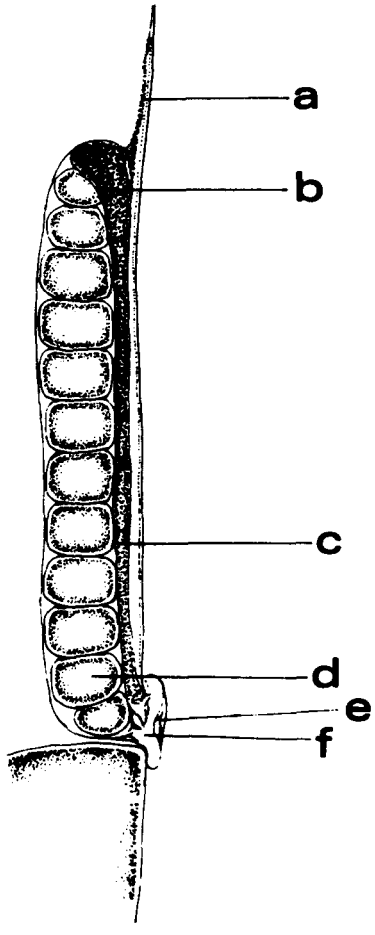

Fig. 1. Diagram of the ovary of a chaetognath (dorso-ventral view). a, Mesenteric conjunctival cord attaching the ovary to the body wall; b, ampulla of the seminal receptacle; c, seminal receptacle; d, ovum; e, vaginal opening (female sexual pore); f, uterus.

and oxygen-uptake of the sperm. This raises some problems concerning metabolism of the chaetognath spermatozoa. Clearly, further critical investigations are required on all aspects of sperm metabolism in chaetognaths, which might allow comparisons with spermatozoa of various invertebrates and vertebrates and on phylogenetic relationships of chaetognaths with other invertebrates.

In aquatic organisms, the output of gametes often achieves prodigious proportions; the animals become gamete-production factories during the breeding season. In chaetognaths, the trunk is almost completely filled with ova, and the tail segment with sperm. Diverse strategies and devices are used by animals to facilitate the encounter of partners and gamete union. They can be grouped into three broad categories: (1) elaboration of chemical agents to attract or trap the male gemetes;

(2) mechanical juxtaposition of gametes; (3) synchronization in production and release of gametes. The most useful and common patterns involve processes belonging to at least one of these categories, and in many cases a high level of efficiency is attained. However, the coupling of gametes involves also some elements of chance. Chaetognatha are hermaphrodite animals, and fertilization is by copulation (see Section III). Cytological, physiological, and histochemical details of the fertilization process are scarcely known. The chaetognaths expend sizeable portions of their biomass in the formation of the gametes, such that most of them die after reproduction.

III. MODES OF INSEMINATION

As outlined above (Section II), in chaetognaths, the spermatozoa are transferred by the vas deferens from the testis to the seminal vesicles where they are stored until copulation. During copulation, the sperm pass from the seminal vesicles into the seminal receptacles of the reciprocal partner. Muscular activity of the gonads may serve to accelerate the entry of sperm and the filling of the seminal receptacle; some chemotactic action may also take place.

Some hormones, secreted probably in the ovary in response to proximity of the sperm stored in the seminal receptacle, may induce oocyte growth and ovulation. Meanwhile, the sperm in the seminal receptacle reach the level of maturity needed to successfully fertilize the ova. The ova, released from the ovary, are carried into the uterus and vaginal cavity by a fluid current and by muscular contraction of the ovary. Fertilization *per se* seems to take place in the uterus or in the vaginal cavity, where opens the seminal receptacle (Fig. 1).

Statements by several authors (e.g. Ghirardelli, 1968) that the sperm pass through fine ducts from the seminal receptacle to the ova, stacked in rows along the ovary, are not accurate. There are no direct communications between the ovary and the seminal receptacle. Adult specimens have always their sperm duct filled with sperm, and no sperm is found inside the ovary proper. The ova do not develop into fertilized eggs while still in the ovary. In other words, no insemination occurs before the ova have been extruded to the uterus and vagina.

Cross-fertilization is the rule in Chaetognatha (Alvariño, 1965a, 1967a; Reeve and Cosper, 1975) though some instances of self-fertilization have also been reported (see Section IIIA below). The male gonads reach maturity earlier than the female gonads, a factor regulating the timing of copulation in these animals. In chaetognaths, the seminal fluid is emitted as a result of stimulation during copulation; only rarely is this discharged directly into the waters. When the sperm come in contact with sea water, the seminal fluid usually coagulates after a short time, and the mass could then be dispersed only with difficulty. Water-borne insemination appears most improbable, since it requires that two processes (viz. unstimulated oviposition and unstimulated seminal discharge) should occur simultaneously. Water-borne sperm in ocean cannot enter efficiently the seminal receptacles in chaetognaths. Under normal conditions, in epipelagic layers, the animals are distributed sufficiently close

to each other with greater chances for encounter and copulation. However, mesopelagic and bathypelagic populations are not so abundant, and under those circumstances some incidental self-fertilization may occur. In *Eukrohnia,* for instance, the dorsal bending and curling of the posterior part of the lateral fins may assist the sperm in their passage from the seminal vesicles to the opening of the ovaries. However, eggs produced without copulation appear to be less viable than normally fertilized eggs.

Specimens of the benthic genus *Spadella,* successfully maintained in the laboratory, have been observed to engage in a behavioural sequence in which copulation occurs. According to Ghirardelli (1968), after a succession of quick movements and pushing, the two animals orient themselves in opposing directions; the seminal vesicles now attach reciprocally to the opening of the oviducts, and the copulating partners fill each others seminal receptacles with sperm.

A. Self-insemination

Self-fertilization appears to be less successful and efficient than cross-fertilization, producing only a small number of normal embryos. Spermatozoa of Chaetognatha are flagellate, but they do not have great powers for swimming, and do not move with great activity in sea water. However, there is a possibility that, aided by water movement, water-borne spermatozoa can effect fertilization at some distance from their point of release, the sperm reaching the seminal receptacle of individuals of the wrong species. But no hybrids have been so far observed in Chaetognatha. In copulating species, interspecific hybridization may be prevented by incompatibility of the genital apparatus.

Ghiselin (1969), who reviewed hermaphroditism in animals, recognized three possibilities in the fertilization process, and only one, the 'classic' low-density model, would apply to chaetognaths. It is evident that the ability to reproduce without the assistance of another animal would greatly increase the reproduction potential of a population of low density and low mobility. But neither of those characteristics would apply to Chaetognatha, abundant animals in the plankton (only second to copepods), mainly at the epipelagic layers, and seldom motionless. Other planktonic carnivores (euphasiids, amphipods) appear less abundant in the ocean than chaetognaths, and those animals are unisexual.

Self-fertilization was mentioned by Reeve (1970a,b) in isolated individuals confined to small dishes. Mature sperm will flow out into and swim about in the surrounding water as the seminal vesicle bursts and some sperm may enter the opening of the oviducts. The fact that this may happen does not imply it is the rule in nature. This is rare in *Sagitta hispida* (Reeve and Cosper, 1975): only 2 per cent of the animals, grown in isolation in small dishes, produced eggs. Self-insemination could nevertheless be more easily artificially induced by breaking open the seminal vesicles. Animals, isolated after they have been inseminated, would only lay one batch of fertile eggs; subsequent batches were nonfertile. These observations suggest that

in chaetognaths self-insemination could provide a short-term survival mechanism in populations temporarily at very low densities. Since the general morphological characters of all planktonic and benthic-hypoplanktonic chaetognaths are similar, it may be expected that they generally resort to cross-fertilization only.

B. Spermatophore

No spermatophores are produced by Chaetognatha. Bundles of spermatozoa may sometimes coagulate to form a ball shortly on contact with sea water, and these have been mistaken by some investigators for spermatophores. Description of the presence of a 'spermatophore' at the region of the corona ciliata, for example by Ghirardelli (1968), and of streams of spermatozoa simultaneously moving caudally is questionable, In nature, it may be recalled, there is a harmonious relationship between anatomy and the mating process, in other words structure and function. What purpose would be served by placing one 'spermatophore' outside the body and releasing sperm free into the water ? It is also not clear why only one 'spermatophore' is produced whereas the animal has two seminal vesicles and two openings of the oviducts to conduct the semen to the seminal receptacle. In chaetognaths, the sperm obviously are passed from the seminal vesicles to fill the seminal receptacle of the recipient, and no sperm have been found stored inside the ovary as such, the tubular organ containing the ova.

In *Sagitta nagae,* a species propagating by cross-fertilization, Nagasawa and Marumo (1978) observed one to four 'spermatophores' attached to the body at the level of the anterior or posterior fins in animals collected at night, but none in animals from daylight collections. In the many hundreds of thousands of chaetognaths I examined (alive and preserved), I have never come across any 'spermatophores', though the seminal receptacles in many instances were indeed filled with sperm. I have also seen agglomerations or bundles of spermatozoa casually attached to various places on the body of the animal, but they were not spermatophores in the true sense of the term.

C. Copulation and Mating Behaviour

Extensive observations have been made by Reeve and Walter (1972b) on copulation and mating behaviour of *Sagitta hispida.* These authors found that two animals became attached to each other by their hoods at the start of the behavioural sequence; their bodies flexed and twisted about each other as they swam upward in spiralling motions, alternating with intervals of passivity and sinking down. The whole performance lasted from a few seconds to about 10 minutes. In about 59 couplings observed (Reeve and Walter, 1972b), the result was consistently that sperm appeared in the seminal receptacle of the animals, and the seminal vesicle in turn was empty.

The presence of peculiar formations on seminal vesicles in chaetognaths is far too constant to be void of any functional significance. These formations may be con-

sidered in some way to be copulatory organs, fitting the female genital orifices, thus making mating impossible between individuals of different species. Differences in morphology of mature seminal vesicles, seen in closely related species, would thus have value as a highly discriminative systematic characteristic.

The inability of various authors to find *Eukrohnia fowleri* or *E. bathyantarctica* with mature seminal vesicles in plankton collections is related to the small number of specimens analysed and to the depth from which the collections have been made. Ripe and full seminal vesicles break off easily, more so in specimens dredged from deep waters such as *E. fowleri* and *E. bathyantarctica*, due to change in pressure when brought to the surface waters.

IV. EGG-LAYING

The ova pass to the lowest part of the ovary, viz. uterus and vagina, where the duct of the seminal receptacle opens and releases the spermatozoa. As the ova reach the vagina they are fecundated by the spermatozoa, a process that apparently takes 20 to 30 minutes. Eggs of species of chaetognaths belonging to the genus of the highest evolutionary rank are probably the best equipped for survival (Alvariño, 1968).

Spadella eggs are laid in clusters of four to 12 or 16, attached to an elastic peduncle over a substratum (Vasiljev, 1924). Secretions from a cement gland form a cuticle over the egg with a stalk at one side, a process that takes about two hours (John, 1933). The eggs, about 0.3 mm in size and enclosed in a thin transparent membrane, are laid, according to John (1933), at low tide to protect them from strong current of the receding waters. Ghirardelli (1968) states laying may happen at any time but Vasilijev (1924) thinks the nights are preferred. In *Eukrohnia bathyantarctica*, eggs are laid into incubatory pouches (also called 'brood sacs' or 'marsupial sacs') at the vaginal opening to the exterior, where the eggs are protected during development. The pouches are also ventrally protected by the bending over of the laminar part of the lateral fins (Fig. 2).

Sanzo (1937) notes the eggs of *Pterosagitta draco* are clumped in a gelatinous oötheca (6.00 mm × 6.04 mm) containing about 200 eggs. I have found these oöthecae, 7.0 mm × 5.8 mm, in plankton samples from California, but with fewer eggs (approximately 50). The jelly substance from which the oötheca is built is apparently produced by the vaginal glands. The oötheca sinks slowly, protecting the eggs from the action of waves, sudden changes in both temperature and salinity, and from predation.

Sagitta hispida eggs are extruded, covered by layers of gelatinous substance, in two linear rows (Conant, 1896) but occasionally may be separated. They do not float and are submerged in the waters. Egg clumps of *S. hispida* and *S. helenae* appear stuck to the wall of the aquaria (Reeve and Lester, 1974; Reeve and Cosper, 1975), merely because of the meniscal physical surface tension. The exact time of laying of eggs appears to depend on temperature, about early in the morning in July but later on during cold days.

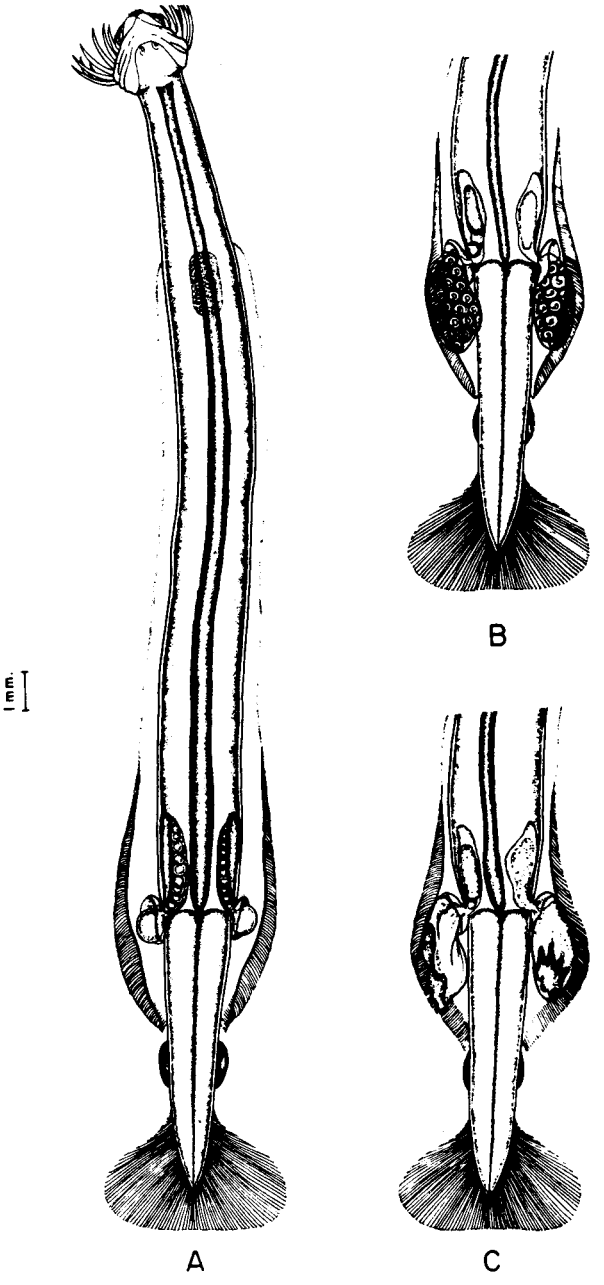

Fig. 2. *Eukrohnia bathyantarctica.* **A**: Complete animal (dorsal view) with incipient marsupial (brood) sacs at the vaginal opening to the exterior. **B**: Marsupial sacs filled with eggs containing embryos in a single coil (Stage III; dorsal view). **C**: Marsupial sacs broken (dorsal view). (From Alvariño, 1968.)

V. DEVELOPMENT

A. Cleavage and Embryonic Development

Cleavage is regular in *Spadella* and *Sagitta* species, where the yolk is uniformly distributed throughout the egg. When a great amount of yolk is present, segmentation is irregular and incomplete, as the yolk generally tends to get concentrated at the vegetal pole of the egg and interferes with the division of the protoplasm at this pole. As a result, the animal pole segments rapidly and the vegetal pole only slowly.

The first few cleavages produce a spherical blastula, with a well-marked blastocoel. The blastomeres are equal and opaque. In *Sagitta,* the blastocoel appears at the 8-cell stage itself, but not in *Spadella* in which the eight-cell-stage embryo is still solid with no trace of a blastocoel (John, 1933). Cleavage proceeds rapidly during the next two divisions. Six hours after laying of the egg, one side of the blastula flattens and invaginates into the blastocoelic cavity. At the end of seven hours, the embryo is a typical gastrula comprising two layers, an outer epiblast and an inner hypoblast. The latter encloses a wide space, the archenteric cavity which opens out by a narrow blastopore at one end. When the embryo is 14-hours old, three areas of the archenteric cavity are clearly seen : germ cells in the middle part of the anterior region, surrounded on either side by the archenteric folds. Some hours later, the two germ cells divide to form four cells, one pair to the right and the other pair to the left of the median line (see Fig. 3).

When the embryo is about 24-hours old, the posterior ends of the two archenteric folds come into contact with each other occluding the opening; the intestine now becomes a closed tube with a narrow lumen, and begins to elongate. The coelomic pouches are separated into right and left body cavity. A small constriction appears at the anterior end of the coelomic sacs and a small ring of mesoblasts is already present at the anterior end of the embryo at about 27 hours; the head is also outlined. Ganglion cells begin to appear, and the embryo starts to curve inside the egg membrane. The embryo elongates, the head becomes thicker and broader, and the tail tapers. In embryos, 35-hours old, the ganglion cells can be clearly observed which multiply rapidly, and the three regions of the body (head, trunk, and tail) are also distinct (Fig. 3). The embryo hatches at the end of about 48 hours as a young 'larva' which resembles broadly the adult: transition to the adult sate therefore involves no metamorphosis.

B. Hatching

The hatching of eggs is a process under the action of various agents and mechanisms. The egg case may be disintegrated by enzyme action; rupture may be due to osmotic swelling of the embryo, by purely mechanical action, or by movement of the embryo (Barnes, 1955).

The first sign of hatching is a slight vibration of the appendages, seen mainly

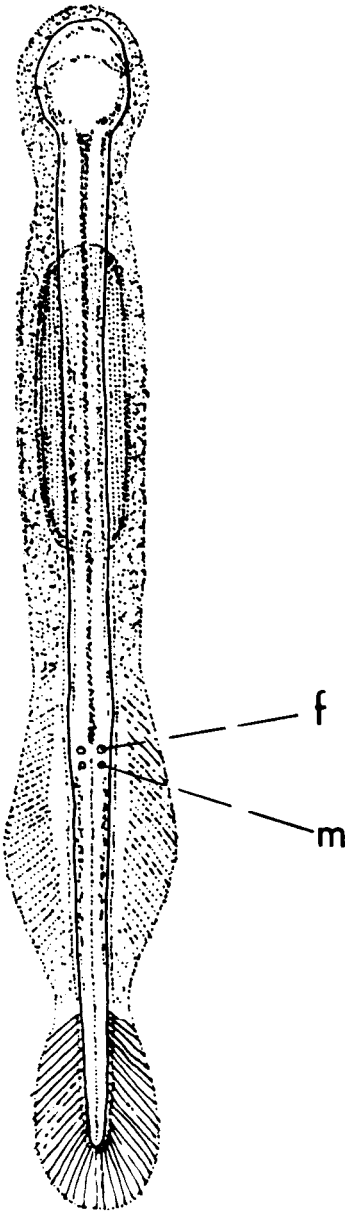

Fig. 3. Diagram of the larva of a chaetognath. The head, trunk and tail are already evident. f, Female germinal cells; m, male germinal cells.

from the ventral side of the embryo. This twitching is first slight but extends later to other parts of the body, resulting in marked flexions of the caudal region and in up-and-down movements of the tail and appendages. The mechanical pressure resulting from these movements produces a distension of the egg case, and eventually leads to its rupture. The larva moves forward by flexions of the caudal sector and usually emerges, head first, with the hooks held close to the sides of the head.

Hatching in *Sagitta enflata* starts with contractions at each end of the embryo, extending to the middle region, producing the effect of uncoiling of the organism, and forcing its tail and head against the egg membrane. The contractions become more pronounced 10 to 15 minutes before hatching, and immediately before hatching, take the form of an uninterrupted series of violent jerking movements.

After hatching, the larvae swim with the same series of darts that characterize the adult chaetognaths. *Spadella* larvae, however, do not swim much; they attach themselves immediately to the substratum by adhesive clusters or palmar devices at the ventral side of their tail.

The two primordial germ cells located in the trunk cavity adjacent to the posterior septum and the other two situated behind are visible soon after hatching. The ovaries develop from the two germ cells in the trunk cavity, and the testes from corresponding cells in the tail cavity.

Immediately after hatching, the alimentary system is relatively undeveloped and the fins are delicate membranes, the whole body being covered by an alveolar epithelium.

C. Larval Development

Development is rapid (at least in warm-water species) at 20° to 30°C. In a few hours the rays of the tail fin are well formed, and those of the posterior part of the lateral fins also appear. The tail fin needs to develop first, as it is the main part in the propulsion system of the animal. In the next few hours, the interstitial tissues of the fins grow progressively from the body wall. the newly hatched animals begin to feed 48 hours after laying of the egg, or within three days.

The 'tangoreceptors', at first few in number, project relatively farther from the body wall, increasing in number while decreasing in relative size to the length of the animal. After several days, the anterior lateral fins in *Sagitta* specimens begin to develop.

Development of *Sagitta crassa* larvae was observed in the laboratory by Murakami (1959, 1966) who noted that lack of adequate food arrested the rate of development.

The major problem in successfully rearing pelagic chaetognaths is the difficulty in obtaining undemaged specimens. Neritic species are better suited for experiments, as they are able to withstand sudden changes in temperature, salinity, and mechanical action than the oceanic species.

Newly hatched two-day-old *Sagitta elegans* larvae (Kotori, 1975) ranged in length from 1.23 mm to 1.42 mm (from the top of the head to the tip of the tail). Only

a pair of the lateral fins, a thick collarette covering the body, and a median vertical septum at the posterior part of the body appear at this stage; the tail transverse septum is absent, and the ventral ganglion occupies about half the length of the trunk (i.e. 23 to 33 per cent of the total length). Seven-day-old larvae (1.69 to 2.20 mm long) have eight hooks at each side of the head and no eyes, whereas in specimens, 2.05 mm and 4.93 mm long, the eyes have already appeared. *Sagitta elegans* larvae, 5.10 mm long, generally have well-defined anterior fins, but according to Kotori (1975), some larvae, 5.20 to 6.45 mm long, still lacked independent anterior fins. Metamorphosis from larva to juvenile takes place at these sizes. In specimens 7.90 mm long, the ovaries begin to appear. The seminal vesicles develop in specimens 18.2 mm long, and become fully mature at 23.9 mm.

1. Stages of development of the larvae

Four stages (I to IV) are described here in development of the larvae of chaetognaths, partly after Kotori (1975):– Stage I: newly hatched larvae, up to the phase when transverse septum (tail-trunk) makes its appearance; Stage II: the stage during which head armature is developed, but eye pigment is absent; Stage III: eye pigment is present; Stage IV: the two pairs of lateral fins have been formed (in *Sagitta* species) but the gonad is yet to be developed.

Stage IV in development of the larvae comprises the beginning of the juvenile period; sexual maturation is marked by the appearance of gonads as small round bodies (female) and thin tubes (male).

2. Evolutionary considerations and the larvae

In *Sagitta,* the larval stage comes to an end as the paired anterior lateral fins appear; in other genera, with no anterior fins, that stage is only indicated by proper development of the particular generic characteristics of the lateral fins. Also at this stage, the beginnings of gonad formation are visible. In *Eukrohnia,* with a long pair of lateral fins, initiation of the juvenile stage is marked by separation of the tail fin from the lateral fins.

Larvae of the genus *Eukrohnia* appear to resemble closely their adults, but less so are those of *Krohnitta, Pterosagitta, Heterosagitta,* and *Sagitta*—in that order.

3. Hatching mechanisms

The emergence of a juvenile animal or larva from the egg membrane or shell is an extremely critical period of its life, as the developing animal is sufficiently protected while within the egg from vagaries of environmental conditions, both biotic and abiotic. The young at hatching time need to remove their protecting covering, and may get damaged and exhausted in the process. Once free, the young rely upon alertness, speed of response, and strength for their survival.

In spite of the importance of the process of eclosion in survival to animals, hatching has been little studied, the observations available often being incidental during the study of other problems. Embryologists should study the nature of egg membranes present at the time of oviposition, but no work of this type has been done on Chaetognatha (see Alvariño Volume I). Though the eggs and embryology of chaetognaths have been described by several investigators, only Murakami (1959) deals with hatching and provides photomicrographs of the different states of eclosion. Obviously, a great deal of investigation is needed, both to ascertain hatching mechanisms in many groups and to check the reliability of the incidental observations that have been reported on the subject. Hatching mechanisms are quite varied among aquatic invertebrates. As far as we know, eclosion from the egg may be strictly mechanical, i.e. by the action of egg buster, hooks, or by non-mechanical means. Possible mechanisms of eclosion include: (1) the bursting of the egg membrane by osmotic intake of water; (2) active uptake of water by the embryo itself, producing an internal pressure that would burst open the egg membrane; (3) action of an enzyme produced by the embryo or larvae, which dissolves all or a limited portion of the membrane; (4) parental help in breaking open the shell or in flushing the embryos out of the broken egg membrane; (5) a combination of the various processes mentioned above (see also Section VI).

4. Larval development and behaviour

The embryo of *Spadella* hatches (John, 1933) in about 48 hours as a yound larva. A few hours before hatching, the embryo shows signs of movement inside the egg membrane. At the time of hatching the egg membrane bursts; the larva wriggles out and straightens itself; and with little further effort sinks to the bottom of the container and tries to adhere to a substratum and crawl.

The eggs laid in a cluster may all hatch at the same time or successively; in any case, all the larvae which come out from the same cluster of eggs adhere to their empty egg membranes for some time. When disturbed they detach themselves from the egg membrane, wriggle for a short distance, and settle back in resting position. Transparent new-born larvae remain in schools and do not move much except when disturbed.

Differences in behaviour of the larvae of *Sagitta* and *Spadella* may be traced back to differences in the life of their adults. Young *Sagitta,* for instance, are transparent, almost invisible, and lie motionless near the surface of the waters. Transparency is a useful characteristic for animals and their larvae with predatory tendencies: unseen by other animals, they can attack their prey. When disturbed the larvae of *Sagitta* swim like the adults. On the other hand, the larvae of *Spadella* have the habit of adhering to surfaces and crawling over the substratum; occasionally they also swim. The adhesive abilities of *Spadella* larvae are essential for survival in the *Spadella* habitat. Adhesion is effected by adhesive capsules or palmate structures developed at the posterio-ventral part of the tail. Corona ciliata, which

may be of vital importance in survival of the animal, appears during the four-day-long larval development.

VI. BREEDING CHARACTERISTICS AND BROOD CARE

Table 1 summarizes the breeding peculiarities of the various genera of chaetognaths (Alvariño, 1968). Nôrdgaard (1905) was the first to describe a brood sac or marsupium in *Eukrohnia* collected at the Vest Fjord from 600–300 m depth; subsequently, Ritter-Zahony (1910) confirmed its presence in specimens of *Eukrohnia,* 30 mm long, collected at 900–750 m depth. Alvariño (1968) described the egg sacs in *E. bathyantarctica. Eukrohnia* species appear to be inhabitants mainly of the deep strata of world oceans and polar regions. Temperatures here are similar to those obtaining

Table 1

Breeding particularities of different genera of Chaetognatha

Genus	Generic characteristics	Breeding characteristics
Eukrohnia	One pair of lateral fins (from ganglion to tail); one pair of sets of teeth	Brood (egg) sac or marsupium
Krohnitta	One pair of rayed fins from tail to the posterior part of the trunk	Probably as in *Eukrohnia*
Heterokrohnia	One set of paired fins from tail to the level of the ventral ganglion; two pairs of sets of teeth	Unknown
Pterosagitta	One pair of paired fins, from tail to the posterior septum; two sets of teeth	Pelagic jelly oötheca
Sagitta	Two paired lateral fins; two pairs of sets of teeth	Free eggs covered by a thick involucrum

in the Bay of Fundy and Gulf of St. Lawrence, but in both localities *S. elegans* only lays free eggs and various stages of their development have been observed by Huntsman and Reid (1921). It appears that the eggs of different species of the most evolved genus, *Sagitta,* are better equipped for survival by virtue of the chemical composition of their vitellus (Alvariño, 1968) or by the nature of the involucrum covering the egg.

It is well known that Arctic animals brood their eggs or provide some other method of protection of the egg until the embryo develops into a large larva or young animal. In this way the larval period is cut short. On the contrary, species inhabiting temperate, equatorial or tropical waters lay only small eggs that produce small larvae. Large larvae with a short larval period are generally obtained only if the eggs

are large or the eggs develop in incubatory folds, sacs, etc. under the protection of the parent. Species of *Eukrohnia* brood the eggs until the young are 3 mm in length (*E. bathyantarctica*: Alvariño, 1968; *E. bathypelagica* identified as *E. hamata:* Dawson, 1968; *E. hamata:* MacGinite, 1955). The sacs are in communication with the respective oviducts by a fine tube.

Alvariño (1967a, 1968) illustrated some pieces of sac-like remnant hanging from the oviduct of *Eukohnia fowleri,* and in 1968 observed specimens of *E. bathyantarctica* from the Antarctic and Subantarctic regions with sacs containing eggs. The brood sacs were of different sizes indicating the eggs within were in different stages of development in different animals. Eggs in the marsupial sac were at different stages of development, ranging from the formation of the blastomeres and various phases of development of the embryos up to the larval stage ready for eclosion. Some sacs were full of larvae already hatched from the eggs. Five stages (I to V) have been distinguished by Alvariño (1968) in the brooding phase:

Stage I : brood sac developing;
Stage II : brood sac filled with eggs developed up to the gastrula stage;
Stage III : brood sac with eggs containing embryos in a single coil;
Stage IV : brood sac with eggs containing double-coiled embryos;
Stage V : brood sac filled with larvae, or broken after the extrusion of the larvae.

According to Ritter-Zahony (1910), brood sacs are not present in the genus *Krohnitta,* but Schilp (1941) noted small membraneous sacs at level with the trunktail septum, in *K. subtilis.* Sanzo (1937) observed the pelagic oötheca of *Pterosagitta draco* containing mature eggs. The gelatinous substance protects both eggs and larvae from the various physico-chemical changes until eclosion. Gelatinous egg clusters measured 6.0 to 6.4 mm in diameter, and the spherical eggs therein 0.40 to 0.46 mm (Figs. 4 and 5).

Species of *Sagitta* lay their eggs free in surface waters (Fig. 6). The eggs are pushed out by ovarian contractions and extruded in two rows, one from each oviduct.

Eclosion and its mechanisms have been briefly described in Section VB and C 3. In many animals, the 'oviducal membrane' is broken by the action of a powerful proteolytic enzyme (protease) reportedly secreted by the embryo at the time of its release (Barnes and Barnes, 1977). In the genus *Eukrohnia* with brood sacs, extracts of the adult could stimulate and synchronize hatching if conditions in the environment are adequate for the survival of the young (presence of phytoplankton and young calanoids).

More information is needed on mechanisms involved in breaking of the membrane of the brood (egg) sacs. The following possibilities may be considered: (1) bacterial activity within the sac cavity; (2) action of some substance released by the adult. If a second cycle of maturity occurs, nutrients will be used for restoration of the gonad and for formation of new gametes, a process that requires a high degree of oxygenation. The egg sac, which receives far too little oxygenation, cannot be sustained and disintegration takes place; (3) action of a substance released by the larvae, or mechanical action of the larvae, eclosed from the egg.

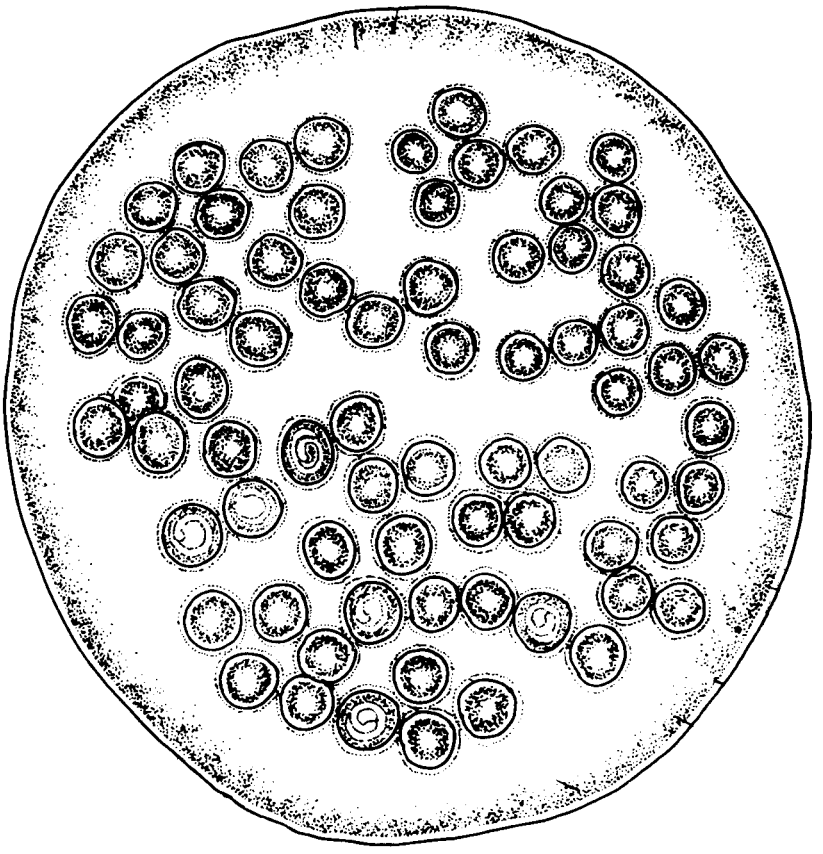

Fig. 4. Jelly oötheca of *Pterosagitta draco*, with eggs at various stages of development up to single-and double-coiled embryos.

Since the breakdown of the brood sac synchronizes with the 'maturity' of the larvae, all the three possibilities may be in action. The larvae may be producing the necessary enzyme(s) to destroy the sac in response to some hatching factor (Barnes, 1957) or stimulation produced by some chemical on the adult; bacterial action may play a part mainly in disintegration of the jelly oöthecae.

VII. SIZE DISTRIBUTION AND BREEDING SEASONS

Environmental factors affecting the breeding seasons are: temperature, illumination, and nutrition. Reproductive phases in many animals are dependent upon corresponding changes in quality and quantity of the food available during their development and life span. The production of plants and the grazing ability of animals are subject to seasonal variations. Most species breed in the spring. Breeding cannot begin earlier than the vernal development of the phytoplankton, the food of small *Calanus*, the primary prey of Chaetognatha.

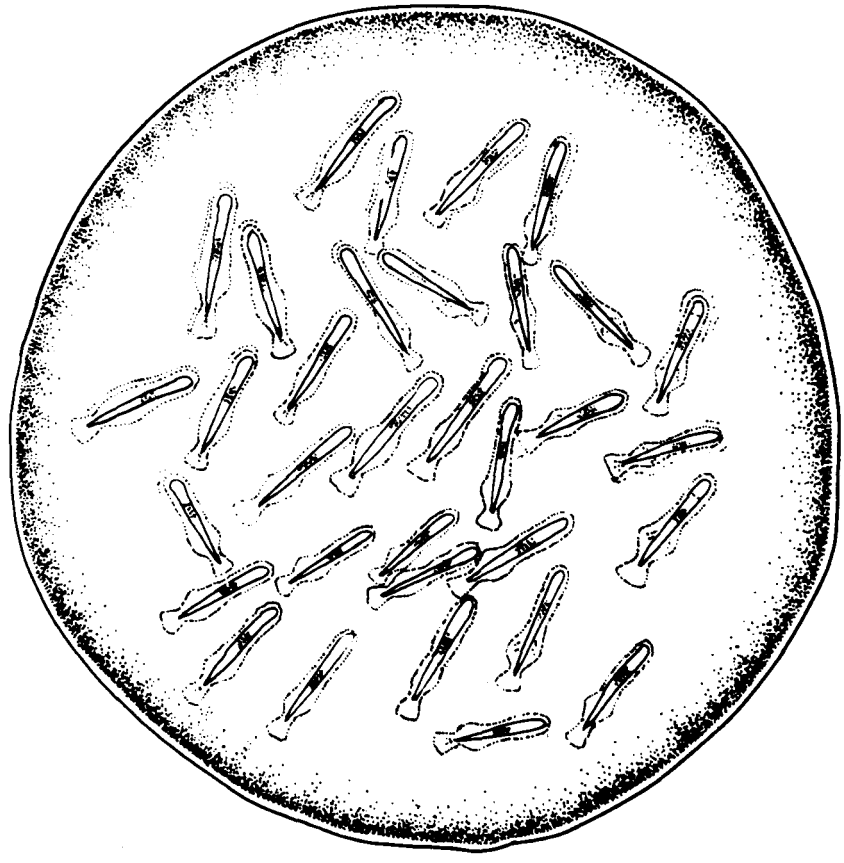

Fig. 5. Jelly oötheca of *Pterosagitta draco*, with hatched larvae.

In species that reproduce all year round, the size of the broods varies with the supply of phytoplankton, on which depend the copepods. However, these variations in carnivorous zooplankters are insignificant when compared with those in herbivorous plankters (population controlled by the predation pressure and food supply). In tropical regions, reproduction is a continuous process along the year.

The breeding season of a species is the period of the year, when most individuals in a population have ripe gametes in abundance, ready to be released, and is usually indicated by months or seasons. In most chaetognaths, there is only one gametogenic cycle in the life of each individual. The gametes may be released all at once, or intermittently during the few days of the season. The extent of the breeding seasons increases from the high to the low latitudes, which is a function of temperature and the quantity and quality of food available. Table 2 indicates the breeding seasons for most species of Chaetognatha, and the regions they inhabit.

Juvenile, immature, and mature individuals all show seasonal trends in their biochemical composition. This indicates that environmental and trophic conditions and changes in gross biochemical composition play a role, more than the seasons

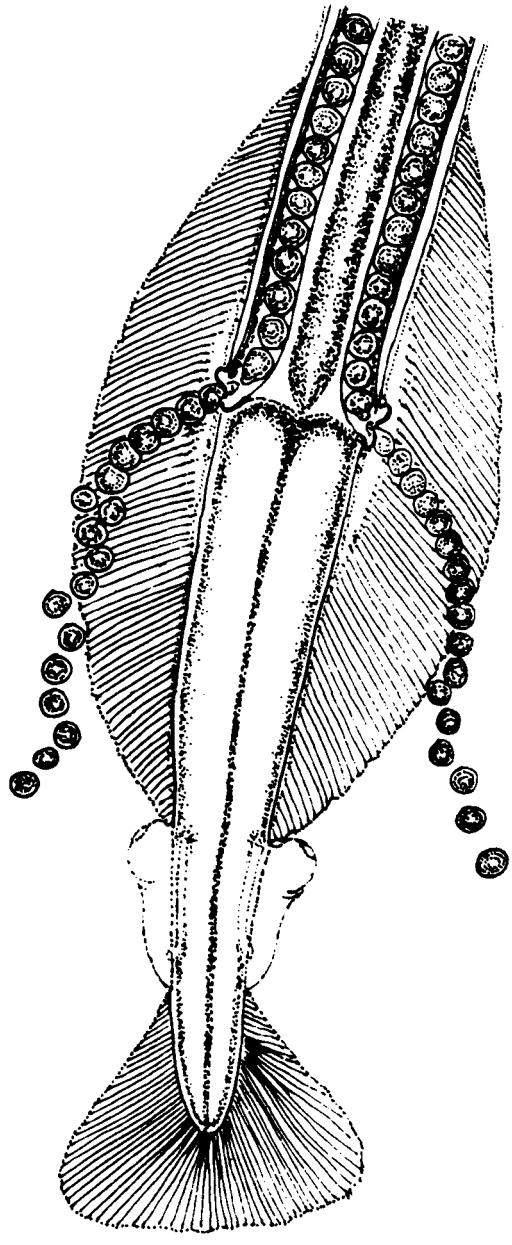

Fig. 6. Free pelagic egg-laying in species of *Sagitta*. The vaginal opening (female sexual pore) is at the dorsal edge on each side.

per se, in determining the breeding cycle. It is not known how the final adaptation timing the cycles, in order that the production of larvae or juveniles is synchronized with periods of favourable feeding, is reached.

Eggs of *Sagitta elegans* were identified in the Bay of Fundy and Gulf of St. Lawrence (Huntsman and Reid, 1921) with double-coiled embryos, in April and

Table 2

Seasons of reproduction of species of Chaetognatha in various oceanic regions

Species	Region	Breeding period	References
Spadella cephaloptera	Marseille	Spring to autumn	Furnestin and Brunet, 1965
	Naples	Spring to autumn	Ghirardelli, 1959
	Roscoff	Spring to autumn	Nouvel, 1935
	Villefranche-Sur-Mer and Naples	All year round, peaks in spring and summer	Vasiljev, 1924
Eukrohnia bathyantarctica	—	—	—
E. bathypelagica	—	—	—
E. fowleri	—	—	—
E. hamata	Greenland	Summer	Kramp, 1939
	Korsfjorden, Norway	April to November	Sands, 1977
E. minuta			
Krohnitta mutabbii	Florida	All year round	Owre, 1960
K. pacifica	Tropic-equatorial Indo-Pacific	All year round	Alvariño, 1965a
K. subtilis	California	Spring to summer	Alvariño, 1967b
	Florida	Summer to winter	Owre, 1960
Pterosagitta draco	California	Spring to summer	Alvariño, 1967b
Sagitta bedfordii	Indonesia	All year round	Alvariño, 1965a
S. bedoti	Tropic-equatorial Indo-pacific	All year round	Alvariño, 1965a
S. bierii	California	January to October	Alvariño, 1967b
S. bipunctata	Central Pacific	January to October	Alvariño, 1967b
	Florida	Late winter to early spring	Owre, 1960
S. bombayensis	Eastern India	March to September	Lele and Gae, 1936
S. bruuni	Gulf of Thailand and South China Sea	All year round	Alvariño (unpubl. data)
S. crassa	Seto Inland Sea	Spring, summer, autumn	Murakami, 1959
	Sea of Japan	February to November	Murakami, 1966
	Yellow Sea	March to October	Murakami, 1966
	Chinhae Bay, Korea	March to November	Park, 1970
S. decipiens	California	Spring to autumn	Alvariño, 1967b
	Florida	Summer, winter	Owre, 1960
S. elegans	Gulf of Maine	Spring and summer	Bigelow, 1926
	Martha's Vineyard to Cape Hatteras	Late Winter to early spring	Bigelow and Sears, 1939
	Basents Sea	Summer	Bogorov, 1940
	Georges Bank, Nantucket	April to September	Clarke *et al.*, 1943
	Chesapeake Bay	Late winter to summer	Cowles, 1930
	Delaware	February to May	Deevey, 1960
	Baffin Island, Labrador	June to October	Dunbar, 1941
	Eastern Canadian Arctic	July to December	Dunbar, 1962

Species	Region	Breeding period	References
S. elegans	Woods Hole	March to September	Fish, 1925
	Bering Sea	June to September	Heinrich, 1962
	Eastern Canada	Spring and summer	Huntsman, 1919
	Bay of Fundy, Gulf of St. Lawrence	April to October	Huntsman and Reid, 1921
	Oslofjord	April to September	Jakobsen, 1971
	Greenland	April to September	Kramp, 1917, 1939
	Sagami Bay, Japan	Brought into the area in spring-summer	Marumo, 1966
	North Sea	April to October	Meek, 1928
	Korea	Early spring	Park, 1970
	Irish Sea, Port Erin	January to May	Pierce, 1941
	Gulf of Maine, Georges Bank	Spring and summer	Redfield and Beale, 1940
	Plymouth (Great Britain)	March to September	Russell, 1932a
	St. Margaret's Bay, Nova Scotia	April to September	Sameoto, 1971
	Gulf of Maine	Spring to fall	Sherman and Schaner, 1968
	Eastern Greenland	February to June	Ussing, 1938
	Norwegian Sea	April to May	Wiborg, 1955
	Bedford Basin	Spring to autumn	Zo, 1973
S. enflata	Iberian Atlantic	Most of the year	Alvariño, 1957
	California	All year round	Alvariño, 1967b
	Mediterranean	All year round	Furnestin, 1957
	Miami	March to August, November to January	Owre, 1960
	Kaneohe Bay, Hawaii	All year round	Piyakarnchana, 1965
	Southeast Australia	Most of the year	Thomson, 1947
S. euneritica	California	All year round	Alvariño, 1967b
S. euxina	Roumanian Black Sea	November to May	Elian, 1960
S. ferox	Tropic-equatorial Indo-Pacific	All year round	Alvariño, 1965a
S. friderici	Iberian Atlantic	All year round, peaks in spring-summer	Alvariño (unpubl. data)
S. gazellae	Antarctic-Subantarctic	Spring and summer	Alvariño *et al.*, 1978
	Antarctic-Subantarctic	Late March to autumn	David, 1955
S. helenae	Miami	Spring	Owre, 1960
	Florida	All year round	Pierce, 1951
S. hexaptera	California	Spring-summer	Alvariño, 1967b
	Indonesia	All year round	Schilp, 1941
S. hispida	Miami	April to December	Owre, 1960
	Gulf of Mexico and Florida	All year round	Pierce, 1951

Table 2 (*Contd.*)

Species	Region	Breeding period	References
S. hispida	Biscayne Bay, Florida	November to May	Reeve, 1966
	Biscayne Bay, Florida	All year round except in summer	Reeve and Walter, 1972a,b
S. johorensis	Indonesia	All year round	Alvariño, 1967a
S. lyra	Miami	May to February	Owre, 1960
S. macrocephala			
S. marri			
S. maxima	Greenland, Davis Strait, Uyanak Fjord	Spring and Summer	Kramp, 1917
	Greenland	Summer to autumn	Kramp, 1939
S. minima	California	Spring and summer	Alvariño, 1967b
	Florida	Spring to autumn	Owre, 1960
S. nagae	Suruga Bay	April to September	Nagasawa and Marumo, 1978
S. neglecta	Tropic-equatorial Indo-Pacific	All year round	Alvariño, 1967a
S. oceania	Indonesia, S.E. Asia	All year round	Alvariño, 1965a
S. pacifica	California	Spring and summer	Alvariño, 1967b
S. peruviana			
S. planctonis			
S. popovicii			
S. pseudoserratodentata	California	Spring and summer	Alvariño, 1967b
S. pulchra	Tropic-equatorial Indo-Pacific	All year round	Alvariño, 1965a
S. regularis	Tropic-equatorial Indo-Pacific	All year round	Alvariño, 1965a
S. robusta	Tropic-equatorial Indo-Pacific	All year round	Alvariño, 1965a
S. scrippsae	California	Spring to autumn	Alvariño, 1967b
S. septata	Indonesia, S.E. Asia	All year round	Alvariño, 1965a
S. serratodentata	Delaware	Summer to autumn	Deevey, 1960
	Miami	All year round	Owre, 1960
S. setosa	Villefranche-sur-Mer	Spring and summer	Dallot and Palazzoli, 1976
	Roumanian Black Sea	June	Elian, 1960
	Irish Sea, Jersey Channel	April to August	Pierce, 1941
	Plymouth, Great Britain	February to October	Russell, 1932b
	North Sea	March to September	Wimpenny, 1937
S. tasmanica			
S. tenuis	Florida	All year round, except probably October	Pierce, 1951
S. tokiokai			
S. zetesios	West Greenland	May	Kramp, 1917

May, but disappeared in the middle of June. Their Stage I eggs (up to gastrula) decreased progressively and Stage III (double-coiled embryos) increased until the eggs all disappeared. Small *S. elegans*, 2 mm long, appeared at the end of May and were still found up to the middle of June; by July the smallest were 7 mm long. The sudden disappearance of the eggs in June coincided with an abrupt decrease in the number of adults in plankton hauls. The breeding season of *S. elegans* in the Bay of Fundy (Huntsman and Reid, 1921) appears to be long in so far as eggs have been found in the plankton from April to October. Stages I and II eggs (gastrula to single-coiled embryo) seem to be equally abundant at surface and at 5–7 m depth. There is some indication that Stage III eggs (double-coiled embryo) reach deeper layers than those sampled. The young are more widely distributed in the Bay of Fundy than the adults, and more abundant in the estuaries than in the open Bay.

Sagitta elegans spawns over a long period in the Canadian Eastern Arctic (Dunbar, 1962), from July into winter, probably February. Winter breeding implies that this process is not timed to coincide with maximum abundance of food; the cycle is determined by growth limitations imposed by low temperature that slows down metabolism. In Korean waters, the size composition of *S. elegans* in larger in winter than in other seasons, the mature individuals constituting as much as 40 per cent of the samples (Park, 1970). The main period of reproduction is early spring. *S. elegans* begins to breed early in St. Margaret's Bay, Nova Scotia (Sameoto, 1971). The first eggs appear in the samples in May, and the maximum size of the animals decreases from 32 mm to 30 mm in April. The reduction in length is due to breeding and brooding activities of the large animals: the laying of eggs continues into late July.

Table 3 from Sameoto (1971) gives useful data on spawning and maturity and

Table 3

Relationship between life span and mean ambient temperature in *Sagitta elegans* (modified from Sameoto, 1971)

Date of birth	Date of maturity	Life span in days	Mean water temperature	Degree/days*
7 October 1968	1 May 1969	206	4.2°C	865
25 October 1968	15 May 1969	200	3.8	760
25 November 1968	1 July 1969	219	3.6	788
15 December 1968	15 July 1969	213	3.5	745
15 April 1969	1 September 1969	142	5.2	738
1 May 1969	15 September 1969	137	6.1	866
15 May 1969	9 October 1969	147	6.8	1000
1 July 1969	25 October 1969	115	7.4	851
15 July 1969	26 November 1969	133	8.1	1077
1 September 1969	5 December 1969	95	9.0	855
15 September 1969	12 December 1969	91	9.1	822**

*Total temperature the animal has been exposed to during the life span;
**See text for discussion.

the relationship between the length of the life span and temperature of the waters in *Sagitta elegans*. It may be noted that the population born on 15 September 1969 and exposed to 822 degree/days, matured by 12 December 1969 and ceased to grow further; some of their offspring in fact could receive only 549 degree/days (Sameoto, 1971). Therefore, this overwintered population had not matured and it was the first to breed in 1970. This provided the clue to determine the minimum degree/days needed by *S. elegans* to reach maturity. Low mean temperatures, during the development of the animals, increased the length of the growing period and the time to reach maturity (Table 3).

Several chaetognaths, including, *Sagitta elegans*, have been long used as indicator organisms of water masses (Russell, 1932 a,b, 1936; Alvariño, 1965 a, b). The knowledge that *S. elegans* needs a minimum of 738 degree/days to reach gonad maturity (Table 3) is used as a base to calculate the length of the life cycle as a function of mean water temperature. The length obtained at maturity and the time of breeding of *S. elegans* will provide a useful clue to the temperature of the waters inhabited by it and in identifying the water masses in which it originates (Sameoto, 1971).

VIII. SUCCESS OF REPRODUCTION AND GROWTH

However, in these estimations (Section VII), the kind of food and their availability were not considered. Long-term studies have shown that a relationship exists between the size of the copepod (or other prey) population and that of *Sagitta elegans* population. In coastal waters of the Gulf of Maine (Sherman and Schaner, 1968), this species has a prolonged period of breeding, from late spring through the autumn. The abundance of specimens at Stages I and II of maturity suggested that no significant breeding occurred in winter. *S. elegans* in this region has only one breeding period per year.

The number of generations produced in a year obviously varies with the species, but is also correlated with the environment. Generally, the number of generations produced by a species in a year, increases with the distance from the poles (Owre, 1960). Thus *Sagitta elegans* (Ussing, 1938; Kramp, 1939; Alvariño, 1965a) reproduces once a year in the Arctic and Subarctic regions. *S. gazellae* also breeds likewise only once a year (David, 1955) with abundant reproduction in spring (Alvariño *et al.*, 1978). *S. elegans*, however, reproduces two or five times a year in the north Atlantic while at Port Erin (Pierce, 1941) only once from January to May. In the North Sea (Wimpenny, 1937) and off Nantucket and Georges Bank, there are two breeding periods, one in spring and the other in autumn (Clarke *et al.*, 1943). Differences in length among specimens in fully mature stages have been related to variations in temperature in the course of the year, the longest individuals being found in the colder periods.

The life cycle of *Sagitta elegans* off Plymouth, according to Russell (1932 a,b, 1933 a,b), is completed in 43 days, based on which he suggests five generations

could exist each year in the waters of south England. The reproductive cycle of *S. elegans* in the eastern Canadian Arctic has been studied by Dunbar (1941, 1962), who observed that this species has a life span of two years. The spawning period is long, lasting from July into autumn and winter. The breeding cycle is two-phased or alternating in the species population, such that three size-structure populations appear together during the breeding seasons. The smallest may be the offspring of the largest; the intermediate-size population (adolescent group), born the previous year (one-year old), will breed the following year (Dunbar, 1962). The breeding cycle is determined by the slow growth rate at low temperature, to which there has been no adaptation. The young are born during a period of maximum abundance of food.

Hydrographical differences, though not great, are nevertheless reflected in the biology of *Sagitta elegans* from the Arctic and Atlantic waters. This seems to be of some importance in deciding the timing of sexual maturity. In the specialized environment of Ogac Lake, which is warmer than the proper Arctic, the growth rate is rapid and the breeding cycle single-phased; or it could be alternating as in cold waters. In any case, maturity is reached at half the body length required for cold-water animals (Dunbar, 1962).

Environmental factors also have a great influence on the size of the individuals and their life span. In extreme cold waters, for instance, zooplankton organisms only develop slowly, but reach a large size, and live longer than related species in warm waters (McLaren, 1966). It is believed that generation length in the Arctic is determined by marked seasonality of food supply, corresponding to high fecundity, large size of the individuals, and slow development.

Sagitta gazellae, an Antarctic-Subantarctic chaetognath, grows 5 mm per month (David, 1955) during winter and spring, but faster in summer. The life cycle appears to last one year, and the animal reaches 60 mm in 10 or 11 months (David, 1955). In this connexion, a comparison of the length at which sexual maturity is attained by *Sagitta* species in the Arctic and Antarctic regions would be of interest. *S. elegans* from the Arctic reaches maturity in two years at a length of 30 mm, whereas *S. gazellae* from the Antarctic region does so in one year at length of 90 mm. If these data are reliable, the reported difference between the two regions may be related (to species differences apart) to differences in the quality of food supply and to the quantity and quality of hormones and trace elements favouring accelerated development and growth. This could be put to better test by studying the development of populations *Eukrohnia hamata*, a species common to the Arctic and Antarctic. In Korsfjorden (Norway), *E. hamata* reaches its maximum length during the first year of its life (Sands, 1977), and sexual maturity develops during the second year. The positive correlation between weight and lipid proportion, found for autumn and spring populations, reflects the differences in lipid content between the juveniles and the slow-growing maturing animals. *E. hamata* breeds from spring to the end of autumn in Korsfjorden, with peaks in May and October–November (Sands, 1977).

Sagitta crassa, in the Sea of Japan, has three alternating main breeding periods: February–March, May–July, November–December. The period from laying of eggs to hatching changes with water temperature and chlorinity. A minimum of 15 hours was recorded at temperatures above 27°C and an optimum chlorinity of 17–18 per cent salinity of 31–33%. This species breeds in Chinhae Bay, Korea from March to April and from July to October–November (Park, 1970). In the Yellow Sea, breeding occurs during May–October, especially in July and August. Several generations of *S. crassa* show phenotypic variations: for instance, type C with large collarette is adapted to sudden changes in temperature and salinity, type N (with collarette mainly at neck) prefers waters of high temperature, and type I is intermediate in nature (Murakami, 1966). In Biscayne Bay, Florida, *Sagitta hispida* presents only one breeding season extending from November to March; this is followed by a period of summer inactivity; a period of rapid growth and maturity starts again in the new generations (Reeve, 1966). In species with only one maturity cycle, mixed populations are common due to flow of recruits from other areas. Fluctuations in *S. hispida* populations appear to be related to fluctuations in abundance of food: when the number of adult copepods increases in October, the population of *S. hispida* shows a significant gain in size, maturity, and abundance.

Sagitta enflata exhibits marked polymorphism in relation to stages of maturity and size (Alvariño, 1963a; Piyakarnchana, 1965). Furnestin (1975) thinks two cycles of maturity may occur in the Mediterranean populations; in tropical Atlantic, three or four could be attained. In the Indian Ocean, Rao and Kelly (1962) observed variations in size of this species during the year, larger sizes coinciding with abundance of copepods. In the Agulhas Current, specimens of *S. enflata* from neritic waters generally contained more ova than from oceanic waters (Stone, 1966). This difference may be advantageous in producing sufficient reproductive potential in maintaining populations over a wide range of variations in physical and biological parameters.

Spadella cephaloptera reaches maturity in two months, and it is uncertain if specimens born in autumn overwinter, retiring to the bottom (Ghirardelli, 1959, 1960, 1963). Furnestin and Brunet (1965) at Marseille, Nouvel (1935) at Roscoff, and John (1933) at Plymouth, have confirmed that *Spadella* lie concealed in the bottom silt during the winter months, and that the ones collected in winter are smaller than those collected in spring. *Spadella* living in the prairies of Posidonia show a direct correlation between body growth and number of ova, and the environmental conditions. In both spring and summer, the populations grow fast by producing a large number of eggs

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