

8. CHAETOGNATHA

A. ALVARIÑO

*National Marine Fisheries Service,
Southwest Fisheries Science Center,
8604 La Jolla Shores Drive,
P.O.Box 271, La Jolla, California 92038-0271, U.S.A.*

I. INTRODUCTION

Asexual propagation does not occur in chaetognaths. When a chaetognath is broken, regeneration occurs only of the part that includes the head and the ventral ganglion. If the head is missing, the ventral ganglion assumes the direction of the regenerative process. However, there is no production of other individuals, only a regeneration of the missing part of the animal.

II. REGENERATION

Few experiments have been conducted on regeneration in chaetognaths. Kulmatycki (1918) and Ghirardelli (1968) found that *Spadella cephaloptera* could regenerate the whole caudal section, and *Sagitta helenae* and *S. enflata* the head (Pierce, 1951).

In animals there appears to be a close correlation between regenerative power and the stage at which segregation of the germinal line occurs (Ghirardelli, 1968). Animals with precocious determination of the primordial germ cell have usually limited regenerative ability, insufficient for the reconstruction of complete new individuals from a portion of the body, and they cannot regenerate important and large portions of the body. They also lack the power of asexual reproduction by fission or budding (Ghirardelli, 1956, 1959a). In Chaetognatha, segregation of the germinal-line determinant occurs early in development of the egg (see Alvariño, Volume IVB of this series). Deficiency of regenerative power seen in chaetognaths is shared by animals with RNA-rich ova, a characteristic associated with absence of asexual reproduction (Ghirardelli, 1959b, 1965). Different animals of analogous evolution (e.g. Rotifera, Cladocera, Copepoda, Chaetognatha, Anura Amphibia) do

not have the totipotent, or at least pluripotent cells which constitute the so-called embryonic reserve (Ghirardelli, 1968). Based on these observations, Ghirardelli (1958) stated that the regenerative ability of chaetognaths could not be as marked and effective as claimed by Kulmatycki (1918) and Pierce (1951).

Ghirardelli (1968) performed experiments on *Sagitta enflata* and *Spadella cephaloptera* from Villefranche-sur-Mer and the north Adriatic Sea, by cutting the animals at various levels of the body. Regeneration of the caudal fin is always rapid (from two to four days) if the posterior part of the body is not damaged. Epithelial cells in mitosis migrate towards the wound, and reconstruct the fin rays (Ghirardelli, 1959a). The lateral fins may be regenerated in seven to 10 days. The caudal region, if sectioned at a level *anterior* to the seminal vesicles, does not regenerate. The sectioned muscles fold in a scar made of alveolar stratified epidermis, reminiscent of an epithelial collarette. In some cases, the lateral fins fold towards the wound and fuse with the midline of the body, and there is no formation of seminal vesicles in the wounded caudal coelom, although normal development of the sperm proceeded. In such animals the sperm, however, cannot be extruded due to want of seminal vesicles. Therefore, no new cycle of male gametes would be possible as implied by Kulmatycki (1918) and Pierce (1951). On the contrary, if the cut passes through immediately *behind* the seminal vesicles, only a rudimentary regeneration of the caudal fin occurs.

Ghirardelli (1958) obtained regeneration of the caudal fin of *Spadella cephaloptera* beheaded immediately after amputation of the posterior end of the body, 56 per cent fin regeneration in decapitated animals against 36 per cent in those not decapitated. This may suggest that the presence of the head inhibits the regenerative process of the caudal fin, and that regeneration is only possible via the ventral ganglion.

Regeneration of the head does not occur, according to Ghirardelli (1956, 1959a), in *Spadella cephaloptera* and *Sagitta* (probably *S. bipunctata*). However, Pierce (1951) and other authors have observed specimens of *Sagitta setosa*, *S. minima*, *S. enflata*, and *S. euneritica* with heads that are abnormally small, and bearing no teeth or hooks. It is not clear from their accounts if that condition was produced by regeneration or what they saw was only a wounded head. Species of *Sagitta* may be beheaded by predators and, if the amputation occurred at the level of the ventral ganglion or in front of it, a sharp stump could be formed with histological features of a scar. This would indicate a lack of differentiation and of the regeneration process. Duration of the regeneration process and the chances of survival of the wounded animal are not known. The stumpy head is more rounded and the eyes can be seen, and there is doubt whether it is a case of true regeneration or only one of repair of a lesion on the cephalic region.

Pierce (1951) indicated that *Sagitta helenae* and *S. enflata* found with their heads cut off, together with a short section of the trunk, were at various stages of head regeneration. This condition was first attributed to accidental damage encountered in the net, but analyses of plankton samples have shown many specimens at

various degrees of head regeneration. No regrowth of the posterior part of the body and tail was found. After the loss of the head, the trunk tissues contracted tightly together at the wounded end, giving the appearance of a sausage. The head began to form inside the contracted end, the eyes appearing first, followed by the mouth and the hooks (Alvariño, 1965).

Pierce (1941) stated that although he had examined hundreds of *Sagitta setosa* and *S. elegans* from the northern latitudes, no evidence of head regeneration was observed in these species.

Ghirardelli (1959c) reported young chaetognaths, probably *Sagitta bipunctata* and *S. enflata*, showing the beginnings of regeneration of the head. I have observed regeneration of the head in *S. elegans*, *S. enflata*, *S. euneritica*, *S. pacifica*, *S. neglecta*, and *S. pulchra* (Alvariño, unpublished).

III. PARTHENOGENESIS

This form of reproduction has not been investigated in chaetognaths. However, laboratory experiments with isolated individuals (Reeve, 1966), in which no copulation would occur, have shown that bursting seminal vesicles ejected sperm to the water, some of which would enter the receptaculum seminis. Only a few extruded ova were fertilized and those produced larvae, while the unfertilized ova invariably degenerated. It could therefore be assumed that parthenogenesis proper does not occur in Chaetognatha.

IV. FECUNDITY

The fecundity of *Sagitta elegans* has been calculated (McLaren, 1963, 1966) by setting ovary length against body length, and in turn relating the number of ova to ovary length. It appears that egg production by *S. elegans* is the function of adult size. The brood size is the result of the number of eggs produced by a functional female population. Egg number is equivalent to the number of ova carried by the parent, and it is a function of the size of the animal and the capacity of the ovary filled with ova. Comparisons must be made between animals of the same size, if a calibration were to be set up between parent size and egg number. The standardized number of eggs may then be used to compare the reproduction potential of a given species under different environmental conditions, within a restricted locality or over various areas in the wide distributional region of the species.

Breeding may be restricted to one or several seasons, or a succession of broods may be produced, as in *Sagitta enflata*. Therefore, simply put, the rate at which eggs are produced will be termed 'fecundity'. The number of eggs produced per standard animal per species per unit of time (season) could be determined. Different species reach various adult sizes, in each of which the number of eggs is a function

of the size of the animal. Fecundity can thus be defined as 'the number of eggs produced per individual per species and geographic location'.

Determination of the number of ova is easy in chaetognaths, the animals being transparent. The number of ova can be plotted against standard body weight or body length. Variability within species, time of year, and locality and over the years can so be observed. Differences are likely an expression of long-term cyclical fluctuations in reproduction level from year to year, related basically to food supply. Such differences and annual variations in egg production may be of importance in competition and dominance of chaetognath populations. The number of ova produced by chaetognaths is usually higher in 'poor' areas and in species living under stress (e.g. bathypelagic and cold-water species). Small numbers of ova—flat, elongated, and scattered along the ovaries—are observed in tropical populations carried out of their normal environmental living areas because of either scarcity of food or infestation with parasites (e.g. *Sagitta bierii* off Central American Pacific, *S. bedfordii* in some Indonesian locations). This confirms that food supply is a basic factor in the success of reproduction in chaetognaths as in many other animals. The number of ova in epipelagic populations is related to the size of the population: in large populations, the number of ova produced could be lower than in small populations.

To compare relative reproductive efficiency, there is a need to take into account the metabolic process, the number and size of eggs produced, and the time required for the production and hatching of eggs. Certain species can withstand severe climatic conditions advantageously by a marked seasonal breeding period, and by production of a relatively small number of large eggs. However, the same annual cycle could be maintained with a relatively large number of small eggs, leading to greater fecundity, and consequently greater competitive power. Large eggs produce larvae which are almost as large and as advanced in development as the juveniles—strong, able to feed, and better suited to survive.

V. STERILITY

Sterility, or poor reproductive ability, of *Sagitta scrippsae* off California (Alvariño, 1983) appears to be related to lack of adequate food to provide for the development of the gonads. *Sagitta bierii* inhabits the eastern Pacific from the United States to Chile, but populations off Central America do not seem to reproduce there due to high temperature and/or lack of the right kind of food in the area; the animals are all small with few flat ova (Alvariño 1964b, 1965, 1967). This observation leads us to suggest that *S. bierii* of Central American Pacific are likely descendants of specimens inhabiting the north and south of the region, mainly from the California- and Peru-Currents domain of the species (Alvariño, 1965, 1967). How higher temperatures can inhibit breeding is illustrated by *S. hispida*, a species unable to breed in the Biscayne Bay during the high water temperature of the summer.

Parasitism is another cause of arrest in gonadal development of chaetognaths, at least in some areas of the world: e.g. Gulf of Siam (*Sagitta bruuni*, *S. bedoti*, *S. pulchra*), the Caribbean (*S. enflata*), the Mediterranean (*S. enflata*), and off California mainly in the neighbourhood of Los Angeles (Alvariño, unpublished; and *S. scrippsae*: Alvariño, 1983). A high percentage of Chaetognatha here are infested with parasites (trematodes, cercarias), a strong indication of man-made pollution.

VI. REPRODUCTIVE CYCLES AND STRATEGIES

In *Sagitta friderici*, there is only one reproductive cycle, at the end of which the animals die (Cavaliere, 1963). Studies of abundance, distribution, and seasonal reproductive cycles of *S. elegans* indicate a life span of three months in Georges Bank (Clarke *et al.*, 1943); the animals die soon after breeding. In Georges Bank there is only one main breeding period per year. However, two populations of *S. elegans* may coexist there at least during part of the year, one indigenous to the area, and the other carried south from northern waters with the Labrador Current. Therefore, a wide size-range of maturity stages is encountered for *S. elegans* in the American North Atlantic. In the Georges Bank area, reproduction of *S. elegans* generally starts in April. Stage I animals present in September may represent the end of the spring and summer reproduction; those overwintering will produce a new generation next spring.

Two generations of *Sagitta elegans* were found in Bedford Basin by Zo (1973) with different life-history tactics: a spring generation which reached maturity in mid-September and reproduced during the rest of the year and an autumn generation (born from the spring generation) which apparently overwintered and reproduced during the next spring. Most of the young developed to maturity between June and September. This suggests that the successive hatching of eggs in spring provides a continuous recruitment of adults. The autumn generation, i.e. animals hatched during the autumn-winter period, grow slowly and reach maturity in the spring with increase in temperature and food availability. The larvae measure 1.28–1.30 mm. Autumn adults developed at 3.8°C have a mean length of 19.7 mm, while spring adults developed at a mean water temperature of 2.3°C are more than 25 mm long.

Sagitta enflata, which is abundant in temperate and tropical oceanic waters and has also invaded neritic regions, is probably the only epipelagic chaetognath to resort to the tactics of multiple cycles of maturity during its life span. As a result of this, the fecundity reaches a high level and the population becomes large and agglomerated in space leading to severe competition for food among the individuals. *Sagitta enflata* is also the chaetognath presenting the highest degree of cannibalistic behaviour, a possible regulator of population size.

Uninterrupted reproduction takes place in tropical and subtropical chaetognath populations; the rate of survival of the fall generation, however, is higher than that of the winter generation. Breeding index in the tropics is not constantly maintained

through the year, and variations in density of the populations result from biotic and abiotic changes in the environment. Neritic species inhabit a region of drastic environmental fluctuations along the year, and consequently they show greater variation in density of population than oceanic species distributed over wide ranges. *Sagitta euneritica*, off California, exhibits great seasonal variation through the year (Alvariño, 1967). In species studied over a wide latitudinal range of their distribution, such as *S. bipunctata* and *Pterosagitta draco*, reproduction occurs throughout the year in the tropics, but only in spring and summer at temperate locations. This means that the reproductive span shortens coincidentally with the termic variations, which also affect changes in the food supply.

Annual breeding seasons are common to both Arctic and Antarctic regions. A large proportion of polar species brood their embryos and larvae (e.g. *Eukrohnia*) and release them as juveniles, when food is available. In species inhabiting deep waters, maturity takes place once a year as in polar species, but their life span may include, at least occasionally, several maturity cycles.

A. Reproductive and Developmental Delays

One mode of ensuring optimum reproductive and developmental success for a species is by temporally scheduling these processes to take place when conditions for survival of the progeny are favourable. Coming to strategic delays in reproduction and development, in *Eukrohnia*, 'diapause' in development of eggs and larvae may be regulated to favour hatching process at the right time for survival of the species as we have just seen above. Overwintering population of *Sagitta crassa* delay reproduction until food is plentiful for the larvae. Russel (1936) suggested that normal delay in development of gonads of late summer broods of many planktonic animals, including chaetognaths, is frequently accompanied by a descent of that population to deep strata, provoked by the removal of some essential factor "from the water during the summer, which becomes available again after a period of time or is perhaps lacking in the diminishing food supply". The significance of carotenoids, vitamins, and related substances in the plankton has only been tentatively investigated, but it is known that the carotenoid, vitamin and sterol constant varies greatly, not only in relation to the plankton but also to the season. Carotenoids and vitamin A within the plankton (Gillam *et al.*, 1939) begin to rise just about or at the spring diatom peak, the maximum being during the autumn. The peak coincides with the main breeding period of the plankton (Lucas, 1947).

It is well known that water-borne metabolites may influence reproduction. The conditioning of the environment through external products may bring about community integration through adaptation of animals to the products of others. The production of certain compounds may be related with reproduction of planktonic animals and induce particular stages of their life history. Local concentration of such compounds might tend to stimulate the development of maturing animals and the fertilization of eggs (Alvariño, 1989). Carnivores do not

eat plants, but some of the substances available in plants are obtained by them through their prey. It would be of interest to develop research on the biological factors responsible for the variation and constitution of plankton communities and their influence in reproduction, spawning and breeding, hatching, and survival.

Water masses may have similar parameters of salinity and temperature but, in keeping with different plankton populations they harbour, differences in rate of reproduction between chaetognath species are not uncommon. These variations may depend on vital metabolites and other substances released to, or removed from, the waters. This is best illustrated by *Sagitta elegans* and *S. setosa*, dominant in plankton off England. Abundance of *S. elegans* is accompanied by plankton assemblages different from those of *S. setosa*; also, successful fish-larvae populations are related to dominance of *S. elegans* in plankton of the region. Appropriate combination of experiments suggests the presence of a 'beneficial' substance in both Celtic and Biscay Bay waters, and its lack in the local waters characterized by an abundance of *S. setosa*. The English Channel waters are characterized usually by *S. setosa* community, and the Celtic Sea and Bay of Biscay by *S. elegans* and other different planktonic communities. It appears that the Celtic and Biscay waters supply some necessary ingredients for successful reproduction, resulting also in an abundant fish population (Wilson and Armstrong, 1952). Alvarino (1989) showed that certain plankton assemblages ensure high reproductive success and high survival of anchovy larvae.

B. Breeding and Spawning Strategies

Reproductive success can be guaranteed only if suitable strategies are evolved by the species to synchronize breeding and spawning activities of its members and thereby to increase the chances of fertilization and production of the young. The simplest method of estimating reproductive activity of any species is the observation of breeding of animals in the field or in the laboratory. Such observations are imprecise but they produce important data on the presence of mature gametes, sperm, and ova. Spawning is not easy to induce when gonads are not gravid, but when the animal is gravid almost any stimulus may cause spawning, and also egg laying.

There is need to determine the factors inducing spawning in nature. It may be argued (see Giese and Pearse, 1973 for discussion) that in nature no spawning stimuli *per se* are required, and that spawning and breeding are spontaneous after the gonads have become mature. This hypothesis is, however, disputed as changes in biotic and abiotic factors and hormonal milieu are definitely known to play a role in inducing spawning in animals (see Volumes I and II of this series). *Sagitta tasmanica* specimens reaching the Gulf of Maine area grow larger than normal with large ovaries and well-developed full seminal vesicles, but there is no evidence of breeding perhaps because there the spawning stimulus is wanting. The animals

may die and disappear either with no breeding or with a young population that does not survive. In any case, no *S. tasmanica* eggs have been reported from that area.

It is well known that light induces spawning and breeding (Knight-Jones, 1951; Kume and Dan, 1968; Segal, 1971) in animals. Exudates from green algae (Myazaki, 1938), diatom blooms (Barnes, 1957), and chemical exudates from males and females of the same species have been shown to synchronize breeding. Probably some of the most mature individuals, the best receptors of stimuli, are first induced to breed in nature and produce exogenous stimulants to other individuals in the population, until the synchronization phenomenon reaches epidemic proportions ensuring maximum fertilization.

Studies on bathymetric distribution of chaetognath species indicate that young and small specimens inhabit the upper oceanic layers, while full-mature and large individuals extend into deep waters. In other words, there is an ontogenic vertical distribution of the population down the water mass (Alvariño, 1964a, 1965). Our analysis of the bathymetric distribution of *Sagitta scrippsae* (open-closing net collections), off California, included specimens 10 to 50 mm long. Small-sized individuals appeared in the upper 225 m, and the largest in strata below. Young, Stage I individuals of *S. gazellae* inhabit the upper 250 m (Alvariño *et al.*, 1983) whereas Stage II appears mainly at 500 m to 1,000 m depth (David, 1955). Distribution of *S. elegans* in Bedford Basin (Zo, 1973) also showed an ontogenic bathymetric pattern of the populations. Observations on the ontogenic stratification of the chaetognath populations (Alvariño, 1964a) indicate that fecundation and laying of eggs take place in deep layers, and eggs and young are brought up to upper layers. Studies by Reeve and Coper (1975) on *S. hispida* populations in the shallow waters of Biscayne Bay, Florida, indicate that surface waters rarely contain mature animals. In the eastern Canadian region, young *S. elegans* and *Eukrohnia* appear in the upper layers, while large individuals are at deep strata (Huntsman, 1919).

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