Shortened binder title:

"Studies on *Sagitta elegans*
Verrill and its Parasites"

ABSTRACT

'Studies on the Relationship Between *Sagitta elegans* Verrill and its Endoparasites in the Southwestern Gulf of St. Lawrence'

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The life cycle of *Sagitta elegans* in the southwestern Gulf of St. Lawrence takes two years. The growth rate and vertical distribution change during the cycle: growth slows during the winter months and there is a changing relationship between body and ovary lengths; individuals settle lower in the water column with increasing maturity. *S. elegans* is concentrated near the bottom over a range of depths. The role of this hyperbenthic distribution was discussed.

Metaphrya sagittae, a ciliate, and the metacercaria of *Hemiurus levinseni*, a hemiurid trematode, are common parasites, while the metacercaria of another hemiurid, *Derogenes varicus* is less common and the larva of *Contracaecum*-type nematode and the cestode larva *Scolex pleuronectis* are quite rare. *H. levinseni* has a seasonal cycle of abundance, which was correlated with the maturity dependent changes in the hosts' vertical distribution. Although low incidences of *M. sagittae* are the rule, the largest size-classes of *S. elegans* sustain very high incidences.

Studies on the Relationship Between *Sagitta elegans* Verrill and its Endoparasites in the Southwestern Gulf of St. Lawrence

Martin Weinstein

Ph.D. Thesis
Marine Sciences Centre
McGill University
November, 1972

To all my Teachers

"I wonder, though, whether
silence is not the true state
of affairs in the Universe..."

The Keys to December

Roger Zelazny

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I. Introduction

The purpose of this study was to determine the relationship between Sagitta elegans and its parasite fauna and to elucidate the role played by this plankter in the life histories of its parasites. Holoplanktonic organisms, crustacea, coelenterates, and chaetognaths long have been recognized as important intermediate hosts in the life cycles of some of the most common marine helminths, but the functicnal aspects of these hosts in the parasites' life cycle has received little attention. Most of the literature consists of catalogues of the parasites found, with a description of the parasites' morphology. This study is an attempt to define the factors determining the make-up of the parasite fauna of one species of plankton and the causes of the variations in numbers of the parasites within the host populati on.

The environment of parasites with complex life cycles is manifold; it includes the internal environments of a number of physiologically distinct hosts as well as the external environment. Thus there can be two different, but equally important, ecological approaches, one of which is

primarily physiological and the other ecological in the traditional sense of the word. Although both approaches are interrelated closely, the questions they ask and the methods they use are quite different. For example, if we look at the important problem of host-parasite specificity two questions can be defined which together provide answers. One question is concerned with the problems of transfer from one host to another and the other with the hosts' acceptance of the parasite. The latter resolves into lesser questions of the parasites' responses to the hosts' physico-chemical environment and the immunological and defensive reactions to the foreign organism, while the former examines the problems of host-parasite proximity (geographical ranges, bathymetric distribution, and migratory behaviour of the hosts; the parasites' behavioural and morphological adaptations for finding the host) and entrance (behavioural and morphological adaptations of free living infective stages for gaining entrance into a host; in the case of food-chain-transfer, the hosts' feeding behaviour).

The environmental-ecological approach to parasitology has been emphasized recently. V. A. Dogiel (1964) and his collaborators in the Soviet Union stressed that environmental

factors can be as important or more important than the purely phylogenetic factors of compatibility of a parasite to the host's environment in determining a host's parasite fauna. Most of these ecological studies in the marine environment have concentrated on fishes. Pioneer work was done by Dogiel, Polyanski, and many others in the Soviet Union; by Manter, Noble, and Sindermann in the United States; by Kabata and Llewellyn in the United Kingdom; and by Margolis in Canada.

There are many uses to which such information can be put. Margolis (1963) has attempted to determine the area of geographic origin of Pacific salmon caught in the high seas using parasites as indicators. Kabata (1963) attempted to separate stocks of haddock and whiting on the basis of differences between their myxosporidian parasites. In general, parasites can be used to give supplementary information about the host's biology. They can be used to supply information much finer than can be obtained using current methods. For example, parasitic stages which are transferred down the food chain can be used as predator-prey labels. To evaluate information obtained using parasites as indicators or labels, however, the details of the life cycle and the host specificity of the different stages, as well as the factors responsible for the geographic

distribution and changes in incidence and intensity in the host populations must be understood.

Like so many other marine animals, parasites make use of a planktonic existence for the dispersal of their eggs and larval stages. Free-living stages in the plankton cover the full spectrum of possibilities, from the eggs and oncho-spheres of cestodes to the cercariae of trematodes and the adults of mostrillid and caligid copepods.

To ensure successful contact between successive hosts, parasites have evolved either huge reproductive potentials or life-patterns which increase the probability of contact between host and parasite. Most of the known life cycles of helminth parasites of pelagic vertebrates include planktonic organisms as intermediate hosts. Increased accuracy in finding hosts precludes the necessity of massive egg production and permits maximum parasite population size without an energy drain which may damage the definitive host and subsequently prove fatal to the parasite population. The migratory habits of planktonic intermediate hosts may also facilitate contact between a series of hosts distributed through different levels in the water column and in shallow water between benthic and pelagic hosts.

The effect of parasites on the productivity of zooplankton is completely unknown. One of the parameters necessary for an understanding of productivity is mortality, which is the sum of predation and "disease". The latter term is generally overlooked in productivity studies because of the lack of information about the effect of parasitic organisms on zooplankton mortality or reproduction.

There are several factors which make chaetognaths ideal organisms for this type of study. The group has been relatively well worked and, with the exception of physiology, a large amount of information about the basic biology of the group has been accumulated. The role of chaetognaths as both predator and prey places them in an interesting position in the marine food web and therefore in parasitic life cycles. Theoretically, they should concentrate those parasites occurring in their prey, the copepods, which are not rejected. The transparency of this host also greatly facilitates parasitic examinations. One would expect them to be good intermediate hosts for any parasite which can gain entrance, finds the internal environment compatible, and has a possibility of being transmitted to its next host.

Sagitta elegans has been the most thoroughly investigated

chaetognath. Its life cycle, growth, and distribution has been studied intensively from different regions along the North American Atlantic coast with the exception of the Gulf of St. Lawrence. The inshore waters of the Gulf provides a temperature environment which annually and vertically duplicates arctic and temperate conditions. The preliminary collections led to the discovery of large shoals of S. elegans just above the bottom and subsequent collections were modified to study the species' vertical distribution and how it influences the dynamics of the parasite fauna. The thesis is divided into three parts; the parasites of S. elegans, the biology of the host in the Gulf of St. Lawrence, and the relation between the biology of the host and the dynamics of its parasites.

The hyperbenthic distribution of Sagitta elegans has been frequently mentioned in the literature, but no studies have been conducted to determine what portions of the population are involved in this distinctive distribution, what physical and/or biological conditions lead to this type of behaviour, and what effect this particular interface environment may have on a planktonic organism which is adapted to a physically uniform environment.

II. Acknowledgements

I would like to express my gratitude to the many people who have helped and encouraged me throughout this study.

The field work was carried out at the Station de Biologie Marine, Grande-Rivière, Gaspé, Québec. The facilities and assistance supplied to me by Dr. Alexandre Marcotte, the director of the Station, are especially appreciated.

I would like to thank the technical and biological staff of the Station; in particular, Drs. Guy Lacroix and Pierre Brunel for giving me valued advice and continual encouragement. M. Robert Boudreault and M. Richard Couture provided a forum for the frequent discussion of biological and oceanographic problems. I am especially indebted to M. Yves Boudreault for offering advice on the equipment used and for guiding my appreciation of the uniqueness of the Gaspé.

The 1968 field program was carried out in conjunction with Dr. Pierre Brunel, M. Daniel Granger and M. Lucien Poirier, to whom I am indebted for the success of this program.

M. Adelard O. Dubé and M. Albert Couture assisted in the design of the nets used; the nets were constructed by M. Albert Couture. Collections of the material used in this study were greatly facilitated by the assistance and cooperation of the captains and crews of the many draggers used. I am particularly indebted to Captain Allain and the crew of the Jean d'Arc for the assistance they provided in making the collections in 1968.

Mr. William Pennell, Mr. Tom Newbury and Dr. M. J. Dunbar made specimens available for examination.

The nematodes were identified for me by Dr. Betty June Myers, of the Southwest Foundation for Research and Education, San Antonio, Texas.

I would like to thank the staff and students of the Marine Sciences Centre, McGill University, all of whom provided assistance throughout this study. I am especially indebted to Mr. William Pennell for his assistance, advice and companionship in the field, at Grande-Rivière, and in Montreal.

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Finally, I would like to thank my wife, Ilona, without whose assistance and encouragement this study would never have been completed.

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III. Methods

III.A. Field Methods

Sampling was carried out in 1965, 1966 and 1968 at the mouth of the Baie des Chaleurs. During 1965 preliminary investigations on the parasites of various benthic and planktonic invertebrates were done. Encouraged by abundant parasitized Sagitta elegans found in September, the 1966 sampling program was set up to examine the seasonal variations in the parasite fauna of S. elegans and the life cycle of the host. A more sophisticated sampling program in 1968 stressed the vertical distribution and hyperbenthic behaviour of S. elegans.

Samples were collected in September 1965 and from May to November 1966 using a beam trawl with ½-metre number 0-mesh nylon plankton nets attached above and below the trawl beam. Each net-frame measured 26" long by 6" high, and sampled plankton from 6" to 18" off the bottom. These samples were supplemented by vertical and oblique plankton tows. The trawl was played out under steam, towed for 10 minutes at about 3 knots, then the boat was stopped and the net retrieved.

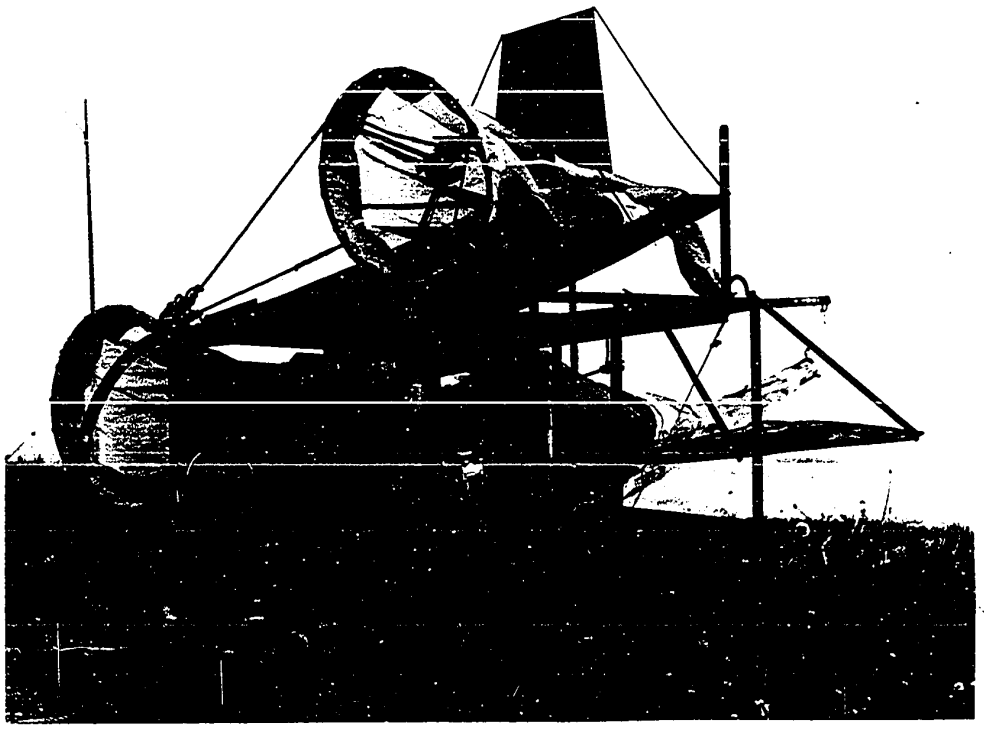


Fig.1. The opening and closing hyperbenthic net used in the 1968 sampling. (Modified from a design by C. T. Macer 1967.)

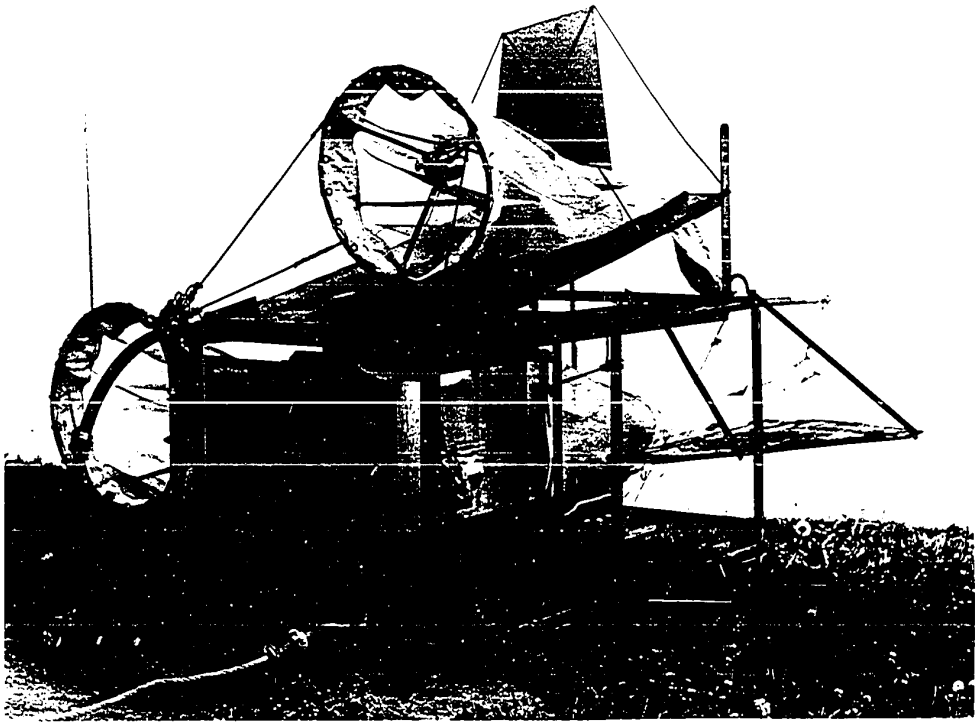


Fig.1. The opening and closing hyperbenthic net used in the 1968 sampling. (Modified from a design by C. T. Macer 1967.)

The successful sampling of small organisms near the sea floor presents many difficulties. Many non-closing hyperbenthic nets have been designed (Russell 1928; Beauchamp 1932; von Elster 1933; Walford 1938; Colman and Seagrove 1955; Frolander and Pratt 1962; Clutter 1965). Closing hyperbenthic nets intended to exclude mid-water plankton, all of which incorporate different problems in net construction, operation, and/or deployment at sea, in the design, have been built by Werner (1938), Bossanyi (1951), Wickstead (1953), Beyer (1958; personal communication), Macer (1967), and Bieri and Tokioka (1968). The hyperbenthic net designed by C. T. Macer was modified and used for the collections in 1968 (Fig. 1). The net-frame was scaled up proportionally from Macer's design to take a 57-cm plankton net (Fig. 2). Fins (8 & 9) were added and the depressor (7), constructed out of marine plywood to ensure that the net would land right-side-up on the bottom. A sheet-metal plate (11) was welded to the underside of the frame so the net could be used on rocky bottoms without damage. The spring opening-and-closing mechanism was also modified. In the original design the door (3) was secured in the closed position by a pin (14) which was activated by a spring-loaded lever (13). When the net hit the bottom the lever was depressed, the pin retracted, and the door swung to the open position, where it was blocked by another pin (15),

Legend

Fig. 2a. View of the apparatus from above.
2b. Lateral view of the net chassis with the net box removed.
2c. Net box, with a cut-away view of the opening and closing mechanism. (The portion of the net box posterior to the door was rendered transparent to show the opening and closing mechanism.)

1. Net sledge
2. Net box
3. Door
4. Pulley
5. Rubber tubing
6. Extension pole, for supporting the plankton net
7. Depressor plate
8. Vertical stabilizer fin
9. Horizontal stabilizer fins
10. Runners
11. Bottom plate
12. Hook for the towing warp

13a Activating lever, depressed (net on bottom; door open)
13b Activating lever, extended (net off the bottom, door closed)

14. Door closing pin (shown in the closing position,as though the activating lever was extended)
15. Door opening pin (blocks the door in the open position when the net is on the bottom and the lever is depressed)
16. Compression spring (extends the lever when the net is off the bottom)
17. Lever pivot
18. Flowmeter
19. Frame, for the attachment of the plankton net

Note: The additional nets shown in Fig. 1 were added to the hyperbenthic apparatus for auxiliary collections and were non-closing.

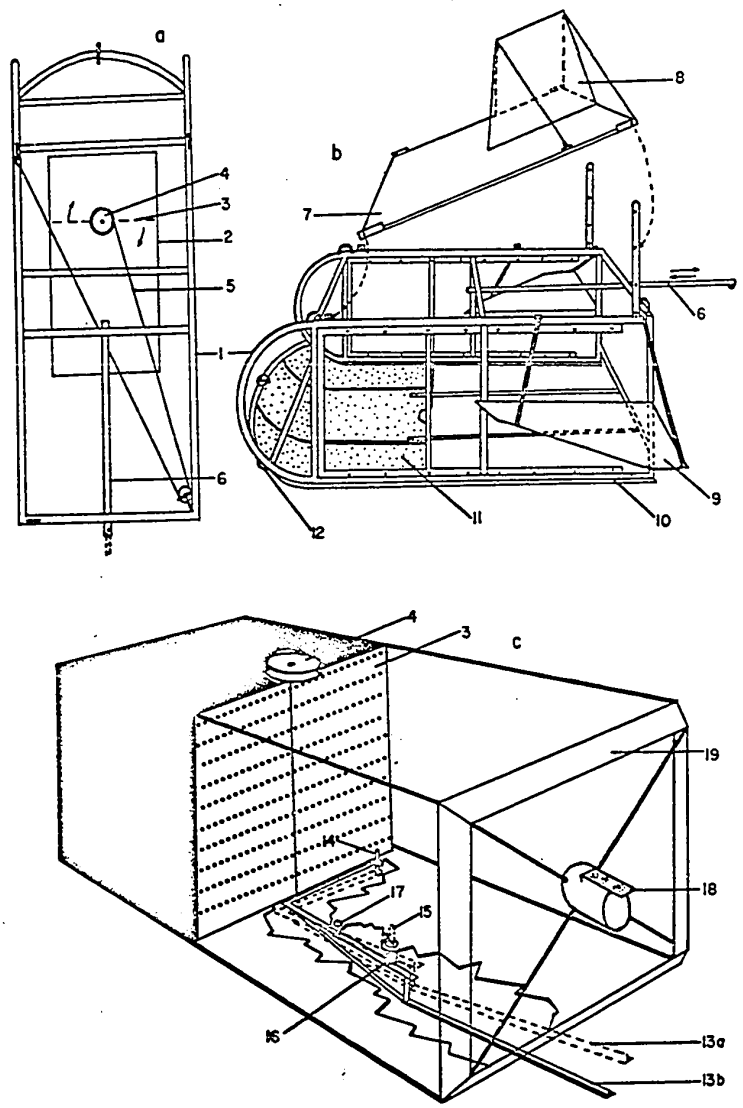


Fig. 2. Plan of the modified 'Macer' hyperbenthic apparatus. (Drawing from Poirier, Granger, Weinstein, and Brunel 1969.)

which had been extruded when the lever was depressed. On leaving the bottom the compression spring (16) expanded, the lever extended, and the position of the two pins was reversed, resulting in a closed door. The door was mounted on a central vertical axle stressed by a torsion spring. To improve closing-opening efficiency and to simplify the preparation of the net for each tow, this spring was replaced by a long piece of surgical rubber tubing (5) attached to a grooved pulley (4) which sat above the pivotal axis. With spring closure the door had to be wound while "pumping" the trip lever, which was quite difficult on a moving surface. To set the modified net, the rubber band was wound around the pulley.

A non-closing 57-cm plankton net was attached to the hyperbenthic net depressor plate (Fig. 1) for comparison with the 1966 samples.

Tests on the modified Macer Net using a clockwork depth recorder showed that the ascent time was slightly shorter than the descent time (Table 1). The tests indicated that stopping the boat during retrieval, rather than towing, resulted in the net being dragged along the bottom until the warp shortened, and then being raised in a near vertical trajectory. This procedure cut down the contamination of organisms through the gaps necessary for the door's unimpeded rotations during opening and closing. This fishing procedure was also used with

the non-closing trawl in 1965 and 1966 and probably resulted in relatively little mid-water contamination.

TABLE 1. Ascent and descent times for the modified Macer net.

Bottom Depth (M)	Descent Time (Min.)	Ascent Time (Min.)
119	3½	3½
	4	2½
	5	2½
	4	½
110	5	½
	4	1
	2	3
	2	2
	3	3
	3	2
75	2½	1
	2	½
54	1	½
	1	½

Following the recommendations of the Joint ICES, SCOR, and UNESCO Committee on Zooplankton Sampling Methods (Fraser 1966), 57-cm diameter plankton nets were used in the 1968 program. The use of 57-cm nets, which filter a 0.25 m^2 column, simplify the calculations of the volume of water filtered by the net.

A series of stations over progressively deeper bottoms, out along a course of 160° magnetic from the Grande-Rivière buoy, were occupied more or less regularly at 2-3 week intervals in 1966 and 1968 (Table 2; Fig. 3). (In 1966, stations at depths of 60, 50, 40 and 30 fathoms were occupied when possible. When necessary, the program was cut short and stations at 60, 45 and 30 fathoms were occupied. In the calculations the samples collected at the 50, 45 and 40 fathom stations were combined and considered as from the intermediate depth station, HP 24). The stations were designed to study the influence of various depth bottoms on the hyperbenthic behaviour of S. elegans. Difficulties in renting draggers, the time necessary to test modifications in the gear, and a shipyard strike in the spring of 1968 all contributed to some irregularities in the timing of the program.

Surface and bottom temperatures and salinities were taken in 1966 and 1968 and a bathythermograph was lowered at each station.

Sampling in 1966 consisted of a 10-minute hyperbenthic trawl and vertical and oblique plankton tows at each station.

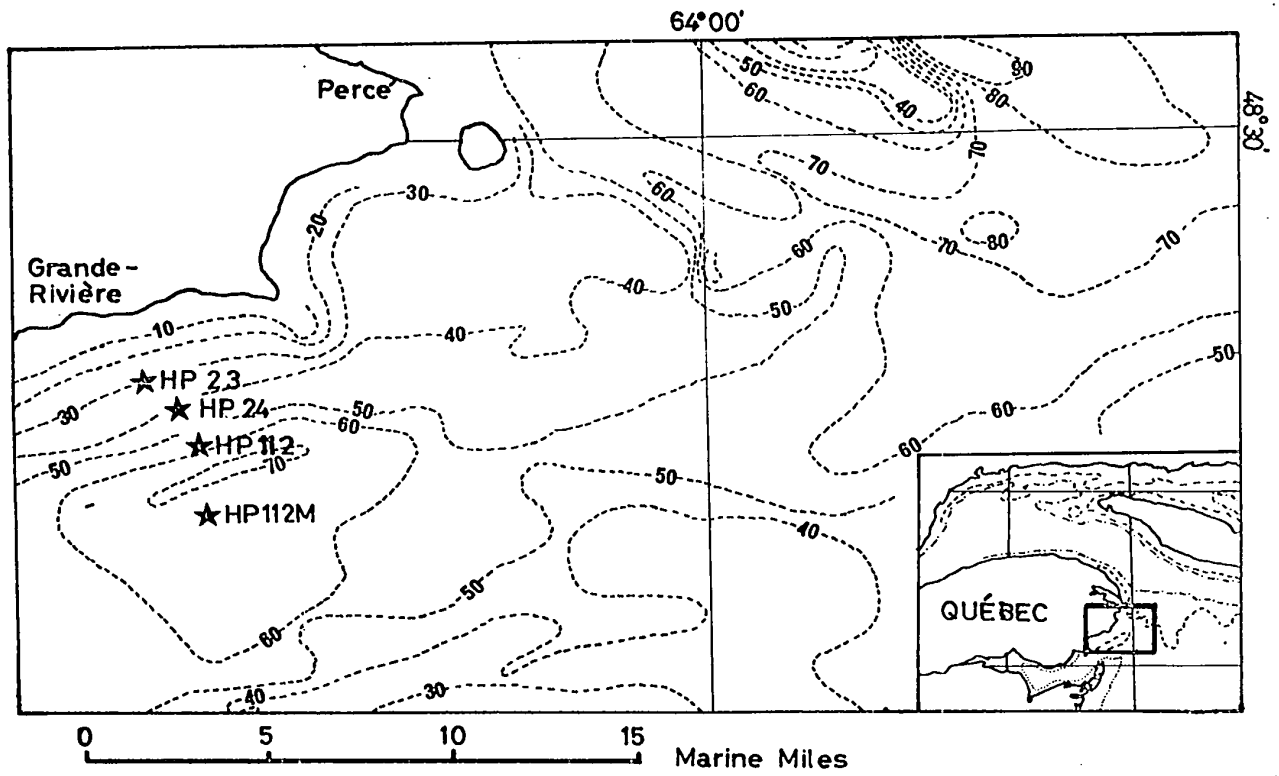


Fig. 3. Map of the sampling area at the mouth of the Baie des Chaleurs.

TABLE 2. The stations sampled during 1968.

Station	Depth Fm.	Depth Meters	Latitude North	Longitude West
HP 112M	65	119	48°18'	64°21'
HP 112	60	110	48°20'	64°22'
HP 24	41	75	48°21'	64°23'
HP 23	30	54	48°22'	64°26'
68 Labrador 1	266	488	47°52'	60°16'
68 Labrador 2	223	408	48°24'	61°21'
68 Labrador 3	204	373	49 16'	64°08'

Sampling in 1968 was designed to make it possible to compare animals caught planktonically and hyperbenthically at the same depths (see Fig. 4). A 10-minute hyperbenthic sample using the closing net and a series of 10-minute horizontal plankton tows with the 57-cm plankton nets spaced at 25 meter intervals were taken at each station.

A series of vertical and oblique plankton samples was collected in April 1968 from the Icebreaker LABRADOR at stations along the Laurentian Channel and at Station HP 112 (Table 2; Fig. 5). Vertical plankton samples collected at these same stations in March 1967 were supplied by Mr. W. Pennell. These collections were made with #6 mesh plankton nets.

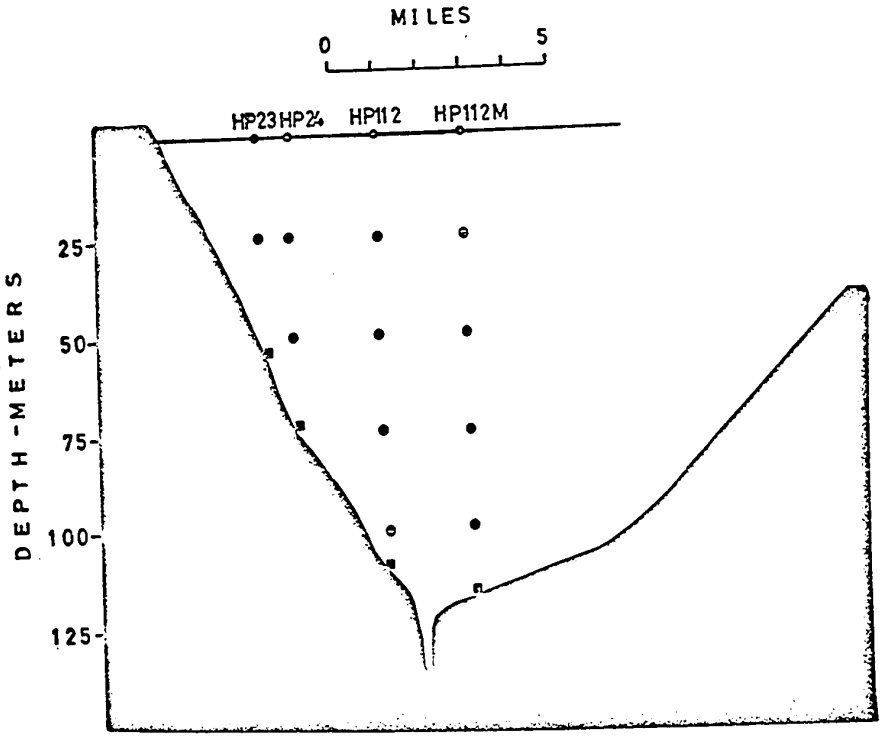


Fig. 4. Section through the mouth of the Baie des Chaleurs along the transect course, showing the position of the hyperbenthic and plankton samples collected during each of the 1968 cruises.

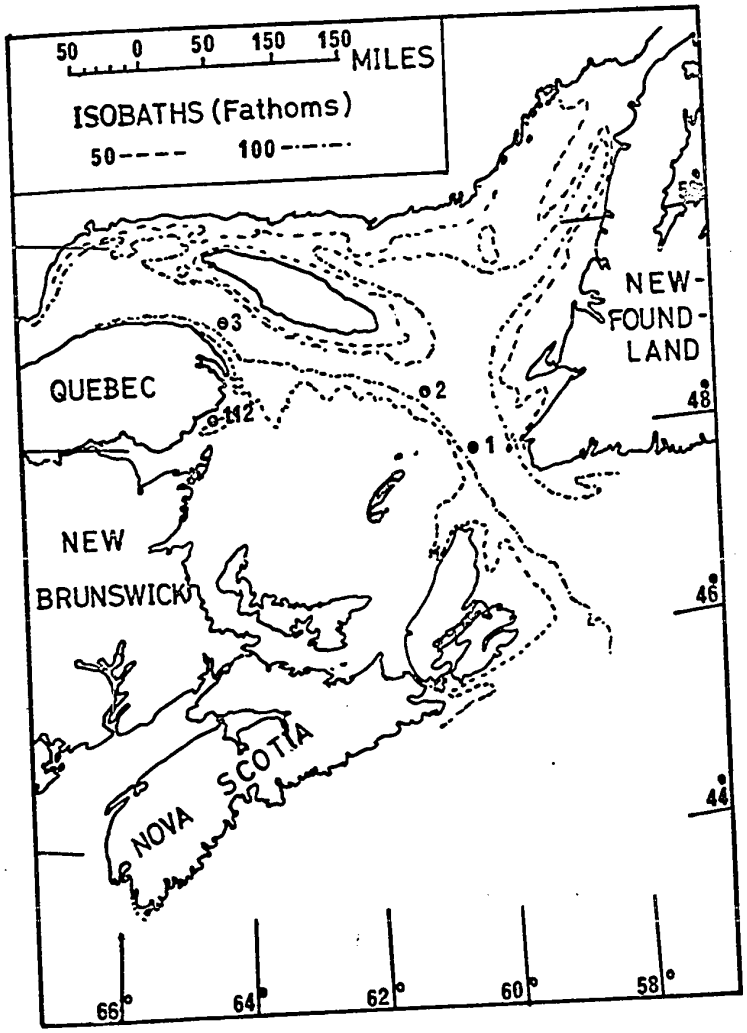


Fig.5. Map of the Gulf of St. Lawrence, showing the position of the 'late winter' Icebreaker stations.

III. B. Treatment of the Samples

Samples were preserved in 5% formalin while on board ship. Several samples were taken back to the laboratory unpreserved to observe the parasites of *S. elegans* while alive.

The chaetognath portion of the sample was sorted by picking out large individuals and examining the remainder of the sample under the binocular microscope for the smaller sagittae. About one-half of the 1968 samples were sorted by the COIDC in Ottawa.

Several hundred of the chaetognaths from each of the 1966 hyperbenthic samples collected at Station HP 112 were identified, measured, staged, and examined for parasites. The total body length, excluding the tail fin, was measured under the binocular microscope to the nearest millimeter. Ovary lengths were measured to the nearest 0.1 mm. Sub-sampling was done by swishing the sample bottle with an irregular twist of the wrist and plunging a long pair of forceps to the bottom of the bottle and removing a mass of chaetognaths. This procedure was repeated until a sufficient number of chaetognaths was in the dish.

Thirty chaetognaths from each of the 1968 plankton

and hyperbenthic samples were measured, staged, and examined for parasites. A sub-sample of 200 S. elegans from the open hyperbenthic net sample from Station HP 112 were similarly treated, as a comparison with the 1966 samples.

III. B.1 Determination of Maturity Stages

Chaetognaths are protrandric hermaphrodites. The ovaries originate near the tail-trunk septum and extend anteriorly within the body coelom on either side of the intestine. The testes are two band-like bodies attached to the lateral wall of the tail coelom. In juvenile individuals, before any sexual development has taken place, one can see minute testes and ovaries extending away from each other on opposite sides of the septum. The testes mature first and release spermatogonia into the coelom of the tail segment. In the juveniles, the ovary is small and undifferentiated; following development of the male system, the ovaries enlarge and ova begin to appear as swellings along the length of the ovaries.

There is confusion over how fertilization occurs. Several authors have stressed the possibility of self-fertilization (see Ghirardelli 1968), while several others feel that mating is necessary for fertilization. Ghirardelli, who

reviewed the literature on sexual maturation and reproduction, gives one the impression that, although self-fertilization may occur, it is the exception. Cross-fertilization actually has been observed in a few species and Ghirardelli published a series of remarkable drawings (by Kaj Olsen) of the mating behaviour of the benthic chaetognath Spadella cephaloptera.

Attempts have been made to distinguish general patterns of maturation for the phylum and to designate these as discrete developmental stages. The systems devised have been based either on morphological examination of the ovaries and testes through the transparent body wall or on cytological examination of the developing germ cells in the ovaries and testes. The cruder morphological examinations generally are used in population studies, where large numbers of individuals are examined, since the latter system requires staining and sectioning of the organisms. Russell (1932a), Dunbar (1940), and Pierce (1941) stained batches of chaetognaths to determine maturity stages for their population studies. However, staining of thousands of individuals, taking the care necessary to avoid shrinkage and distortion,is impractical and most authors have dispensed with it after becoming familiar with the pattern of gonadal development.

Kramp (1939) recognized five stages, based on the

development of testes and ovaries: Stage I, gonads of both sexes are unripe; Stage II, some sperm in tail and ovaries unripe; Stage III, sperm in tail coelom and some eggs large; Stage IV, sperm at least partly evacuated and ovaries filled with ripe eggs; Stage V, sperm evacuated and eggs evacuated (spent). Russell (1932a), on the other hand, recognized three stages for Sagitta elegans and S. setosa: Stage I, sagittae "in which not a single sperm mother cell was visible lying loose in the tail cavity"; Stage II, individuals with at least some sexual development of the male organs, but showing no enlarged ova; Stage III, chaetognaths with fully ripe or ripening ovaries. The practical difficulty in both of these schemes is in distinguishing Stage II without cytological examination. Stage II in both systems is based on the onset of male sexual development, and no distinct macroscopic criteria exists to delimit the onset of this stage. Dunbar (1962) noted this difficulty and in some cases, lumped Russell's Stage I and Stage II together; "in practice Stage I and II are often difficult to distinguish, because they grade into each other imperceptibly, whereas the differences between Stage II and III are marked." This certainly suffices for most purposes.

Dunbar (1962) examined Russell's and Kramp's staging systems and found that they were not incompatible. For Sagitta

elegans the two systems are essentially identical, because individuals at Kramp's Stages IV and V are very rarely found. Dunbar took Kramp's Stages III, IV, and V as corresponding to Russell's Stage III, and modified Russell's system and included seminal vesicles as a staging criterion. His Stage II included individuals with spermatocytes in the tail segment, with developing seminal vesicles, and with small ovaries and uniform ova.

The system used here is:

Stage I - Ovaries small, no distinguishing structure apparent, tail coelom seen to be clear under reflected illumination.

Stage II - Tail coelom partially or completely opaque under reflected illumination. No differentiation seen in the ovaries.

Stage III - Tail coelom opaque. Some ova enlarged.

Stage IIIs- Large individuals, with no seminal vesicles, a clear tail coelom, and long ovaries, but no enlarged ova.

III. B.2 Treatment of the Parasites

Except for the parasites brought back to the laboratory for live study, all parasites were fixed in 5% formalin *in situ* within the chaetognath host. Ideally the parasites should have

been removed from the host and fixed in a proper fixative. It was, however, impossible to do this without rendering the host material unsuitable for further studies. The in situ fixation caused considerable contraction of the contractile organisms. Measurements of contractile organisms are comparable throughout any study where methods are uniform, but it is doubtful if the absolute measurements can be compared to other studies.

The chaetognaths were examined under 15X magnification using reflected light. Using this method, the dense-bodied helminths stood out within the transparent host.

Prior to staining, trematodes and cestodes were moved progressively into 70% alcohol for hardening. They were brought back into 30% alcohol or distilled water depending on the alcoholic content of the stain. Specimens were stained in Mayer's paracarmine, Erlich's haematoxylin, Partsch's alum cochineal, Gower's carmine, or Grenacher's alcoholic borax carmine using Lynch's Precipitated Carmine Method (Galigher and Kozloff 1964). There was some difficulty in getting the stains into hemiurids and in completely dehydrating the animals due to their heavy, impermeable cuticle. The most satisfactory and consistent staining results were with Mayer's paracarmine and Grenacher's borax

carmine. The hemiurids were very gradually dehydrated after differentiation in 1% acid alcohol, and then cleared in xylene or terpeneol and toluene and slowly brought into Permount for mounting.

Difficulties in transferring the small helminths through the numerous solutions were minimized by retaining them within the hosts until differentiation. Thereafter, gentle swirling of the petri dish concentrated the freed parasites in the centre of the dish, helping to minimize losses during transfer.

The ciliates were treated similarly, but were stained in Heidenhain's haematoxylin or Mayer's paracarmine. Silver impregnation using both Klein's dry film method and the Chatton and Lwoff method was unsuccessful, probably due to the fixation of the ciliates.

Nematodes were transferred into glycerine alcohol after fixation, the alcohol was evaporated and the specimens transferred to lactophenol for clearing and examination.

Following identification of the parasites, length and width measurements were taken. The diameter of the oral and ventral sucker, the pharynx, and the size and number of the eggs in the trematodes were noted.

IV. Hydrography

IV. A. Introduction

Topographically, the Gulf of St. Lawrence is an extensive shallow bank with a deep submerged river channel running through its centre. The Laurentian Channel runs from the mouth of the Saguenay River out onto the continental shelf south of Newfoundland. Arms of the channel extend part way into the Strait of Belle Isle, as the Esquiman Channel, and between the eastern end of Anticosti Island and the North Shore of the Gulf. Depths over 250 fathoms have been recorded in the main channel and 150 and 180 fathoms in the Anticosti and Esquiman Channel, respectively.

The southwestern Gulf is a large bank with depths averaging about 30 fathoms. This bank descends precipitously into the Laurentian Channel along most of its length. At the mouth of the Baie des Chaleurs and along the northwestern coast of Cape Breton Island the descent is more gradual (Fig. 5).

The Baie des Chaleurs gradually widens and deepens as it extends out from the Restigouche River. The Baie deepens at the mouth to form a wide trough with a flat bottom ranging from 60 to

65 fathoms in depth. A small, narrow slit in which depths of up to 102 fathoms have been recorded runs along the northern side of the depression.(Figs. 3 and 4). Past Cap d'Espoir, on the Gaspé coast, the bottom rises again to 30 - 45 fathoms before the descent into the Laurentian Channel.

Outflow from the estuary, as the variable Gaspé Current, passes along the Gaspé coast and a portion enters the Baie des Chaleurs, forms intermittent eddies and flows back out (Boudreault, personal communication). Fresh water enters the Baie from the Restigouche River and the numerous smaller rivers along the coast. Movements of the deeper waters are less known; the deeper waters in the trough are subject to tidal oscillations (Boudreault 1966) and in some years warmer waters formed by mixing of the intermediate and deep layers may spill into the trough (Brunel 1968).

The stations occupied for this study extend from the north side of the trough (Fig. 3). In a way the trough represents a special environment within the western Gulf, but the shallower stations occupied (HP 23 and HP 24) are probably representative of the bottom conditions on the extensive Magdalen Shallows.

The choice of this sampling area was advantageous in several other respects. The closeness of the sampling area to

the Station de Biologie Marine permitted a larger sampling program than would otherwise have been possible with the available ship time. The area about Station HP 112 has been well worked hydrographically and biologically by the Station de Biologie Marine (e.g. Brunel 1968; Lacroix 1968). Hydrographic data for this station are available from 1952 (Boudreault 1967).

IV. B. Results

There are two vertically stratified water masses in the Gulf, a variable surface layer and a deep warm and saline layer. During the summer, due to the build-up of a thermocline which splits the upper layer into a warm and a cold component, three layers are generally distinguished. "In winter, however, the upper layers merge into a single mixed layer of sub-zero temperature overlying the deep warm layer." (El-Sabh, Forrester, and Johannessen 1969). Lauzier, Trites, and Hachey (1957) defined the intermediate layer as the waters bounded by the 0.0°C isotherm. For this study, however, the intermediate layer refers to the water layer between the bottom of the thermocline and the warm (>1°C), saline (>33‰) deep layer. The intermediate cold layer is thought to originate by cooling and mixing of the surface waters during the winter months, rather than coming in from outside the Gulf as was earlier suggested (Forrester 1964).

Boudreault (1967) examined bathythermographs recorded at Station 112 from 1952 to 1961 and found a well-defined thermocline between 3 and 8°C at depths of 25 to 40 meters which was present from mid-July to mid-August. The thermocline became less distinct and sank to progressively greater depths following autumnal surface cooling. Bottom temperatures increased gradually from the spring to the autumn (Brunel 1968) and decreased as the thermocline became less distinct in the late autumn.

In 1966, the heating of the surface waters continued until 11 August (Fig. 6; Appendix I). In 1968, the highest surface temperature was recorded on 16 July; a period of unseasonably cool weather followed during August and the surface waters warmed again in mid-September.

In 1966, the temperatures just off the bottom at depths from 50 to 75 meters increased until 20 September and then began to drop. At 110 meters the maximum temperature of 0.66°C was reached on 12 October and then began a slow decline. The bottom temperature at the shallowest station (HP 23 - 54 meters) was generally higher than at the deeper stations. Bottom temperatures from 75 to 110 meters were similar until September, thereafter the temperatures above the 75 to 90 meter bottoms increased more rapidly than at Station HP 112 (110 meters).

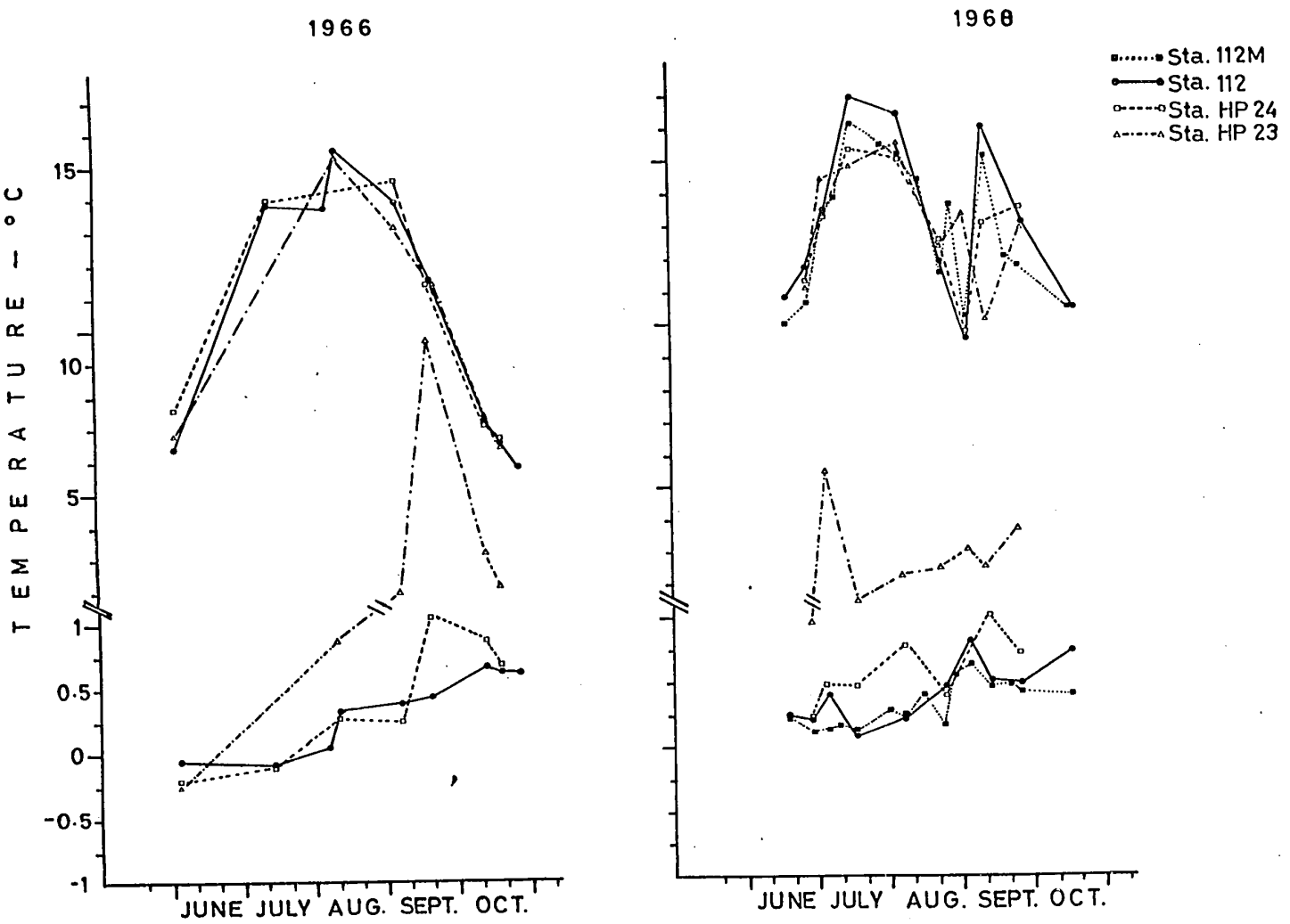


Fig. 6. Surface and bottom temperatures for 1966 and 1968.

The bottom temperatures in 1968 were more variable and generally warmer than in 1966. The maximum temperature of 0.63°C at Station HP 112M (119 meters) and 0.81°C at Station HP 112 (110 meters) was reached on September 3. In August, at the same time as the surface cooling, the bottom temperatures dropped from 0.78 to 0.40°C at 75 meters and from 0.42 to 0.16°C at 119 meters (Station HP 112M). However, at Station HP 112 the temperature rose during August; temperature at this station had dropped in July and early August.

Midwater temperatures at 50 meters tended to be quite variable, due to the presence of the thermocline at about this depth (Fig. 8). The well-formed thermocline present through the sampling period in 1966, began to break up after 20 September. A weak thermocline was still present at 50 meters on 18 October. A deep thermocline between 55 and 75 meters, still existed at the cessation of sampling in 1968. The surface waters were well mixed and had temperatures between 8.9°C and 8.6°C from the surface to 50 meters respectively.

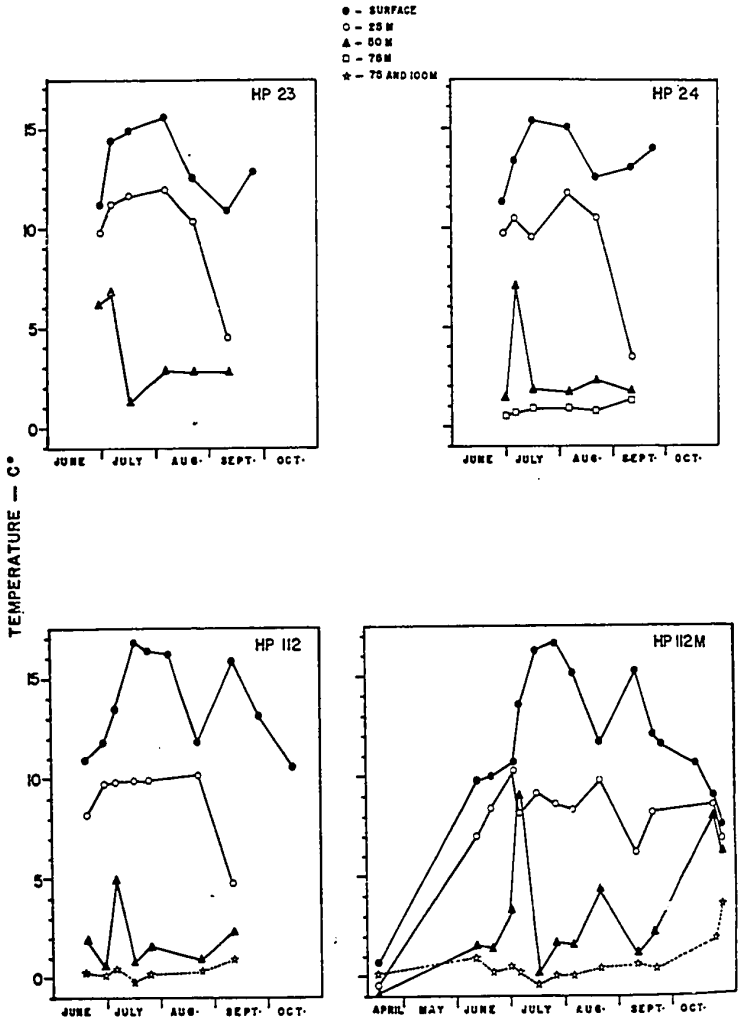


Fig. 7. Mid-water temperatures in 1968.

V. The Parasites of *Sagitta elegans* (Verrill)

V. A. Introduction

Planktonic organisms, like other organisms, provide an environment, complete with special advantages and inherent disadvantages for potential colonizers. The dearth of available information on the parasites of marine zooplanktonic species does not necessarily reflect absence or low diversity of parasites in these animals. Most of the knowledge we have is in the form of notes from investigators who came across parasites while studying zooplankton. Very few systematic searches have been conducted for the parasites of any zooplanktonic taxa.

Chaetognaths are an important element of the carnivorous zooplankton. They occupy the positions of predator and prey and *a priori* should make good intermediate hosts. Although parasites have been found frequently in chaetognaths, there have been no studies on the chaetognath as host.

V. B. Historical Review

V. B.1. The Parasites of Zooplankton

There is a large literature on parasitized zooplankters, but because of the huge number of possible host-parasite taxa

combinations a complete review would be a monumental task. Most of the literature consists of citations of parasitized individuals frequently, but not always, including identification of the parasites.

Several outstanding reviews, generally limited to one zooplankton or one parasite taxon have been written. Dollfus (1923a, 1923b, 1924, 1929, 1931, 1964, 1967) has compiled the records for cestodes in planktonic and other marine invertebrates. Steuer (1928) reviewed the records of appendiculate digenetic trematodes (Hemiuridae) parasitizing marine planktonic copepods and discussed their taxonomy and geographical distribution. Dollfus catalogued all records of digenetic trematodes in chaetognaths (1960), and in marine coelenterates and ctenophores in Indian and Palearctic waters (1963). He attempted to classify the earlier records based on modern systematics; not entirely successfully. Rebecq (1965) discussed the role of zooplankton as hosts for marine trematodes and included lists of trematodes found free as cercariae in the plankton as well as trematodes found in chaetognaths, planktonic coelenterates, and ctenophores. Hyman (1959) and Alvarino (1965) have both reviewed the parasites of the Chaetognatha.

Some comprehensive surveys have been done on the parasite fauna of zooplankters. Apstein (1911a) studied the parasites of

the Copepoda, especially Calanus finmarchicus, in the North Sea. His parasites were discussed and a revised taxonomy suggested by Jepps (1937a). Jepps (1937b) also conducted an extensive study on the protozoan parasites of C. finmarchicus in the Clyde area. Sewell (1951) examined planktonic copepods from the Arabian Sea for epibionts and parasites and Marshall and Orr (1955) included a section on parasites in their Biology of Calanus finmarchicus. Boyle (1966) gave an account of the trematodes and nematodes of the ctenophore Pleurobrachia pileus off New Zealand. Marie Lebour conducted studies on the parasites of Sagitta bipunctata (= S. elegans and/or S. setosa) (1917a), digenea in medusa (1917b), and Hemiurus communis in Acartia (1923; 1935), off Plymouth. Komaki (1970) reported on some parasites from Euphausia similis from Suruga Bay, Japan.

V. B.2. The Parasites of the Chaetognatha

A substantial portion of the studies on zooplankton parasites have been done on the Chaetognatha. As mentioned above, both Hyman and Alvarino included sections on the parasites of the Chaetognatha in their reviews of the phylum.

Representatives of most of the major parasite groups have been found in the Chaetognatha.

V. B.2.a. The Protozoan Parasites of the Chaetognatha

Grassi (1892) observed two amoebae which he called Amoeba pigmentifera and A. chaetognathi in the tail coelom of Sagitta enflata, S. bipunctata, S. serratodentata and Spadella. Janicki (1912, 1928, 1932) transferred them to the genus Paramoeba and Chatton (1953) later created a new genus, Janickina, for them. These amoebae also have been seen by Ramult and Rose (1945) and Ghirardelli (1950a) in S. enflata, and by Hamon (1957) in S. bipunctata. Hyman (1959) concluded that these amoebae "flourished only during male sexual maturity and are probably transferred during copulation."

Horvasse (1924) described a flagellate, Trypanophis sagittae from several Sagitta species. It was studied later by Rose and Hamon (1950) and Hamon (1950, 1951a) in S. hexaptera, S. lyra, and S. decipiens from the Bay of Algiers. As the organism grew the posterior end of the body split off. The anterior portion then lost all differentiation, resembled a gregarine, and attached itself to the intestinal epithelium and encysted. How infestation occurred is unknown.

Leuckart (1861) was the first to see a gregarine in the intestine of a Sagitta. An acephaline gregarine was described

from the gut of a Sagitta and named Lecudina (later Lankesteria) leukarti by Mingazzini (1891). Ramult and Rose (1955) reported finding L. leukarti in the gut of S. enflata and Furnestin (1957) reported Lankesteria from S. friderici and an undetermined gregarine in S. bipunctata and S. hexaptera. A new cephaline gregarine, Tricystis planctonis was described by Hamon (1951b) from the gut of S. lyra and S. bipunctata. Colman (1959) reported finding small multinucleated parasites in the gut of S. hexaptera, which may have been a sporozoan.

Ikeda (1917) was the first to describe a ciliate from a chaetognath. He found large numbers of a lenticular-shaped holotrichous ciliate in the body cavity of a Sagitta sp. and named it Metaphrya sagittae, placing it in the order Astomata. Miyashita (1933), in a postscript, compared Ikeda's parasite to the Apostome ciliate Pericaryon cesticola from the ctenophore Cestus and declared that M. sagittae would be more reasonably placed among the Apostomes. Chatton and Lwoff (1935) in their monograph on the Apostomes, considered that there were insufficient data on the life cycle of Metaphrya to be certain of its taxonomic position and placed it in the Apostomea incertae sedis.

This parasite has been found frequently in a variety of host species and nearly all oceanic waters. Stadel (1958)

described it in Eukrohnia hamata from Antarctic waters and discussed the possibility of placing the organism among the Opalinopsids (genus Opalinopsis). Ramult and Rose (1955) found it in S. enflata from the Bay of Algiers and Furnestin (1957) found it in S. minima and S. enflata from the Atlantic coast off Morocco. Massuti (1954) found it in S. bipunctata off the Spanish coast and Ghirardelli (1950b, 1952) saw it in S. minima. Alvarino (1965) described a parasite from S. enflata in California neritic waters which may have been M. sagittae. It has also been described in S. elegans from the western Atlantic (Weinstein 1967).

V. B.2.b. The Helminth Parasites of the Chaetognatha

The helminths are the most frequently encountered parasites of the Chaetognatha. Larval trematodes and nematodes are reported most often, cestodes are encountered only rarely. A sizable literature has developed on the chaetognath trematodes. Dollfus (1960) cited 50 references and concluded that the trematodes parasitizing chaetognaths are the metacercariae of non-encysting cercariae, generally belonging to the superfamilies Hemiuroidea, Lepocreadioidea, and Accocoelioidea. Only one case of an encysted metacercaria has been recorded.

Various "older authors" (Busch 1851; Leuckart and

Pagenstecher 1858; Claparède 1863; Gourret 1884; MacIntosh 1890; Steuer 1910) described trematodes from the coelom, intestine, or gonads which were later identified as hemiurids by Hyman (1959) and Dollfus (1960); most frequently belonging to the genera Hemiurus, Derogenes, and Aphanurus. Many of these authors simply had noted observing "a larva of a Distome". Dollfus attempted to ascribe these "Distomes" to their modern equivalents, but the descriptions were often either too sketchy or did not include the taxonomic criteria now used.

More recently Lebour (1917a) found Derogenes varicus in S. bipunctata (?); Linton (1927) discovered egg producing Hemiurus sp. in S. elegans; Meek (1928) found a Hemiurus sp. in S. setosa (probably H. communis according to Lebour 1935); Hutton (1954) reported a D. varicus in S. enflata and S. serratodentata from the Florida Current; Myers (1956) found egg producing H. levinseni in S. elegans; and Zaika and Kolesnikov (1967) reported that between 20-40% of the S. elegans arctica in the Barents Sea in August 1960 were infected with a sexually mature trematode, which they suspected to be Derogenes varicus.

Reports of Lepocreadioidea have not been as numerous as for the hemiurids. Lebour (1917a) reported Pharyngora (=Opechona) bacillaris from S. bipunctata (?), off Plymouth.

Accacoelioidea trematodes have been reported more frequently. Dollfus, Anantaraman and Nair (1954) described an accacoeliid metacercaria, possibly belonging to the genus Tetrochetus, from S. enflata. Hutton (1954) described a new metacercarial species, owreae, in S. enflata, S. lyra and S. hexaptera from the Florida Current. It also was reported in S. enflata off Cuba (Gaabro, 1955), S. hexaptera in the Caribbean (Dawes 1958), and in S. pulchra, S. enflata, S. hexaptera, S. bipunctata, and S. serratodentata atlantica off east and west Africa (Furnestin and Rebecq 1966). Dawes (1959) considered the trematode a cercaria rather than metacercaria and renamed it Cercaria owreae, tentatively referring it to the genus Accacladocoelium.

A list of the trematode parasites of the species of Sagitta based on Dollfus' exposition was prepared by Rebecq (1965).

As mentioned above, cestode larvae rarely have been found in chaetognaths. Lebour (1917a) mentioned finding two cestode larvae in S. bipunctata (?) from Plymouth. Grey (1930) drew what he described as a "cysticercus" from the body coelom of S. friderici from the Society Islands. Dollfus, Anantaraman, and Nair (1954) made the notable find of two "Scolex" type larvae of an undetermined tetraphyllidean attached to the cuticle of an

accacoeliid metacercaria in S. enflata from Madras. Dollfus (1964) also reported on a personal communication from Gilbert Ranson, who found a larval tetraphyllidean in S. enflata from Nhatrang. Dawes (1958) briefly mentioned a cestode larva in S. tenuis from South America. Da Costa(1970) included a photograph of what appeared to be a "Scolex" type tetraphyllidean larva found in S. friderici from Brazil, but labeled it as an unidentified trematode larva.

Nematodes, on the other hand, have been found frequently and relatively high incidences have been common. Most of the nematodes have been identified as larval ascaroids, but the specific identity is difficult to determine because of the similarities of the larval forms of the ascaroid genera. A nematode in a chaetognath was first reported by Ulianin, in 1871. Nematodes were reported by MacIntosh (1890), Scott (1896), Moltschanoff (1909), Pierantoni (1913), Lebour (1917a), Meek (1928), Wülker (1929), Grey (1930), Thomson (1947), Russell (1932), Elian (1960), and Ass (1961). The nematodes usually have been placed in the genus Contracaecum, although Grey identified Camillanus trispinosus in S. friderici and Furnestin (1957) reported chaetognaths as intermediate hosts of Agamonema. Elian found 2% of S. euxina in Roumanian waters infested with nematodes and Russell reported 7%

of S. setosa off Plymouth similarly infested. M. Ya. Ass reported 33% of the Sagitta sp. from the Black Sea infested with larval Contracaecum sp. and suggested that Sagitta functioned as the intermediate host of this ubiquitous parasite.

V. B.2.c. Ectoparasites

Several ectoparasites have been reported. Oye (1918) saw peritrichous ciliates on the surface of chaetognaths. Thomson (1947) found a copepod on S. decipiens and Ghirardelli (1948) found a copepod on S. hispida and S. bedoti. Tregouboff (1949) and Ghirardelli (1953) have reported an obscure parasite, possibly a protozoan, which consisted of vesicles with an indefinite histological structure on the surface of Mediterranean Sagitta.

V. C. The Parasites of Sagitta elegans in the Gulf of St.Lawrence

Subphylum Ciliophora Dolfein, 1901
Class Ciliata Perty, 1852
Subclass Holotricha Stein, 1859
? Order Apostomatida Chatton and Lwoff, 1928
? Family Foettingeriidae Chatton, 1911
? Subfamily Pericaryoninae Chatton and Lwoff, 1930

Metaphrya sagittae Ikeda, 1917
(Fig. 8)

Large numbers of holotrichous ciliates frequently were

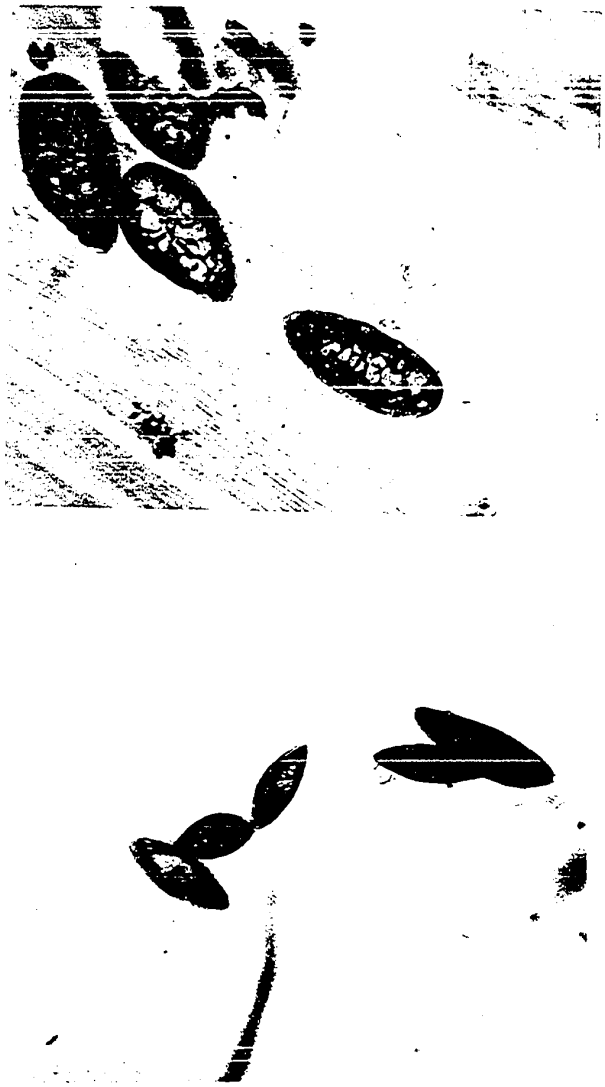


Fig. 8. Metaphrya sagittae, from two different Sagitta elegans.

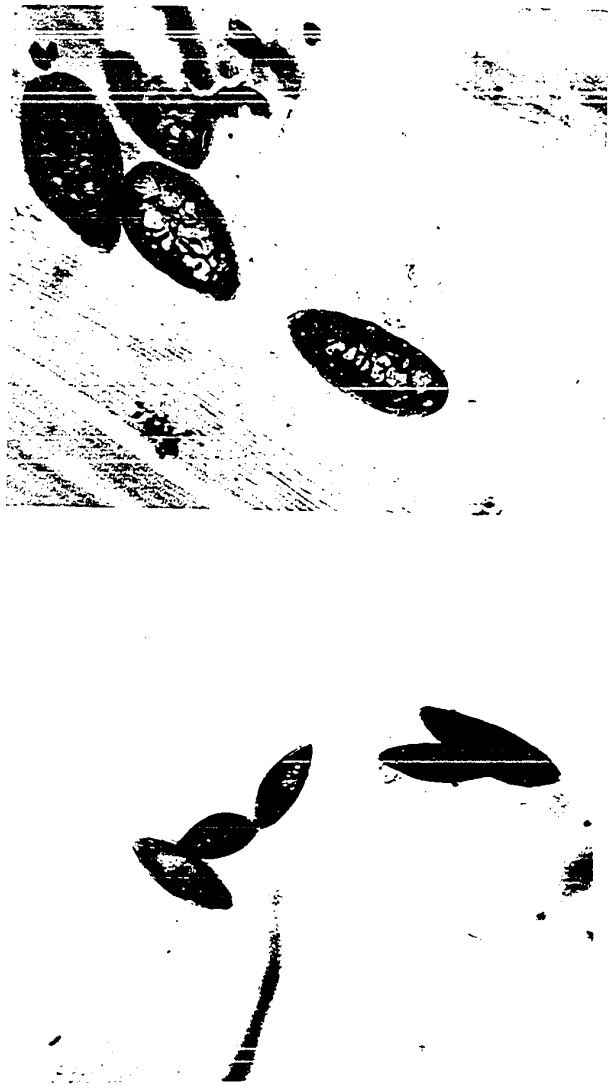


Fig. 8. Metaphrya sagittae, from two different Sagitta elegans.

seen in the coelom of S. elegans. These ciliates were studied live under phase contrast, or fixed in formalin within the plankton sample and later stained with Meyer's paracarmine, Erlich's haematoxylin, or iron haematoxylin and mounted in Permount.

The animals when alive were colourless, transparent, elongate, nearly ellipsoid bodies with 10 to 12 ciliary grooves spaced equidistant along the longitudinal axis. They were tapered toward the anterior and blunted at the posterior end. The surface was remarkably uniform; no mouth or other opening was seen. The ciliates generally numbered several hundred per host and densely packed the coelom of infected Sagitta; infestations of single ciliates were never seen. When viewed under an ordinary light microscope, the cytoplasm was filled with refringent granules which circulated about the interior of the cell.

Ciliates from twenty S. elegans were stained and mounted. Several representative individuals from each of these chaetognaths were measured. The stained individuals varied in shape from spheroid to fusiform. Generally, the ciliates of any one sagitta were similar in size and shape, but there was considerable variation between hosts. The sizes varied from 363µ long to 127µ wide for the largest animal to 130µ long by 20µ wide for the smallest. The size range compares well to previous descriptions of the

parasite (Table 3). (Except for Ikeda's figures, the sizes are the extremes of all ciliates measured and are not representative of the actual proportions of any particular animal.) With the exception of Ikeda's cilates, the range of the ciliates from the Gulf of St. Lawrence was greater than that from other regions; probably because more material was available. Ikeda found three separate size ranges (larger individuals measuring 250 x 130 μ and two smaller measuring 20 x 10 μ and 40 x 20 μ) in a single chaetognath. This has not been noticed in the Gulf chaetognaths.

TABLE 3. The size range of Metaphrya sagittae.

	Length (μ)	Width (μ)
Gulf of St. Lawrence	363 to 80	158 to 20
Barents Sea	211 to 93	109 to 31
Antarctic Ocean (Stadel 1958)	300 to 64	105 to 24
Japan (Ikeda 1917)	250 to 20	130 to 10

The macronucleus is a large and characteristic structure having the appearance of a basket-work-like reticulum concentrated at the cell's periphery, with some projections extending into the interior. A micronucleus was not seen. In some individuals the nucleus consisted of a single closed loop. In dividing ciliates,

the daughter cells were nearly equal in size. No change was seen in the nucleus during division; the reticulum simply constricted at the plane of division. Ramult and Rose (1945) found a small oral opening in living M. sagittae which was not seen in fixed specimens; no opening was seen here in living or fixed specimens. The ciliates were always found dispersed throughout the host's body coelom. None were ever seen in the digestive tract. In a few chaetognaths they were also found in the tail coelom, but here the cell density never approached the congestion regularly seen in the main cavity.

V. C.1.a. Discussion

Since Ikeda's discovery of ciliates parasitizing a sagitta, they have been seen repeatedly in several chaetognath species and in most of the world's oceans (Table 4). Ikeda described the ciliate and named it Metaphrya sagittae and placed it in the family Anoplophryiidae Leg. & Dub. of the Order Astomata Scheviakoff. The organism had twelve uniform ciliary rows, no oral opening, and a reticulated macronucleus; the only significant difference between Ikeda's ciliates and the animals seen in the Gulf of St. Lawrence was that his cells were pear-shaped, bending slightly at the anterior end. Stadel (1958) found ciliates in 1 of 1100 Eukhronia hamata caught at 69°41'S and

TABLE 4. Geographical range and host distribution of *Metaphrya sagittae*.

Host Species	Location	Reference
Sagitta sp.	Japan	Ikeda 1917
S. enflata	Mediterranean Sea	Ghirardelli 1950b, 1952
S. minima	Bay of Algiers	Ramult and Rose 1945
S. bipunctata	Spain	Massuti 1954
S. minima *S. enflata*	Morocco	Furnestin 1957
Eukrhonia hamata	Antarctic Ocean 69°41'S 1°17'E	Stadel 1958
S. enflata ?	California	Alvarino 1963
S. elegans	Gulf of St. Lawrence	
S. elegans	Barents Sea	

$1^{o}17'E$ in the Antarctic Ocean. They resembled M. sagittae except for the shape of the anterior tip, which ended in a distinct papilla. Stadel discussed placing his animals as a new species of the apostome genus Opalinopsis, since M. sagittae had no papilla. Ramult and Rose (1945), however, had pictured both live and fixed M. sagittae found in S. enflata from the Mediterranean Sea, showing that when live the shape was ellipsiod with a slight twist at the apical end, while the fixed and stained animals had a straight apical papilla, suggesting that the papilla was an artifact due to fixation. Stadel finally concluded that the ciliates he found in E. hamata were probably M. sagittae.

Considerable variation between shape and size was found in ciliates from different S. elegans in the Gulf of St. Lawrence, both living and fixed. Nevertheless, their ciliary structure and the appearance of their nucleus were identical. It is not possible to say whether these variations are taxonomically significant or if they are simply clonal differences. A distinct apical papilla was not seen on any of the specimens from the Gulf of St. Lawrence. The ciliates of several infected S. elegans from the Barents Sea, which were given to me by Mr. T. K. Newbury, had characteristic apical papillae. In all other respects they were identical to the Gulf ciliates.

Considering the extremely wide geographical and host ranges of these ciliates, it is remarkable that they are so similar. Some clonal and geographic differences are to be expected.

There is a great deal of confusion about the taxonomy of these animals. Ikeda placed them in the holotrichous suborder Apostomata Scheviakoff. Miyashita (1933) proposed placing the species in the subfamily Pericaryoninae of the Apostome family Foettingeriidae due to their resemblance to Pericaryon cesticola, a parasite of the ctenophore Cestus. "In both the macronucleus is superficially situated and of basket-like structure. The cytoplasm forms only a thin superficial layer and the interior of the body is occupied by a clear fluid-like substance." Chatton and Lwoff (1935) have since considered M. sagittae in the Apostomea incertae sedis due to lack of knowledge of its development and life cycle. De Puytorac (1954), in one of his papers on the revision of the order Astomatida, agreed in the placement of Metaphrya as an Apostome. The very large "order" Astomatida was thought by Corliss (1961) to be taxonomically of uncertain status. The order Apostomatida, on the other hand, is a smaller, more cohesive taxonomic group with a striking polymorphic life history with two hosts often involved. Placement of M. sagittae in its correct order requires details of its life cycle and other forms,if it is polymorphic.

Phylum Platyhelminthes
Class Trematoda Rudolphi, 1808
Order Digenea Carus, 1863
Family Hemiuridae Lühe, 1901

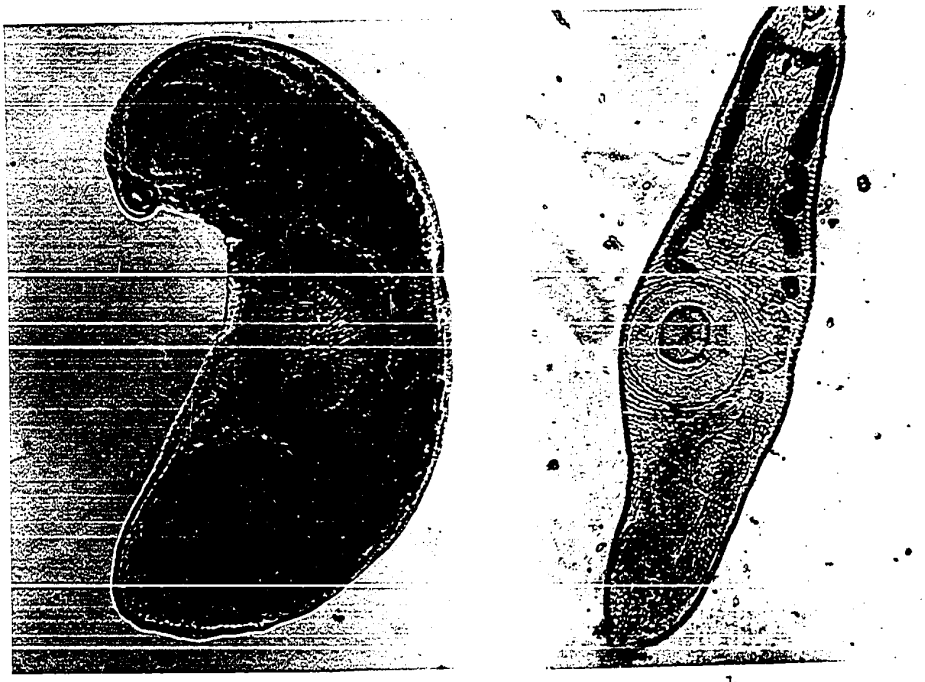
Subfamily Derogenetinae Odhner, 1927
Genus Derogenes Lühe, 1900

Derogenes varicus (O.F. Müller 1784) Looss, 1901

Syn. Fasicola varica Müller, 1784; F. varica Rudolphi, 1802; Distoma varicum Zeder of Rudolphi, 1809;
Distomum dimidiatum of Creplin, 1829 (in part); Derogenes varicum (Müller) of Olsson, 1869; D. varicum of Levinsen, 1881; D. minor Looss, 1901; D. plenus Stafford, 1904; D. fuhrmanni Mola, 1912; D. crassus Manter, 1932.

(Fig. 9)

Derogenes varicus is undoubtedly the most common and most widely distributed marine fish trematode. It has been found in forty-three species of fish from British waters alone (Dawes 1956). It has been seen in five fish species from the Argentine coast (Szidat 1961), nine fishes from New Zealand (Manter 1956), five hosts in the Tortugas (Manter 1947), and twenty-one species in the Barents Sea (Polyanski 1955). It has been found also in various fishes from Iceland (Rees 1953), Greenland (Odhner 1905), Puget Sound (Lloyd 1938), the Sea of Japan (Lyaimen 1930), and the Galapagos Islands (Manter 1940). Manter (1955) concluded the species had a "continuous three-dimensional distribution from Arctic to Antarctic but only by way of the deeper waters." He found it conspicuously absent from the upper waters of the warm seas, but often found in fishes at depth.



a b

c

Fig. 9. Derogenes varicus
a. Progenetic D. varicus from S. elegans, fixed and stained
b. D. varicus from S. elegans, live under phase contrast
c. Calanus finmarchicus with a D. varicus in the haemocoel

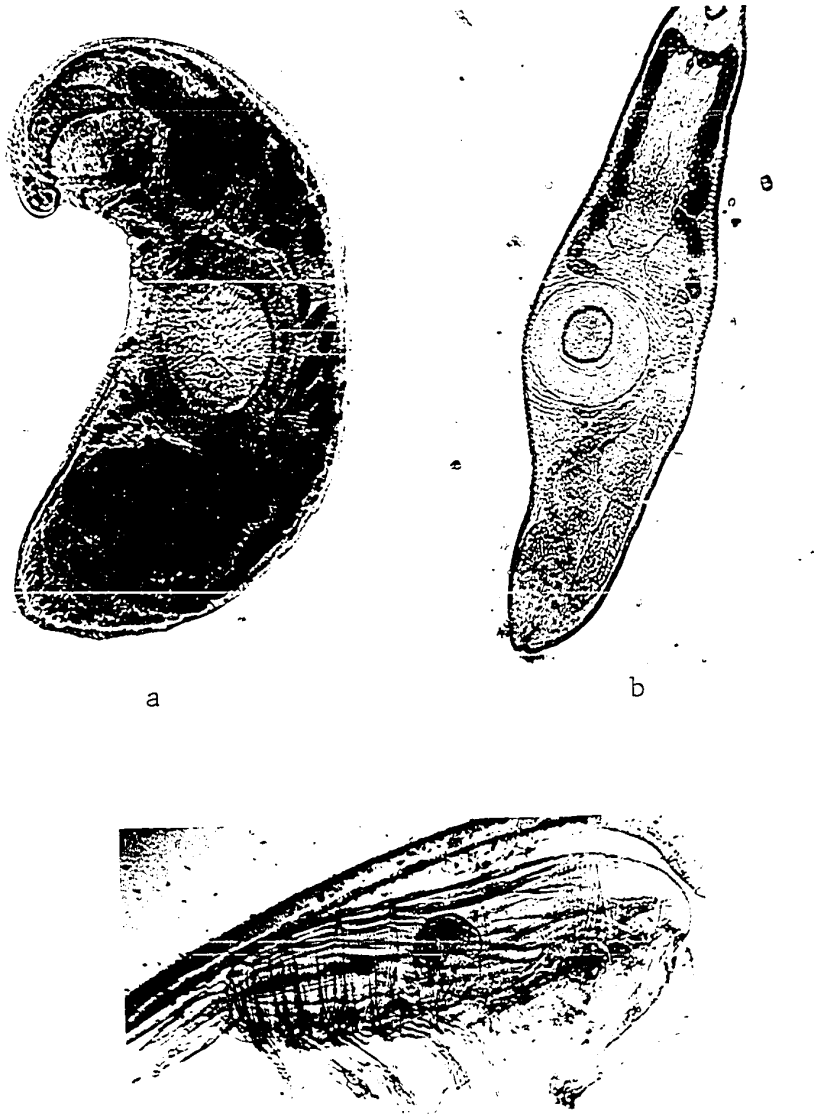


Fig. 9. Derogenes varicus
a. Progenetic D. varicus from S. elegans, fixed and stained
b. D. varicus from S. elegans, live under phase contrast
c. Calanus finmarchicus with a D. varicus in the haemocoel

In the Gulf of St. Lawrence it has been seen in Gadus morhua, Osmerus mordax, and Salmo salar (Heller 1949) as well as in Hippoglossoides platessoides, Limanda ferrunginea, Liopsetta putnami, and Pseudopleuronectes americanus (Ronald 1960). Manter (1926) found it in Gadus morhua, Urophycis chuss, U. tenuis, Anarrhichas lumpus, Hippoglossus hippoglossus, and Myxocephalus octodecimspinosus in the adjacent Gulf of Maine. Scott (1969) saw it in Argentina silus off the Nova Scotia coast and Trelfall (1969) found it in Squalus acanthias and Raja radiata from Newfoundland waters.

Derogenes varicus metacercariae were seen regularly in the Sagitta elegans in the Gulf of St. Lawrence, although they were not encountered frequently (see Section VIII. B.). This parasite was only found in the host's body coelom and was only found singly. A complete description of the anatomy has been given by Odhner (1905) and Dawes (1956).

The specimens were fixed in situ in the plankton sample with formalin and stained in Meyer's paracarmine or Grenacher's carmine and mounted in Permount. The body lengths ranged from 0.43 mm to 1.23 mm and the widths from 0.20 mm to 0.50 mm (Table 5). The smallest individuals had undeveloped testes, ovaries and vitellaria, while the largest were egg producing (progenetic).

TABLE 5. Measurements of several representative Derogenes varicus from Gulf of St. Lawrence Sagitta elegans.

Length (mm)	0.43	0.63	0.83	1.23
Width (mm)	0.20	0.28	0.39	0.50
Oral Sucker (μ)	84	124	158	200
Ventral Sucker (μ)	146	198	282	350
Pharynx (μ)	46.5x40.3	58.9x49.6	?	77.5x77.5
Eggs (μ)	---	46.4-52.7x 12.4-15.5	52.7-55.8x 31.0	40.7-18.5x 22.2

The size of the oral and ventral suckers and the pharynx increased in proportion to the body size of the parasite.

Hemiurid trematodes, probably D. varicus, were found in some S. elegans from the Barents Sea, supplied by T. K. Newbury. The size, shape, general appearance, and the appearance of the eggs were those of D. varicus, but the shape and position of the vitellaria, ovary, testis, and secondary sexual apparatus, which are necessary for proper identification, were obscured by uteri full of eggs. Progenetic D. varicus were also seen in some S. elegans from Godthaab Fjord, Greenland, caught by M. J. Dunbar.

Lebour (1917a) mentioned small spines on the surface of larval D. varicus from S. bipunctata (?) off Plymouth. No spines were seen on any of the S. elegans D. varicus; the cuticular surface was as smooth as the adults'.

Calanus finmarchicus was also infested by D. varicus in these waters (see Appendix II: Some helminth parasites of Calanus finmarchicus in the Gulf of St. Lawrence). No progenetic metacercariae were seen in C. finmarchicus. All infestations consisted of a single parasite lodged in the host's haemocoel (Fig. 9c). The size range of Derogenes in Calanus was very narrow. Forty individuals caught over a five month period were measured and all of the

measurements ranged between 0.30 to 0.48 mm long by 0.13 to 0.19 mm wide. The state of differentiation in these animals ranged from organogeny to early gametogeny. No spines were seen on the cuticle. The length-width locus defined by all forty of these Derogenes lay near the "origin" of a straight line drawn through the length-width points of the D. varicus from S. elegans (Fig. 10). None of the trematodes from the chaetognaths were in the same size range as the copepod trematodes; the smallest was just slightly larger than those in the copepod and the largest was within the size range encountered in the definitive host. The points for the fish D. varicus lay to the right of the line drawn through the points for chaetognath D. varicus; i.e. they were proportionately longer than the S. elegans worms. This length-width relation representation is at best an approximation for age or size. Unfortunately, with contractile animals such as these, linear parameters are an unsatisfactory measurement for size. Presumably, similar treatment in fixation will produce similar degrees of contraction. This seems to hold for D. varicus fixed in situ in the plankton sample, since the length-width points lie along a line; but it is doubtful if animals treated differently can be meaningfully compared. The two points for fish D. varicus in Fig. 10 were taken from purely parasitological studies and the worms probably were relaxed prior to fixation, resulting in these worms being more elongate and less broad than those from S. elegans or C. finmarchicus.

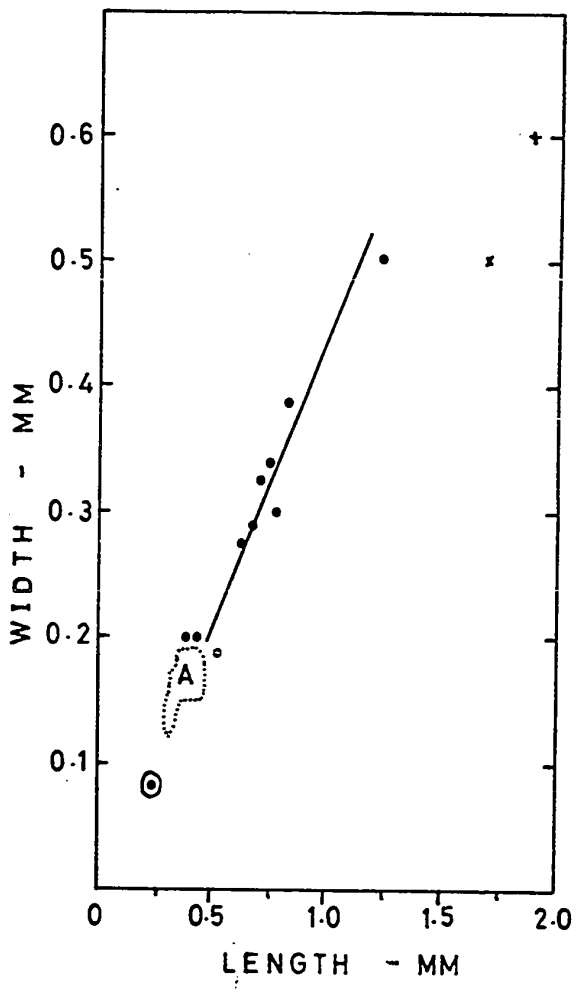


Fig. 10. The length-width relationship of Derogenes varicus from different hosts. · from S. elegans in the Gulf of St. Lawrence; 'A' the size range of forty individuals from C. finmarchicus in the Gulf; ⊙ D. varicus(?) from Aglantha in the Gulf; X average size D. varicus from Gulf of Maine cod (Manter 1926); + average size D. varicus from Puget Sound ling cod and sculpin (Lloyd 1938).

Egg producing hemiurid metacercariae have been recorded frequently in chaetognaths (Lebour 1917a; Linton 1927; Myers 1956; Weinstein 1967; Zaika and Kolesnikov 1967) and other invertebrate intermediate hosts (Dollfus 1927, 1955; Chabaud and Bignet 1954). All of the chaetognaths found with progenetic hemiurids were S. elegans, with the possible exceptions of Lebour's "S. bipunctata" which may have included S. setosa. Smyth (1966) discussed the use of the term "progenesis" for this phenomenon and defined it as "gametogeny in the larval condition". There is some confusion as to what a metacercaria with eggs actually is; an adult maturing in the intermediate host or a sexually mature larva. Since the terms for larval maturation, 'paedogenesis' and 'neotony', do not really cover the special problems of the Trematoda, where many complex environmental (both the hosts' and the external) and genetic factors may determine sexual development, progenesis has been regularly used. 'Progenesis' is used here exclusively for metacercariae which are producing eggs in their intermediate hosts.

None of the D. varicus found in Calanus were progenetic, but the larger ones from Sagitta were. The eggs were ovoid and had a golden yellow hue. The number of the eggs in the uteri of the latter worms was directly proportional to the worms' size (Fig. 11). The threshold size for egg production was 0.6 mm. It

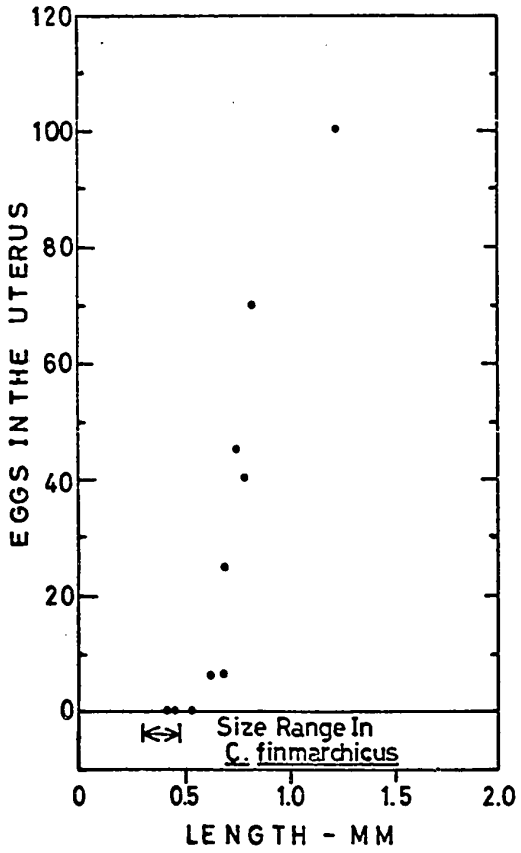


Fig. 11. The relationship between size, progenecity, and egg production in Derogenes varicus hosted by Sagitta elegans and Calanus finmarchicus.

was not possible to determine if the eggs were viable. However, the size range of their eggs was much more variable than those of worms from the definitive hosts (Table 6). The size of the eggs was smaller than those produced in the definitive host except for the two largest worms, which produced eggs of comparable size. Dawes (1956) remarked that the eggs are "always largest in that part of the uterus in front of the ventral sucker". It may well be that the eggs produced first are normally smaller than those produced later.

Except for the size range and the ranges of the body parts of these juvenile trematodes, their appearance conforms to the description of D. varicus given by Dawes (1956). Two of the prime diagnostic features of the species, the ratio between the diameters of the oral and ventral suckers and the position of the ventral sucker, agree precisely. The ventral sucker is centrally to posteriorly located and the sucker ratios are about 3:5 for the worms from both Sagitta and Calanus.

V. C.2.a. Discussion

Although Derogenes varicus has been found in most surveys on the helminth fauna of marine fishes very little is known of its biology; its history is still a mystery. Parts of the cycle can

TABLE 6. A comparison of *Derogenes varicus* from different hosts.

	Sagitta elegans Gulf of St. Lawrence	*Calanus finmarchicus* Gulf of St. Lawrence	Ling Cod and Sculpin (Puget Sound; Lloyd 1938)	Cod; Average Sized Specimens (Gulf of Maine; Manter 1926)
Length (mm)	0.43-1.23	0.30-0.48	1.9-2.0	1.7
Width (mm)	0.19-0.50	0.13-0.19	0.5-0.6	0.5
Oral Sucker (μ)	65-248	62-96	230-250x 280-320	220
Ventral Sucker (μ)	105-350	96-158	380-400x 370-380	370
Pharynx (μ)	40.3-75.0x 46.5-75.0	31.5x33.3	80	85x85
Eggs (μ)	12.4-31.0x 27.8-58.9 (average = 45x20)	none	52-56x 26-28	50x28-30

be pieced together from the literature.

It matures in a wide range of marine fish species and a few invertebrates. Levinsen (1861) found metacercariae in the polychaete Harmathöe imbricata from Greenland and Lebour (1917a) found it in Sagitta bipunctata (?) from Plymouth. It has been seen repeatedly in various chaetognaths, over a wide geographical range (see Sect. V. B.2.b.). Stafford (1905) found metacercariae in Acartia sp. in eastern Canadian waters. Dollfus (1954) made the remarkable discovery of a progenetic metacercaria in Lernaeocera lusci, a copepod parasitic on Gadus lusci. He suggested that the copepod had become infected as a free-living copepodite stage. Zaika and Kolesnikov (1967) found a progenetic hemiurid in 20-40% of the Sagitta elegans arctica from the Barents Sea, which they described as "possibly D. varicus".

In the Barents Sea planktonophagous cod fingerlings were infected with D. varicus, suggesting to Polyanski (1955) that copepods serve as intermediate hosts. It is surprising then that copepods infected with D. varicus have been seen so rarely. The only records of D. varicus in copepods, besides the C. finmarchicus discussed above, were the two records mentioned above. Dragonfly nymphs and copepods have been shown to act as second intermediate

hosts for fresh water hemiurids (Sinitizin 1911; Krull 1935; Thomas 1934, 1939) in experimental life history studies and copepods for marine hemiurids (Hunninen and Cable 1943).

The nature of the first host in Derogenes' cycle is the prime mystery in the life history of this ubiquitous marine parasite. It is probably a mollusc, as it is in nearly every species of digenetic trematode. Most digenetic trematodes have a high degree of specificity to their molluscan hosts. If this is the case with Derogenes, then the mollusc must be as widely distributed as the parasite. There is a possibility, however, that Derogenes varicus is actually a species-complex with a variety of primary hosts over its range. If genetic population differences were non-morphological then no differences would have been noticed in ordinary microscopic examinations.

Very few hemiurid life cycles have been worked out, probably because of the nature of the hemiurid cercariae. All known hemiurid cercariae are the non-encysting cystophorous type (Dollfus 1923). These larvae emerge from the molluscan host as "pre-encysted" cercariae, with several appendages, at least one of which is said to function as a lure and one serves as a delivery tube or injection tube. The parasite shoots out of the "cyst" through the latter tube with considerable force when a slight pressure is applied to the capsule. Several of the other appen-

dages may serve to anchor the cyst or delivery tube to the wall of the digestive tract. The tube pierces the intestinal wall delivering the larva into the haemocoel or coelom of its invertebrate intermediate host (Hunninen and Cable 1943; Macy, Cook and DeMott 1960); the larva then lives as a non-encysted metacercaria in its host's body cavity. These specialized cercariae could be ingested by a filter-feeding or a predaceous plankter, while free living.

The size of the emergent cercaria of Lecithaster confusus, (one of the two marine hemiurids whose life cycle is known) is minute (.085 x .02 mm) (Hunninen and Cable 1943). It showed very little differentiation; even the suckers were poorly defined. At this early stage it would be impossible to recognize a natural infection unless there were corroborative evidence from experimental studies. The smallest D. varicus found in Calanus finmarchicus was 0.30 x 0.13 mm. During the sorting of a plankton sample,however, a small, cylindrical metacercaria was noticed in the manubrium of an Aglantha digitale. It had little internal differentiation, and no ecsoma or cuticular markings. Its length, when stained and mounted, was 0.23 mm, the breadth was 0.08 mm, while the diameter of the oral sucker was 0.043 mm and the ventral was 0.062 mm, giving a ratio of 3.5:5 for the suckers. It is possible that the worm was a Derogenes, but without information on the structure and arrangement of the internal organs specific assignment can only be

conjecture. Since the Derogenes found in Calanus had well-differentiated internal organs, it is probable that they were older metacercariae. The ceiling in the size range of these metacercariae and the fact that it is copepods which have been shown to be the second intermediate hosts in hemiurid life cycles suggests that the animals in Calanus grow to a size maximum and then stop growing. Smaller D. varicus may have been present in the Calanus but they would have been overlooked if their hosts did not produce the red cuticular pigment, which was used as a highly selective indicator to spot the parasitized Calanus (see Appendix II).

Since S. elegans were randomly searched for parasites, it is probable that the size range found is representative of the parasites as they occur in this host. The smallest animals found in Sagitta were about the same size as the largest found in Calanus, suggesting that the parasites are picked up by the chaetognaths by feeding on infected copepods. The relatively large size and the small numbers of D. varicus in Sagitta elegans (see Sect. VIII.B.) suggest that this host functions as a possible third intermediate host in the parasite's life cycle, but is not an obligatory host for the parasite. Fish probably become infected when eating infected Calanus or Sagitta. The parasite then may be passed to the nonplanktophagous fishes through the food chain. In cases of

lack of host specificity, such as this, life cycles may approach the complexity of the food web.

Subfamily Hemiuridae Looss, 1899
Genus Hemiurus Rudolphi, 1809

Hemiurus levinseni Odhner, 1905

Syn. Distomum appendiculatum of Olsson and Juel (in part); D. appendiculatum of Levinsen; D. ocreatum of Linton.

(Fig. 12)

Hemiurus levinseni was the most common and abundant parasite of Sagitta elegans in the Gulf of St. Lawrence. It was always present throughout the period sampled, but had a definite seasonal peak during the fall months (see Sect. VIII.B.1.). Hemiurus levinseni is similar to other marine hemiurids in having a wide variety of definitive hosts. Yamaguti (1958) listed over seventeen fish species. The species has an interrupted north circumpolar distribution, extending into the arctic. It has been recorded from a variety of hosts from Greenland (Odhner 1905), the Barents Sea, Kara Sea, and the Sea of Japan (see Polyanski 1955), the mid-Pacific (Margolis 1963) and the east Pacific coast (Lloyd 1938; McCauley 1960). On the western Atlantic coast: Linton (1940) recorded it in Gadus morhua, Urophycis chuss, Lopholatilus chamaeleonticeps, Merluccius bilinearis, Pollachius virens, and Cyclopterus lumpus from Woods Hole; Manter (1926) found it in G. morhua and U. chuss in the Gulf of Maine; Scott (1969) recorded

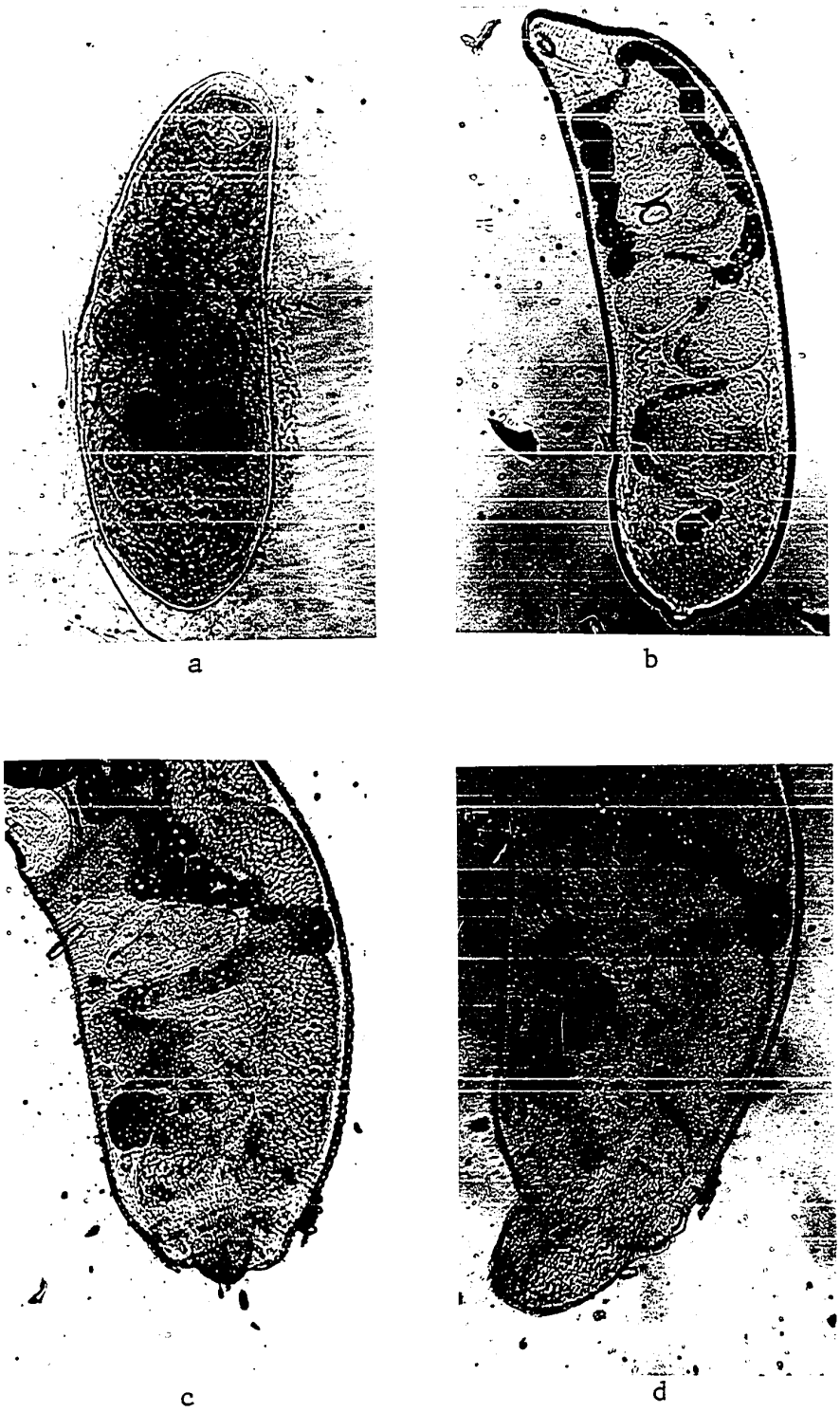


Fig. 12. Hemiurus levinseni from Sagitta elegans
a. Fixed and stained, note retracted ecsoma
b. Live under phase contrast, note partly extended ecsoma
c. Posterior end under phase contrast, with ecsoma partly extended
d. Posterior end under phase contrast, with ecsoma fully extended

it in Argentina silus off the Nova Scotia coast; and in the Gulf of St. Lawrence it was found in G. morhua by Heller (1949), Hippoglossus hippoglossus by Ronald (1960), and Raja laevis and Squalus acanthias by Myers (1959).

A glaring exception to the circumpolar distribution is the apparent absence of the species off Iceland (Rees 1953) and from British waters (Nicoll 1915; Dawes 1956, MacKenzie and Gibson 1970; Williams et al.1970). Pippy (personal communication) found H. levinseni in Salmo salar from England, but was not certain where this migratory fish picked up the parasite.

Specimens were fixed in 5% formalin within their hosts immediately on being caught. They were later stained in Meyer's paracarmine or Grenacher's carmine in situ within the host, to minimize losses. They were removed from their hosts during differentiation, brought into toluene, and mounted in Permount.

This parasite was always seen in the host's body coelom. No H. levinseni were ever found in the digestive tract or in the tail coelom. There seemed to be no special preference for any particular location within the coelom, although some authors (Lebour 1917a; Grey 1930) have reported trematodes commonly in the region of the ovaries. Grey, in fact, reported a "distome" in the tail coelom of a Sagitta sp. It was impossible to determine

the usual disposition of the parasite within the host, since the chaetognaths were invariably dying when caught. When the trematodes were attached to a surface, they were usually bent in an arc around the digestive tract.

The trematodes were identical to specimens found in the definitive hosts, except for the smaller specimens which had poorly developed gonads and vitellaria. The animals were small, cylindrical, elongate hemiurids with characteristic cuticular annuli extending posteriorly to about the level of the vitellaria. The ecsoma, a contractile posterior appendage of unknown function, is usually retracted in the fixed specimens. Figure 12a shows a typical fixed specimen. The diagnostic features of this species of Hemiurus are the 1:1 ratio of oral and ventral suckers' diameter and the structure of the seminal vesicle. The suckers were virtually identical in size, although in some few cases the ventral sucker was marginally smaller than the oral, and the seminal vesicle was bipartite. The ventral sucker lay just anterior to the mid-body.

Hemiurus levinseni found in Sagitta elegans ranged between 0.98 mm long by 0.49 mm wide and 0.30 mm by 0.10 mm. The H. levinseni found in Sagitta were shorter than those found in hake and cod in the Gulf of Maine (Table 7), but the width of these

TABLE 7. A comparison of *Hemiurus levinseni* from different hosts.

	Sagitta elegans	*Enchelyopus cimbrius*	*Scomber scombrus*	Cod and Hake
	Gulf of St. Lawrence	Gulf of St. Lawrence	Gulf of St. Lawrence	(Gulf of Maine; Manter 1926)
Length (mm)	0.98-0.30	0.53	0.69-0.49	1.68-0.99
Width (mm)	0.49-0.10	0.24	0.19-0.15	0.47-0.37
Oral Sucker (μ)	156-59	99	102-81	176-142
Ventral Sucker (μ)	156-53	Collapsed 164x62	105-81	188-136
Pharynx (μ)	77.7x61.1 - 20.4x16.5	?	65.1x68.2 - 49.6x40.3	91x91 - 68x62
Eggs (μ)	27.8x11.1 9.3x3.7 (average = 22.2x9.3)	21.7x15.5	35.2x7.4 - 21.7x6.2	26x10-13; 23-12

Note: *Enchelyopus cimbrius* and *Scomber scombrus* are new definitive host records for *Hemiurus levinseni*.

latter parasites falls comfortably within the range of those from Sagitta. If the same treatment were given to both groups of H. levinseni prior to fixation there would be considerable overlap in the size ranges. Judging from a comparison of the sucker sizes, the animals from Sagitta were generally smaller than those from the fish hosts. Hemiurus levinseni were also found in young four-bearded rockling, Enchelyopus cimbrius, and in mackerel, Scomber scombrus in the Gulf. These are new host records for the species. The size of the individuals found in these planktoniferous hosts were considerably smaller than those found in cod and hake and in fact fall within the range seen in Sagitta.

A large proportion of the Sagitta H. levinseni were progenetic. Individuals smaller than 0.5 mm were rarely egg producing (Fig. 13), while above this apparent threshold the proportion of egg producers increased with increasing size. The largest H. levinseni were, however, not progenetic. The sizes of the eggs, in some cases, were as large as in the specimens from cod and hake (Table 7), but on the whole tended to be smaller. The number of eggs produced by these progenetic individuals increased rapidly with increasing size (Fig. 14).

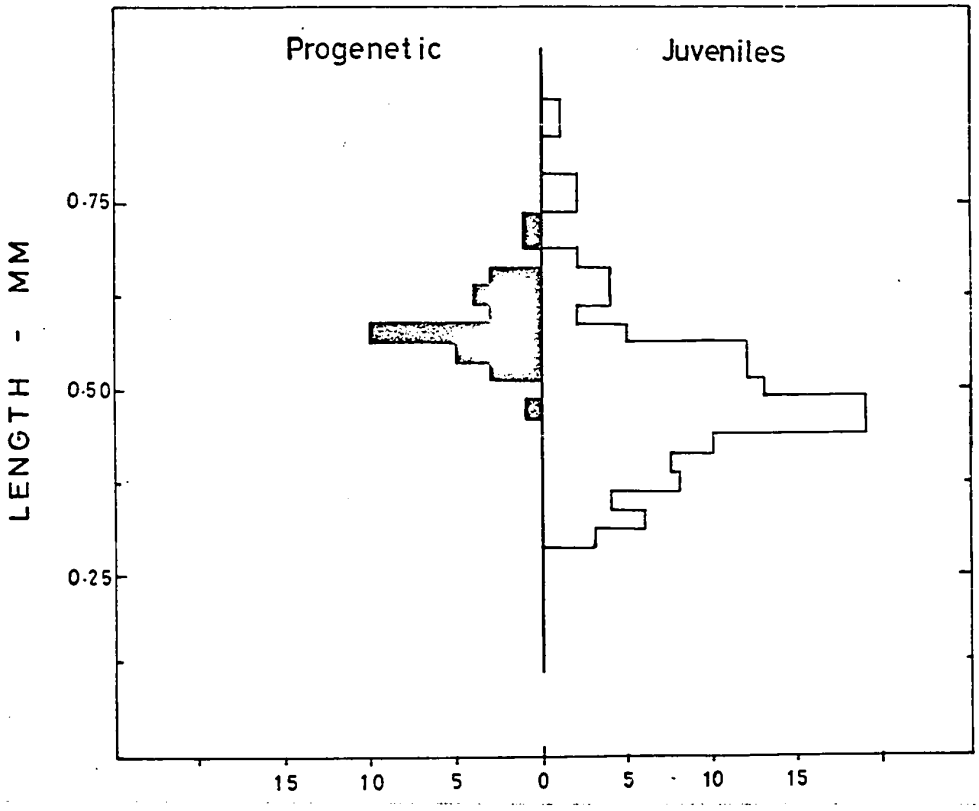


Fig. 13. The relationship between size and progenecity in Hemiurus levinseni from Sagitta elegans.

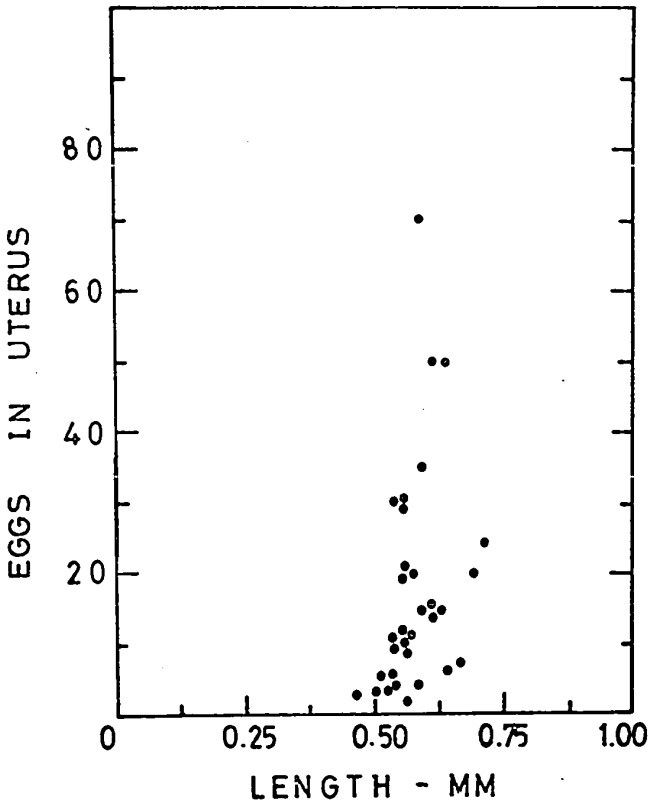


Fig. 14. The relationship between size and egg production in Hemiurus levinseni from Sagitta elegans.

V. C.3.a. Discussion

The genus Hemiurus has a long scientific history. Leeuwenhoek in 1695 saw what is now H. ocreatus in herring at a time when Fasicola hepatica, the liver fluke, was practically the only trematode known and the foundations of taxonomy were just being seeded. For all that this genus has had such a long history and is invariably encountered in studies of marine fish trematodes, its biology is virtually unknown. Not one of the species has had its life history worked out. The general knowledge of the group consists of definitive host records, anatomical studies, and occasional records of planktonic intermediate hosts.

Three species of the genus, H. appendiculatus, H. communis, and H. levinseni, have been found in fishes in the Gulf of St. Lawrence. H. levinseni is a distinctive member of the genus in having its suckers of nearly equal size; most other species have their ventral sucker considerably larger than the oral. Stafford (1904) identified trematodes of the genus Hemiurus with "suckers of equal size" from fishes in Canadian waters as H. appendiculatus. Most of the Hemiurus trematodes found prior to Looss' (1907, 1908) revision of the family Hemiuridea were identified as H. appendiculatus. Manter (1926)

later placed Stafford's Hemiurus as H. levinseni.

Polyanski (1955) found H. communis "very seldom" and H. levinseni "widely distributed" in Barents Sea fishes; no mention was made of H. appendiculatus. He concluded that, as H. communis was one of the most wide spread fish parasites in the Atlantic, it reached the end of its range in the Barents Sea, where it was replaced by H. levinseni, a more arctic form. H. levinseni seems to be absent from warmer water regions of the eastern Atlantic (see Sect. V.C.3), although it has been found in Woods Hole (Linton 1940) and Puget Sound (Lloyd 1938).

Lebour (1935) found Hemiurus communis in Acartia clausi off Plymouth, but no member of the genus was seen in Sagitta bipunctata (?) (Lebour 1917a). Meek (1928), however, found a trematode identified as H. communis by Lebour in S. setosa and possibly S. elegans off the Northumberland coast.

Linton (1927) found two progenetic distomes in a S. elegans from Woods Hole. He attempted to place those trematodes as "Distomum ocreatum Molin, which has been referred by Lander to Hemiurus crenatus (Rud.) Lühe" but Dollfus (1960) noted that "Distomum ocreatum Molin" of Linton was a composite species which

was only a part of Brachyphallus crenatus (Rudolphi) Odhner and that the "Hemiurus crenatus (Rud.) Lühe" of Lander was given the name Brachyphallus affinis by Looss (1907).

Myers (1956) also found a progenetic trematode in S. elegans from St. Andrews, which she identified as H. levinseni. She pointed out the similarities between her trematodes and Linton's and suggested that the latter were also H. levinseni. Linton's drawings resembled the Sagitta H. levinseni from the Gulf of St. Lawrence; except for the large size of his worms, the measurements also match. Although the suckers of Brachyphallus are nearly identical in size, as in H. levinseni, the vitellaria are lobed and the ecsoma is proportionately much larger than in H. levinseni. Linton's drawings showed unlobed vitellaria and the retracted ecsoma which seems to be characteristic for H. levinseni in the preserved state (Fig. 12).

There are no records for intermediate hosts of H. levinseni other than Sagitta elegans. Undoubtedly, some mollusc is the first intermediate host. Dollfus (1960), after commenting on how common distomes were in chaetognaths, posed the question of whether there were any species of trematodes which have their metacercariae only in these hosts. This may be the case for H.

levinseni or it may be that the planktonic crustacea within this parasite's range have not been searched well enough to uncover the parasite. Some of the records of Hemiurus appendiculatus in copepods from the eastern Atlantic may well be mis-identified H. levinseni. Stafford (1904) found H. appendiculatus (?) in Acartia, but it is uncertain if these worms have the equal-sized suckers which would place them as H. levinseni. Cooper (1915) also mentioned H. appendiculatus in Acartia and Pratt (1898) recorded Distomum appendiculatum from "copepods" in Long Island Sound. However, the taxonomic status of all these records is uncertain.

Polyanski (1955) found eight species of hemiurids in Barents Sea fishes, one of which was H. levinseni. The life cycle of one of these species, Lecithaster confusus, was known. Another of the species, H. communis, was seen infrequently. Since the hemiurids have cystophorous cercariae (Dollfus 1950), there are probably at least seven "species" of cystophorous cercariae parasitizing Barents Sea molluscs. Tschubrik (1952) found two different cystophorous cercariae in Natica clausi in the Barents Sea; Cercaria appendiculata Pelseneer and C. naticae sp. nov. The adult form of both cercariae is unknown. The new cercaria was rather remarkable; it was ensheathed in a narrow cone 0.34 mm long

by 0.06 mm wide. At the posterior end of the cyst was a tail (0.15 mm) which bore eight filamentous, noncontractile appendages, each about 0.50 mm long, on the tip. The cercaria itself was 0.28 mm long by 0.04 mm wide. The cercariae were outside the cyst when they left the rediae, but retracted within a few hours. They remained active for about four days in the laboratory. They alternately swam and drifted. Tschubrik speculated on the adaptations of this cercaria for a planktonic life. Presumably this organism left its benthic host and swam upward, spreading its canopy of appendages to prevent sinking while "resting". Thus it would move progressively higher in the water column.

Most of the other known cystophorous cercariae are minute. Generally, the cysts are spherical and under 0.1 mm in diameter (Table 8). Hunninen and Cable (1943) showed that after being eaten by Acartia, Lecithaster confusus grew from 0.08 mm to 0.4 mm in nine days. The small size and spherical shape of these highly specialized cercariae appear to be an adaptation for being filtered from the water by a small filter feeder, such as a copepod. On the other hand, the shape, the size, and possibly the swimming behaviour of C. naticae duplicate those of a copepod. It is possible that this cercaria is adapted morphologically and behaviourally for being picked up by a large predator, such as a chaetognath. Certainly the size of the cercaria makes it

TABLE 8. The sizes of some hemiurid cercaria "cysts".

	Metacercarial Hosts	"Cyst" Diameter (mm)	Reference
Halipegus occidualis	copepods and ostracods (fresh water)	0.085	Macy, Cook, DeMott 1960
Dichadena acuta	unknown	0.070 - 0.075x0.054	Cable & Nahhas 1963
Lecithaster confusus	*Acartia clausi*	0.05	Hunninen & Cable 1943
Bunocotyle cingulata	*Poppella guernei*	0.05x0.06	Chabaud & Biguet 1954
Cercaria sphearula	Cyclops	0.09	Thomas 1934
C. appendiculata	unknown	0.065x0.104	Tschubrik 1952
C. naticae	unknown	0.34x0.06	Tschubrik 1952

improbable that the cyst would be ingested by a copepod.

Knowledge of the place of the Chaetognatha in marine food chains is very scanty. It is almost a cliche that the Chaetognatha are a two-edged sword, predator and prey, but little information is available on chaetognaths as prey. If H. levinseni or some other trematode, which is nonspecific to its definitive host, can be shown to be specific to a chaetognath, then the presence of this parasite in a fish species can be used as a label, much like a radioactive element on a metabolite, to trace the pathways through which chaetognath energy travels in the marine food web.

Class Cestoda Carus
Subclass Eucestoda Southwell, 1930
Order Tetraphyllidea Braun, 1900

Scolex pleuronectis Mueller, 1788

Syn. S. polymorphous Rudolphi, 1819; S. delphini Stossich, 1898.

(Fig. 15)

Two "Scolex pleuronectis" type plerocercoids were found in Sagitta elegans from the Gulf of St. Lawrence. The name Scolex pleuronectis is a generic catchall for unidentifiable tetraphyllidean larvae. Adult tetraphyllidean cestodes are parasites of the spiral valves of elasmobranchs. No life cycle for the group has

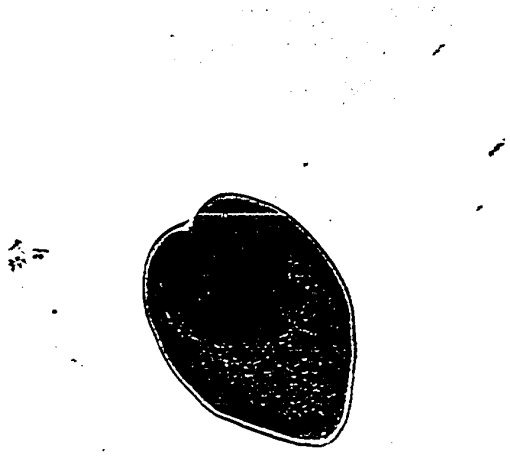


Fig. 15. Scolex pleuronectis from Sagitta elegans.

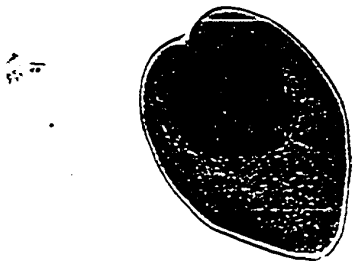


Fig. 15. Scolex pleuronectis from Sagitta elegans.

been completed, but the relatively undifferentiated larvae have been seen frequently in copepods, ctenophores, various decapod crustacea, siphonophores, turbullarians, lamellibranchs, cephalopods, marine mammals and about eighty species of teleosts (Dollfus 1923a, 1923b, 1924, 1929, 1931, 1964, 1967; Wardle and McLeod 1952; Polyanski 1955). Dollfus (as above) has reviewed the literature of cestode larvae in plankton and other invertebrates. Very few cestodes have been recorded from chaetognaths (see Section V. B.2.b).

The cestodes from Sagitta were fixed with 5% formalin in situ within the host, stained in Meyer's paracarmine, and mounted in Permount.

One of the S. pleuronectis was found in a S. elegans off Grande-Rivière; the other was in a S. elegans from the Bay of Islands, Newfoundland. The hosts of both cestodes were about 30 mm long. In both parasites the holdfasts were invaginated; four suckers were seen. The S. pleuronectis from Grande-Rivière was 0.20 mm long by 0.19 mm wide and had suckers 0.053 mm in diameter; the cestode from the Bay of Islands was 0.34 mm long by 0.27 mm wide with 0.062 mm suckers. No calcareous granules or pigmentation were seen.

V. C.4.a. Discussion

The Tetraphyllidea are a group with very uniform anatomy, so that it is almost impossible to identify these adults if the holdfast is missing. It is suspected that the Scolex type larva represents a number of species, since feeding experiments with these larvae have produced adults of different species (Yamaguti 1934; Wardle and McLeod 1952).

It has been suggested that the life cycle is similar to that of the Pseudophyllidea (Hyman 1951), with a copepod as the first intermediate host, and perhaps a fish which is part of the diet of the elasmobranch definitive host, as the second intermediate host. Yamaguti (1959) noted "1st stage probably in crustacea, 2nd plerocercoid stage (Scolex polymorphous) in fish, cephalopods". An experimental study on the life cycle was done by Riser (1956), who fed the eggs of Acanthobothrium hispidum to the splash-pool copepod Trigriopus fulvus. After 15 days, a 0.15 mm procercoid was seen in the haemocoel. The organism had a well-developed cercomere at the posterior end and a "huge apical organ"; no complex holdfast or sucker structure was mentioned or shown in the drawing. If this is the general pattern of development within this group then the Scolex found in Sagitta, with well-developed holdfast and lacking a cercomere, was probably a plerocercoid

stage picked up from an infected copepod. A variety of life cycles are probable in this group, since different species have piscivorous sharks, benthic feeding rays, or planktonivorous elasmobranchs as definitive hosts. It is probable that plankton feeders, such as the basking shark, have tetraphyllidean parasites with life cycles involving only two hosts (see Appendix II).

Since cestodes have been found so rarely in chaetognaths, these hosts must be accidental and probably represent a cul-de-sac for the parasites. Without more information on the life cycle it is impossible to determine the mode of infection of the chaetognath. However, from Riser's results we can expect that the chaetognaths did not become infected through ingesting the egg or onchosphere, since the larvae in this resembles a plerocercoid more than a procercoid. In addition, it is more likely that a chaetognath would have ingested an infected copepod than a minute egg or onchosphere.

It is impossible to determine how long these parasites had been infecting the chaetognaths, but it is probable that the infections were more recent than long established, since if cestode infections "took" in this host, a greater incidence would be expected by simple accumulation. Certainly some rejection of cestode larvae is to be expected, since no tetraphyllideans of the

type seen in Calanus (see Appendix II), were found in Sagitta. If the chaetognath fed randomly on copepods we would expect to have seen this cestode and possibly others in Sagitta, unless they were rejected.

Phylum Nematoda Rudolphi, 1808
Superfamily Ascaroidea Railliet et Henry, 1915
Family Anisakidae Skrjabin and Karokhin, 1946
Subfamily Anisakinae Railliet et Henry, 1912

Contracaecum type larva Myers, 1960

(Fig. 16)

Although high incidences of nematodes have been reported in some Sagitta populations, only two Contracaecum type larvae were found in Sagitta elegans in the Gulf of St. Lawrence. Myers (1960) noted that the digestive tract in the larval Anisakinae resembles the adult stages, but since "many genera possess the same type of digestive tract it is difficult if not impossible to assign the larval stages to genera". The characteristic cephalic structures of the genera and species only appeared after the final, adult moult. She proposed classifying larval stages as Phocanema type, Anisakis type, Raphidascaris type, or Contracaecum type larvae depending on the structure of the digestive tract.

Anisakids are extremely common marine and fresh-water parasites, with adult stages in piscivorous fishes, birds, or

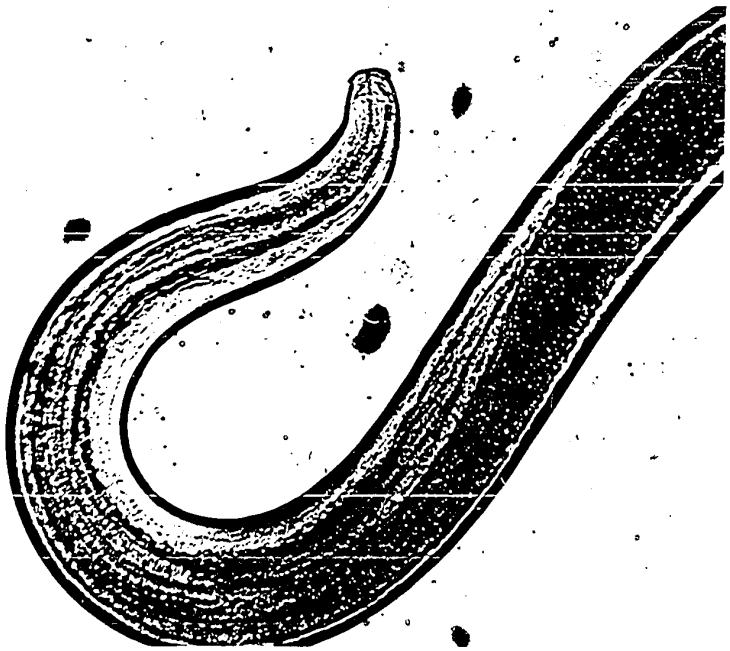


Fig. 16. Contracaecum type larva from Sagitta elegans.

marine mammals. Individuals of the genus Contracaecum are probably the most common. Yamaguti (1961) listed 77 species of the genus in fishes alone. The systematics of the genus are extremely confused and Punt (1941) suggested that many of the species in fishes could be reduced to synonyms. The degree of morphological and ecological plasticity of the genus certainly needs examination. This parasite is apparently cosmopolitan. Polyanski (1955) reported C. aduncum, the most commonly found species, in 37 Barents Sea fishes; Berland (1961) reported it in 20 species of Norwegian fishes as adults and in 32 as larvae.

The nematodes were fixed within the hosts in cold 5% formalin and were cleared in lactophenol. The identifications were confirmed by Dr. B.J. Myers.

Both of the Contracaecum type larvae were found in Stage III S. elegans. They both had a posterior projecting oesophageal ventrical appendix and an anterior projecting intestinal caecum, although the latter was not as easily distinguishable (Fig. 15). These two digestive tract appendages are characteristic of the Contracaecum type larvae. No generative organs were seen, although a set of anal glands were seen in one of the larvae. Both worms were considered to be III-stage larvae, principally due to their size.

V. C.5.a. Discussion

Although the life cycles of the anisakids have not been worked out in elaborate detail, a number of good experimental studies, done mainly on species of Contracaecum, have demonstrated the basic patterns (Markowski 1937; Thomas 1937; Punt 1941; Huizinga 1966, 1967). The principal unknown seems to be the effective roles of the various intermediate hosts. The definitive hosts and the intermediate hosts are relatively unspecific. The successive transfer of larvae between intermediate hosts, has been demonstrated experimentally by Huizinga (1967). If this is also true of the definitive hosts, a web-like life cycle picture must be drawn, with probabilities calculated for the different pathways.

The eggs of the adult female are passed with the hosts' feces. The eggs of Contracaecum spiculigerum (Huizinga 1966) and the eggs and larvae of C. aduncum (Berland 1961) sink. The eggs embryonate and hatch as second stage larvae ensheathed in the first stage cuticle. It generally is assumed that five stages, each separated by a moult, complete nematode life cycles. This free-living larva is ingested by some arthropod or fish. Exsheathing took place in the first intermediate host with no further development. A controversy has arisen over whether one or two intermediate hosts are necessary to complete the life cycle (Berland

1961). Although Huizinga (1966) managed to infect fish and copepods directly with newly hatched C. spiculigerum, a high proportion of the larvae was passed out of the fishes' intestine. He concluded that though cycles can be completed with only one intermediate host, a cycle in which fish pick up the nematodes from infected crustacea was more usual. This was also Berland's opinion. The infective larvae were then passed on to the piscivorous definitive hosts via infected prey.

Larval anisakids, usually identified as Contracaecum sp., have been found in numerous marine invertebrates. Apstein (1911) found larval nematodes in the haemocoel of Calanus finmarchicus, Eucheata sp., and Pseudocalanus sp. from the North Sea which were later identified as Contracaecum sp. by Wülker (1929). Markowski (1937) experimentally infected Acartia bifilosa and Eurytemora affinis with C. aduncum. Scott (1957) found Contracaecum sp. larvae in three mysid species from Bras d'Or Lake. Margolis and Butler (1954), Kruse (1957), Uspenskaya (1960) and Hutton, Ball and Eldred (1962) found larval Contracaecum sp. in shrimp.

Relatively high incidences of nematodes have been reported in some chaetognath populations. Russell (1932) reported 7% of S. setosa off Plymouth infected and Elian (1960) found 2% of the S. euxina from Roumanian waters similarly infected. M. Ya. Ass (1961)

reported 33% of Sagitta sp. in the Black Sea infected with larval Contracaecum sp. He proposed that Sagitta played an important role as intermediate host in the life cycle of the nematode and considering the high incidence in the Black Sea he was certainly justified in his conclusion. Larvae found in chaetognaths generally seem to be III-stage. None of the minute, recently hatched larvae have been reported from chaetognaths. Considering their small (300μ) lengths and minuscule breadth, this is not too surprising. Experimental studies are necessary to determine if Sagitta is an acceptable host for these Contracaecum and if these hosts would actually ingest the hatched larvae. The extremely low incidence of Contracaecum type larvae in the Gulf of St. Lawrence S. elegans suggests that this host plays a negligible role in the nematode's life cycle in these waters. Since the parasite is not specific to chaetognaths, the differences in incidences between the chaetognath populations is probably due to ecological factors.

V. D. Conclusions

Sagitta elegans in the Gulf of St. Lawrence was parasitized by Metaphrya sagittae, metacercariae of Derogenes varicus and Hemiurus levinseni, the plerocercoid (Scolex pleuronectis) larvae of an unknown tetraphyllidean cestode, and Contracaecum type larvae. Metaphrya sagittae and Hemiurus levinseni were

regular parasites of S. elegans, while Derogenes varicus was only an occasional parasite, and Scolex pleuronectis and the Contracaecum type larvae were quite rare. With the exception of the protozoan, all of the parasites were larval stages of organisms with complex life cycles, for which S. elegans functioned as a potential intermediate host. Only in the case of H. levinseni was there evidence for this host being of importance in the parasite's biology.

The larger individuals of both hemiurid species tended to be progenetic in S. elegans. The evolutionary (adaptive) significance of progenesis in these hosts is obscure, since for these eggs to become infective they would have to erode their way out of the host's coelom. The conditions leading to progenesis in these organisms are unknown, but it was shown to be a function of the parasites' sizes (Fig. 11 and 13). None of the D. varicus infecting Calanus finmarchicus were egg-producing, but progenetic hemiurids have been reported from copepods (Chabaud and Biguet 1954). Progenesis may be an adaptation to enable the parasite to become egg-producing directly on entry into the definitive host. Istock (1967) suggested that complex life cycles, i.e. cycles involving "passage through two or more ecologically distinct phases," with the result of loss or suppression of the larval or adult phases. If, however, digenetic trematodes were originally

parasites of molluscs, as has been suggested by Rogers (1962) and others, due to the greater degree of specificity to molluscan hosts than to their vertebrate definitive hosts (the longer the association with a host, the greater the chance for specificity to have developed), then the tendency toward progenesis actually may be a primitive condition rather than a recent adaptation. Knowledge of the stimuli which produce the precocious state might help to clarify its evolutionary significance and whatever adaptive advantages it gives the parasite.

All of the helminth parasites of S. elegans had in common a lack of host specificity in their final host.

Polyanski (1955) pointed out that planktophagous fishes have a parasitic fauna characterized by a low diversity. The parasites of planktophagous fishes in the Barents Sea were exactly the same parasites found in S. elegans in the Gulf of St. Lawrence; "Hemiuridae, Scolex polymorphous, and Nematodes (Contracaecum and Anisakis)". The Hemiuridae, the Tetraphyllidea, and the Anisakidae, with a few exceptions, seem to be the principal parasites with complex life cycles found in marine planktonic organisms. All of the problems of finding a host are greatly multiplied by the three-dimensional nature of the pelagic environment. Few types of parasites which have complex life cycles

involving transfer between hosts seem to have adapted to the pelagic marine environment and those which have are characterized by a low degree of host specificity, suggesting that this is a difficult niche to fill.

VI. The Biology of *Sagitta elegans*

VI. A. Introduction

Sagitta elegans is the dominant chaetognath and one of the major faunal elements of the plankton of the Gulf of St. Lawrence. With the exception of rare catches of young *Eukrohnia hamata*, it is the only species of chaetognath found in the shallower waters of the Gulf of St. Lawrence.

VI. A.1. Geographical Distribution

Although the knowledge we have about its basic biology is scanty, few planktonic organisms have been studied as extensively as *Sagitta elegans*. It has a circumpolar distribution, extending out from the subarctic and arctic coasts of the Atlantic and Pacific Oceans to about the limits of the continental shelf, and similarly ringing the shores of the Arctic Ocean. It is the chaetognath typical of the neritic regions of the more northerly parts of the entire northern hemisphere.

On the West Atlantic coast it has been described from the Gulf of St. Lawrence (Huntsman 1919), the Newfoundland Banks (Alvarino 1956), the Gulf of Maine (Bigelow 1926; Redfield and

Beale 1940), Georges Bank (Clarke, Pierce and Bumpus 1943), and from Martha's Vineyard to near Cape Hatteras (Bigelow and Sears 1939). The southern limit of the distribution along the western Atlantic coast seems to be at the level of Cape Hatteras, although breeding has not been recorded south of Chesapeake Bay. In the East Atlantic, S. elegans has been found as far south as the Bay of Biscay (Alvarino 1965) and from there extending north, around the British Isles (Russell 1932a; Pierce 1941; Fraser 1937; Bainbridge 1963), throughout the North Sea (Apstein 1911), the Norwegian Sea (Wiborg 1954, 1955), and the Barents Sea (Bogorov 1940). The range extends along the Siberian coast through the Kara Sea (Ponomareva 1957).

The major exception to the description of S. elegans as a neritic species is its distribution in the Pacific Ocean. Bieri (1959) found this species right across the North Pacific from the Bering Sea to about latitude 40° or 41°. This facet of the distribution of the species has yet to be explained satisfactorily. Lea (1955) found S. elegans along the British Columbia coast, decreasing in abundance from the shore seaward. However, Sund (1959) did not find this pattern in the Gulf of Alaska. He found a correlation between areas of greatest density "and waters of highest salinity (32.8‰) and moderately warm temperatures (12 - 13°C)". The increase of density seaward agreed well with Bieri's

(1959) trans-Pacific results. He found densities increasing (seaward) into the Pacific Subarctic watermass, with the centre of concentration (densities >1000/1000 m^3) extending out from the southern Alaskan coast to the mid-Pacific at a latitude of about 45^{o}N. A similarly dense area in the western Pacific was found off the Kurile Islands at the mouth of the Sea of Okhotsk. The analog of this trans-Pacific distribution has not been found in the Atlantic Ocean. S. elegans has been recorded off the Faroes (Fraser 1937), off Iceland and through Denmark Strait (Ritter-Zahony 1914), but there does not seem to be any record for this species in the central North Atlantic extending out over the waters of much greater than shelf depth.

In the Eastern Arctic the species has been described from East Greenland waters by Ussing (1938) and the coastal waters of West Greenland by Kramp (1917, 1918) and Dunbar (1940). Its range extends through the eastern part of the Arctic Archipelago (Dunbar 1940, 1962; Grainger 1961) to Hudson Bay (Dunbar 1962) and the western part of the Archipelago (Grainger 1965). Its presence has also been recorded in the Beaufort Sea by Bieri (1959), who found the chaetognath decreasing in density as the ice pack was penetrated. Whether this limitation to the distribution was due to the direct or indirect influence of the permanent pack ice was not clear, but the species does breed in the ice-covered waters of

the Arctic Archipelago (Dunbar 1962). S. elegans has not been found in the Arctic Ocean (Bogorov 1946; Grainger 1965; Harding 1966) beyond the continental shelf. It is especially interesting to note that Grainger (1965) found S. elegans in the South and East Beaufort Sea, Amundsen Gulf, and on the Polar Continental Shelf extending into the Arctic Ocean, whereas no specimens were caught in the Arctic Ocean itself at a distance of about 100 miles from the Shelf stations. The temperature and salinity profiles from all of these stations were nearly coincident.

VI. A.2. Temperature and Salinity Range

Sagitta elegans is a eurythermal and euryhaline organism. It has been found in waters with temperatures ranging from -1.7, the freezing point of sea water, to an extreme of 24°C (Table 9) and salinities of 13‰ to 35.2‰. As can be seen in the table the temperature of 24°C was exceptional. In fact, Cowles (1930) noted that when high temperature conditions were reached in Chesapeake Bay the S. elegans population declined. The normal temperature range seems to extend from the freezing point to about 16°C.

McLaren (1963) has shown that there is an inverse relationship between the environmental temperature and size at maturity in Sagitta elegans and suggested a mechanism by which temperature

TABLE 9. Temperature and salinity environment and depth range of Sagitta elegans

	T° C	S‰	Depth (m)	Remarks
ARCTIC				
West Coast of Greenland Kramp 1939	-1.7 to 5.2		Recorded to 1000-2000m; noted as common between 30 & 45m	Non-closing nets used
Baffin Bay & North Labrador Dunbar 1941	-1.39 to 1.0	28.04 to 32.93		
Western Arctic Islands & Beaufort Sea Granger 1965	-1.7 to 9.0	18.0 to 34		
Ogac Lake, Baffin Island McLaren 1969	6-10 summer	18 to 29	to 30m	Depth of aerobic layer is limited to 30m
EAST ATLANTIC				
English Channel Russell 1931, 1933a	8-16	35.00 ± .2	to 50m	Bottom at about 50m
Scottish Coast Fraser 1952	-0.5 to 13.4	32.75 to 35.5	to 1000 + m	Non-closing nets used. Peaks of abundance at 50m & 1000m
Norwegian Sea Østvedt 1955	0 to 8.6	34.9 to 35.2	100-600m	Never caught in large numbers. Closing nets used. (517 S.elegans in 200 tows)
Oslofjord Jakobsen 1971	6-15	20 to 34	0-164m	Optimum depth of the largest animals - 85 to 90m; majority at 60-120m
WEST ATLANTIC				
Bay of Fundy Huntsman & Reid 1921 * from Vachon 1917	7.6 to 11.3*	30.18 to 32.6*	to at least 175m	Centre of abundance 75-125m
Gulf of Maine Redfield & Beale 1940			to 100m	Scarce offshore beyond the 100m isobath
Georges Bank Clarke, Pierce & Bumpus 1943	2.5 to 16	32.1 to 33.5	to 200m	
Chesapeake Bay Cowles 1930	0-24	as low as 13		
Gulf of St. Lawrence	-0.5 to 13	22 to 32.95	0 to 125m	
PACIFIC				
British Columbia Coast Lea 1955	7 to 19 (surface T)	26.5 to 33		
Mid-Pacific Bieri 1959	3 to 5	33.5 to 34.5	Maximum abundance at about 100m	Found at southmost station in 200-400m net & not in 0-200m net
Gulf of Alaska Sund 1959	12-13 (greatest abundance)	32.8 (greatest abundance)		

might limit the species' range. The warmer the water temperature was, the more quickly the individuals matured and the smaller the size at maturity. Both Russell (1932a) and Dunbar (1940) had related ovary length to body length. They both had found that ovary length increased in a curvilinear fashion with body length. Therefore, the larger, slower-growing, cold water individuals would be more fecund, since they would produce a greater number of eggs. McLaren then calculated the relationship between environmental temperature and the number of eggs produced. Calculations indicated that the intrinsic rate of increase (r) increased with temperature to about 14°C and then dropped sharply. The decrease of r with temperatures above 14°C was due to a drop in egg production at the higher end of the range.

Sameoto (1971) confirmed McLaren's results and suggested that inclusion of a mortality factor in the calculations would lower the temperature at which r=0, thereby lowering the maximum temperature at which S. elegans can maintain a population without immigration. He concluded that the range "will be limited to waters with a mean temperature less than 12°C".

Sameoto also extended McLaren's model to include the effects of temperature on the numbers surviving at various body

lengths and on changes in population size. The lower the temperature is, the longer the time it takes to reach maturity and the fewer the survivors. The number of offspring in the next generation is equal to the product of the number of animals surviving to maturity and the number of eggs produced by each animal, the latter being temperature dependent as explained above.

This analysis agrees very well with observations of the temperature range of the animals. The temperatures listed in Table 9 rarely went above 12°C. The major exceptions were the data from the British Columbia coast (Lea 1955) and Cowles'(1930) findings from Chesapeake Bay. In the former case only the surface temperatures, which cannot be taken as representative of the species' range, were listed. In Chesapeake Bay, Cowles mentioned that the species was abundant only in the cooler months of the year. The remaining temperatures generally fell well below the critical 12°C temperature.

The temperatures of Sagitta elegans in the Gulf of St. Lawrence fell well within the critical extremes for the species. Although the surface waters heated up to 17°, the bathymetric distribution of the species must be taken into account (see Section VII.B.). In general, the younger individuals were found in the surface waters and took up gradually deeper distribution as they

increased in size. Throughout the winter months the water column was isothermal about the 0° mark. Gradual warming took place after the surface ice melted in April, building up a thermocline structure by May. At the mouth of the Baie des Chaleurs the thermocline was at about 50 meters depth through the summer months and with autumnal cooling of the surface waters and deeper mixing due to seasonal storms, it began to decay and descend; on October 23, 1968, the thermocline was at 65 meters. Below 60 meters temperatures remained less than 1° throughout the year, with the exception of the fall, when the colder isotherms descended and the bottom waters warmed.

S. elegans is a euryhaline as well as a eurythermal species. It has been recorded in waters of 13‰ in Chesapeake Bay by Cowles, although this was probably exceptional. McLaren (1969) and Grainger (1965) both have recorded it in the Arctic from waters as low as 18‰. It has been recorded most frequently, however, from waters ranging in salinity from 28‰ to 34‰ (Table 9).

The salinity at the mouth of the Baie des Chaleurs during the sampling period ranged from about 28‰ at the surface to about 33‰ at the bottom of Station HP 112M. Lacroix and Legendre

(1964) recorded catches of S. elegans in August 1962, in the surface waters of the Restigouche estuary near the head of the Baie, where the salinity was 22‰, but not from a station closer to the head where the salinity was 17‰. It was not clear if this absence was an effect of the low salinity, since the general environment at this station was special; the bottom was only seven meters and the turbidity was five times greater than that in the Baie.

The maximum salinity limit in the Pacific, western Atlantic, and Arctic was about 34‰. On the eastern Atlantic there were numerous records of S. elegans from waters at 35‰ plus. Russell (1932a, 1932b) has recorded S. elegans breeding in the well-mixed English Channel waters at salinities of 35± .2‰. The distribution of this species on the East and West Atlantic may be limited by the operation of different parameters.

VI. B. Life History of Sagitta elegans

The growth and breeding cycle of Sagitta elegans has been studied extensively over much of its range. Russell (1932a) and others have pointed to temperature as the causal factor in determining body length at maturity and, since these organisms are semalparous, in determining the length of the life cycle. The

cycle has never been studied in the Gulf of St. Lawrence. Elucidation of the life history in the Gulf was particularly pertinent, since this water body separates the Gulf of Maine, where the species breeds annually (Redfield and Beale, 1940) from the Arctic waters where a biennial cycle has been found (Dunbar 1941, 1962).

Since there are three vertically stratified water layers in the Gulf, different temperature environments would be encountered by the species depending on its vertical distribution. Therefore, a priori, the nature of the species' vertical distribution should play an important role in determining its growth and breeding pattern.

VI. B.1. Historical Review

Russell (1932a) was the first to study life cycles of chaetognaths by using large samples consistently collected at one station over an extended period to construct a time series of length-frequency histograms. In chaetognath life history studies, length is considered a function of age. Since growth is continuous, rather than discrete, as it is in copepods, there is no better way to determine the age of individuals in a natural population than by length measurements. The studies done prior to Russell used clues like the presence of free eggs in the plankton and the

presence of mature individuals to delimit the life histories.

Russell (1932a) studied the biology of Sagitta elegans in the English Channel and concluded that S. elegans produced four or five generations per year. Successive generations were produced in June-July, September, February, and April-May. Russell could not distinguish if one or two broods were produced in June-July. Wimpenny (1936) studied the life history of S. elegans in the North Sea and found two breeding periods and a possible third in October.

Pierce (1941) concluded there was only one spawning period in the Irish Sea, extending from January through May. These findings were based on the appearance and continuance of mature Stage III individuals in the plankton; Stage III S. elegans first appeared in small numbers in December and continued to be caught through May. Pierce's data, however, can be reinterpreted as indicating breeding from March to September, since the 5 mm size class, which is very close to the hatching size (3 mm), first appeared in March and persisted until September. Unless there was continuous recruitment during this period, growth would have removed this size class from the population. The presence of newly hatched individuals into September suggests that mature Stage III animals were present at least until August. Pierce's conclusions

were justifiable based on his catches of Stage III S. elegans, but from the above reasoning it is equally justifiable to suggest that these animals were present into August, but missed by the sampling program.

Jakobsen (1971) sampled the water column in Oslofjord to a depth of 164 meters over a period of several years, using a closing Nansen net and Beyer's Epibenthic (hyperbenthic) Toboggan. Spawning began during April and continued until late summer or autumn. Growth of the new brood progressed linearly at 0.15 mm per day until autumn and began again in the spring. The breeding size of S. elegans in Oslofjord was about 21 mm.

Huntsman and Reid (1921), looking at the development of young and eggs, found S. elegans breeding successfully on the Magdalen Shallows of the Gulf of St. Lawrence, but unsuccessfully in the Bay of Fundy. They suggested that the population in the Bay was maintained by recruitment from the Gulf of Maine. The spawning season in the Gulf extended from May to August, while eggs were found in the Bay of Fundy from April to October.

Redfield and Beale (1940) found Sagitta elegans to be the only endemic chaetognath in the Gulf of Maine and attributed its permanence to "the relatively stable eddy on Georges Bank."

Although the primary concern of their study was the use of different chaetognath species to obtain information about water movements, they concluded that there was an annual breeding cycle in the Gulf of Maine, with the spawning taking place in late spring and the summer. These results were confirmed by Sherman and Schaner (1968).

Clarke, Pierce, and Bumpus (1943) suggested that there were two generations per year on Georges Bank. Their sampling ran from September 1939 to June 1940 and March 1941 to June 1941. Their results led to the conclusion that there was one main spawning period from April to May and a second generation in late summer and early autumn. It is not clear from their data, however, whether the May recruits were responsible for the second generation. In January few Stage III individuals were encountered; by March and April most of the population was at Stage III. Following this, in May and June, the numbers and size of the Stage III animals diminished, suggesting spawning and death. Since 4 mm individuals still were seen in late June the authors suggested a second generation. The sampling spacing and the cut-off of the sampling program in June may have camouflaged a different pattern, such as continuous or discontinuous spawning within the same generation. There is one significant piece of information which suggests that Clarke et al. may have been right about there being more than one generation per year on Georges Bank. A mode of 16

mm Stage III S. elegans was seen in September. All other Stage III modes were around 23 mm.

Zo (personal communication) found two distinct broods per year in Bedford Basin, Nova Scotia; one in the spring and one in the autumn. In adjacent St. Margaret's Bay, Sameoto (1971) concluded that the S. elegans population was polymodal throughout the year, presumably as a result of the rapid flushing rate of the Bay, and suggested that the modes represented subpopulations. An attempt was made to analyze the polymodal histograms by fitting normal curves to each mode. The resulting curves were interpreted as representing four subpopulations resident in the Bay and a fifth which entered from coastal waters and eventually merged with one of the subpopulations. Two generations were produced by each subpopulation during the year, with breeding occurring in the spring and in the fall.

The southern-most record of breeding in the West Atlantic is from Delaware Bay (Deevey 1960). She found S. elegans present in some years and absent in others. Sampling was limited to the surface and sub-surface waters. No mature S. elegans were found when the temperatures rose above 17°C, although immatures were found. She believed that the species spread south from the Cape Cod area in the winter and spring, breeding in areas where the

species' environmental extremes were not exceeded and dying out at the southern limits of its range each year. The maximum size of Stage III animals was similar to that found by Clarke, Pierce and Bumpus for Georges Bank. Both mature Stage III and eggs were found from February to late May. From the histograms presented there may have been more than one brood per year, but the data were insufficient both in time and in the depth of sampling to be certain.

In the Arctic the main breeding takes place during the summer (Ussing 1938; Kramp 1939; Dunbar 1940,1941,1962; McLaren 1969), although Ussing and Dunbar (1941) found evidence for winter spawning. Kramp in West Greenland, and Ussing in East Greenland both found one generation per year, but disagreed on the timing and duration of the spawning period. Kramp claimed breeding from April or May to August or September, with the young maturing through the winter and breeding in the following spring and summer. Ussing found eggs from February to June, with the first adults appearing in August and September and maturation continuing into winter. Kramp suggested the difference between their findings was due to Ussing's using small, fine-meshed nets and only taking shallow tows, thereby undersampling the population. However, considering the current and water-mass differences of East and West Greenland, both of their results may have been correct; then

again, since intensive population studies were not conducted, the real life patterns may have been masked.

Dunbar examined Sagitta elegans from Disko Bay, West Greenland (1940); Baffin Island and Northern Labrador (1941); and Fox Basin, Hudson Bay, Frobisher Bay, and Ungava Bay (1962) and found a two-year and alternating life cycle. He described up to three broods present in the plankton at the same time; "the smallest of which is the offspring of the largest, with an adolescent group of intermediate individual size which will spawn the following year, and which is normally reproductively isolated from the others". Dunbar (1962) believed that spawning and death followed rapidly on maturation. He found spawning individuals from July into the fall and winter.

Bogorov (1940) found that S. elegans in the Barents Sea also has a two-year cycle, with breeding in the summer.

McLaren (1969) worked on S. elegans living in the special environment of Ogac Lake, Baffin Island. Ogac Lake is a landlocked fjord in which the only sea water inflow is over a sill at the mouth of the lake at Spring Tides. Summer temperatures rise above $8^{o}C$ (Dunbar 1962). The lake is divided into three basins, which are overlaid by a layer of fresh water and are anaerobic

and stagnant below 30 meters. The salinity of the lower and middle layers ranges from 20-27‰. S. elegans has an annual cycle in the lake. Eggs were found throughout the entire sampling season, June to September, and "most animals had reached full size but 'suspended' further development to maturity during summer when reproduction would be unsuccessful" (presumably due to lack of available food for the new brood). Ogac Lake's special environment virtually creates laboratory conditions. Sagitta elegans in Ogac Lake grows to less than 20 mm, matures and breeds in a year, whereas immediately outside of the lake the breeding cycle is two years and the individuals grow to over 40 mm.

VI. B.2. The Life History of Sagitta elegans in the Gulf of St. Lawrence

Sagitta elegans has a biennial life cycle in the Gulf of St. Lawrence. Egg-laying takes place over an extended period; probably from the beginning of June to late September. Individuals hatching from the eggs in July grow to an average of about 15 mm by the end of the first year. During the winter months the growth rate is retarded. In the following spring growth resumes at a rate similar to that of the previous summer. By the end of the second summer the brood averages 26 mm in length and goes through another over-wintering period. After April of the second year, ova begin enlarging and full maturation takes place at an average

size of 30 mm. Spawning followed by the death of individuals of this brood takes place throughout the summer. Presumably another breeding group reproduces during the alternative years. The extent of genetic exchange between these two groups can only be speculated upon.

Figure 17 is the length-frequency histogram for Sagitta elegans in 1966-67 and 1968. Stages I and II were grouped because proper discrimination between these two stages can only be made cytologically (see Section III.B.1). The histograms for the 1966-67 season were based on all the S. elegans measured from the hyperbenthic and oblique plankton samples collected during that season's transect program (see figure legend for details). The histogram for March 1967 was the sum of the samples collected from various locations in the Gulf (see Section III.B.for the station list) onboard an icebreaker. On this last date only vertical tows were taken. The histograms for the 1968 season, with a few exceptions, were based on measurements of 30 randomly selected S. elegans from each discrete horizontal depth sampled by the plankton and closing hyperbenthic nets at the four transect stations (Fig. 3 and 4). The graph for April 17 was based on oblique samples taken at Station HP 112M from the Icebreaker Labrador, and the histograms for 19 June and 15 October were obtained from samples at Station HP 112M only. These histograms then, were based on sampling

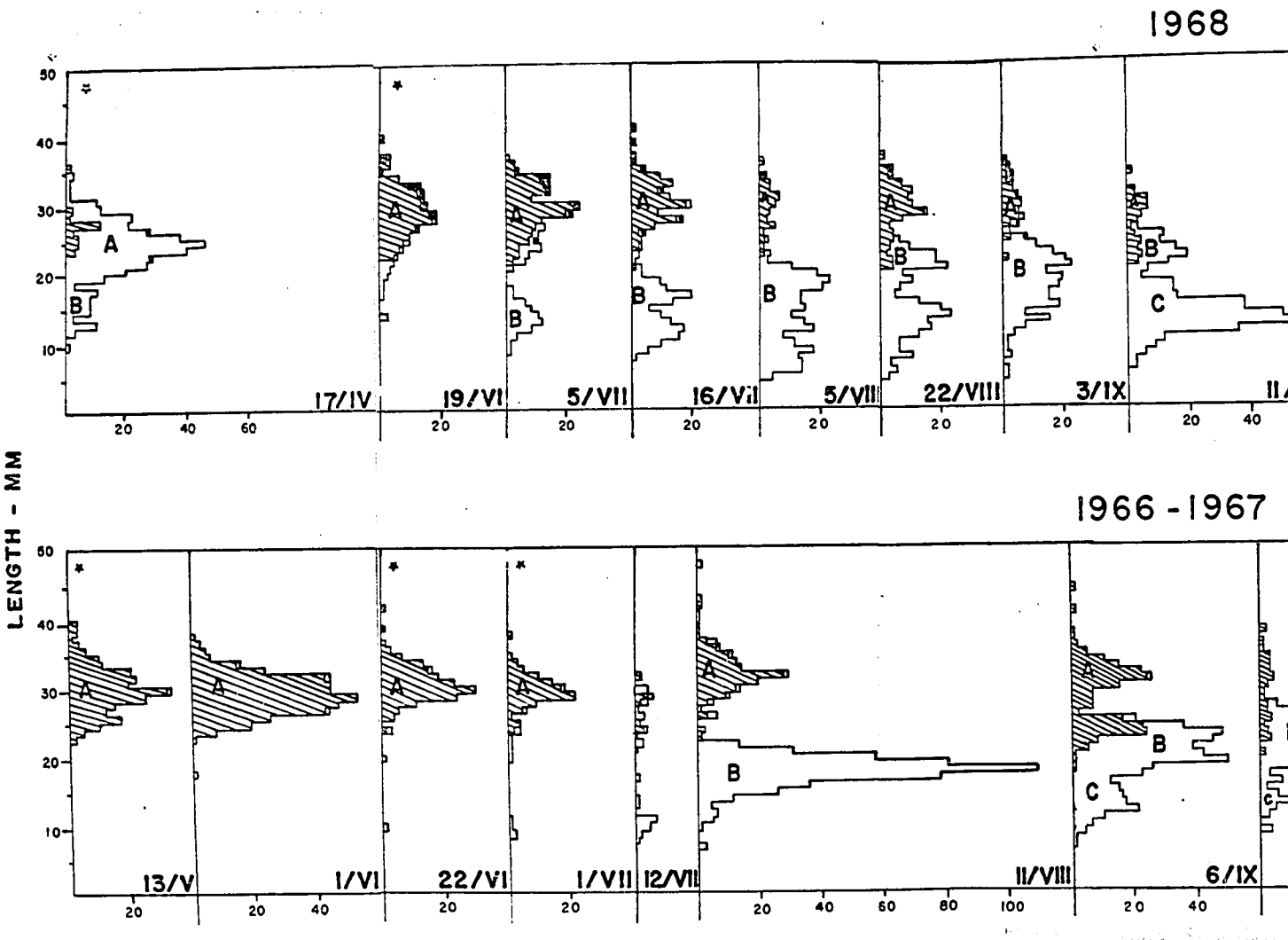


Fig. 17. Length-frequency distribution for Sagitta elegans in the Gulf of St. Lawrence, 1966-7 and 1968.

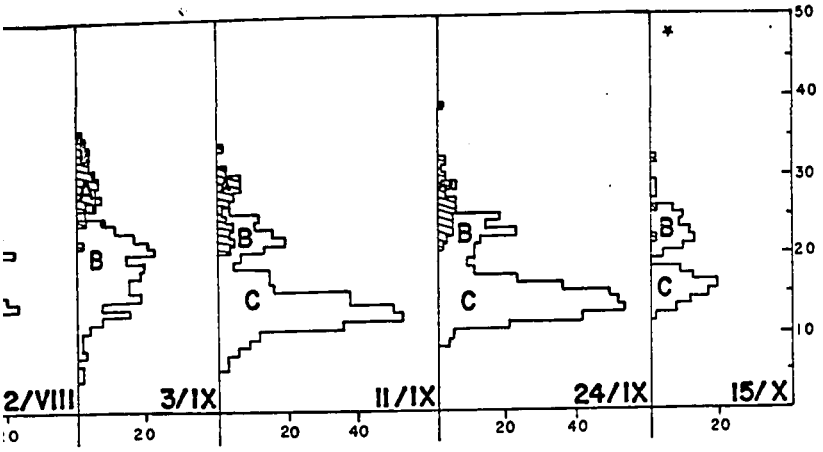
The histograms for 1966-7 were based on oblique plankton samples and hyperbenthic samples collected at the transect stations, except where indicated. The histograms from 13 May to 1 July were taken exclusively from hyperbenthic samples, resulting in the undersampling of the smaller size-classes present in the upper waters at this time of year.

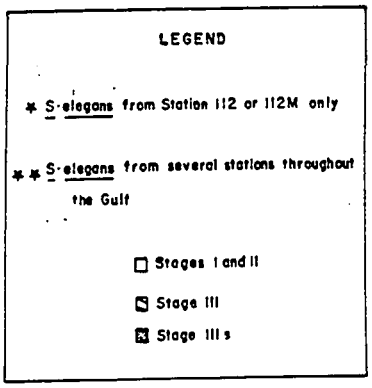
The 1968 histograms were compiled from the 30 chaetognath aliquots from each closing horizontal tow collected at the transect stations on each sampling date.

A, B, and C represent modes of spawning chaetognaths, one year-olds, and the current year crop, respectively.

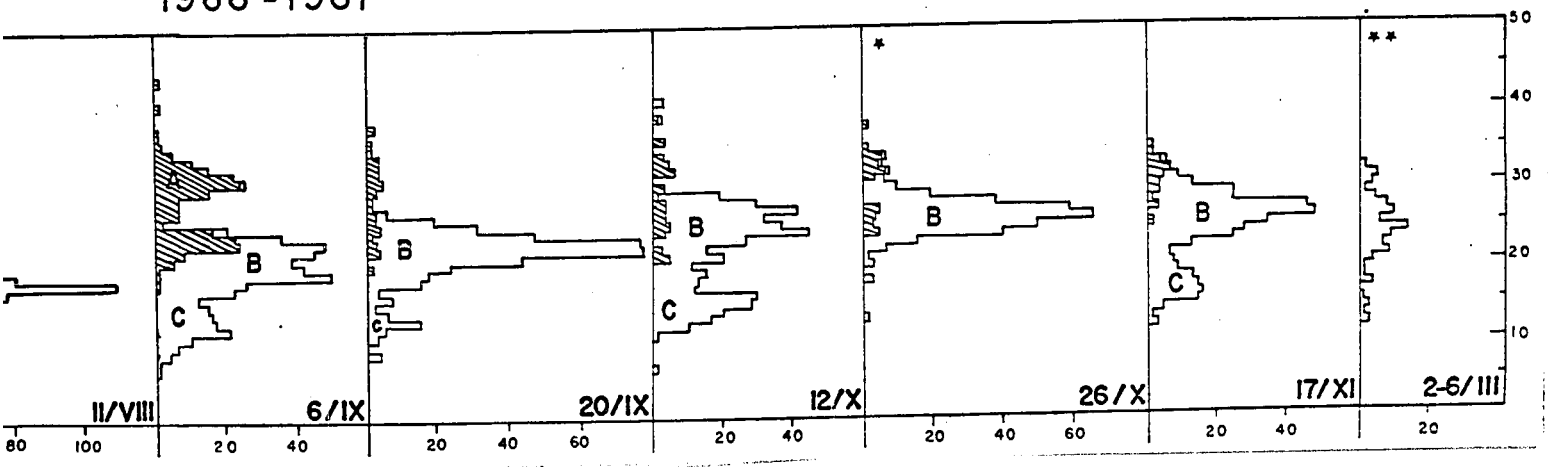
Stage IIIs from 1966-7 were included as Stage III.

1968





1966 - 1967



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through the entire water column. The only obvious bias in the sampling method was in undersampling of the smallest size-classes by the use of #0 mesh nets.

Most of the serial histograms are trimodal, but only one mode is apparent on the histograms from 13 May to 1 July, 1966. These latter graphs were taken exclusively from hyperbenthic samples, which probably had under-sampled the smaller size classes present in the upper waters at this time (see Section VII.B.3 for discussion of the relationship between length and bathymetric distribution).

Three modes were present through the mid-summer period and decreased to two in the late autumn following the spawning and death of the Stage III animals. It was difficult to establish when a third mode, representing the newly hatched animals, re-appeared in the spring because of the under-sampling of the smallest animals by the large mesh size. It can be seen from the graph that chaetognaths smaller than 10 mm were not sampled satisfactorily by the #0 mesh.

Following Dunbar's (1962) notation, the mode representing the spawning chaetognaths has been labeled 'A' in the figure; the mode of one year-olds has been labeled 'B' and the mode for the

youngest sagittae labeled 'C'.

Huntsman and Reid (1921) claimed that the life cycle of S. elegans in the Gulf of St. Lawrence took one year. If the life cycle was annual, we would have expected to find only two modes during the breeding season: the "spawning" mode, remaining static in size but decreasing in number as the mature animals spawned and died; and a mode representing the newly hatched S. elegans, increasing in size and frequency. Only one modal group would have been present after the spawning period.

In Figure 17, the 'A' mode remained approximately stationary at about 29 mm throughout the spawning period, then declined during September-October, and was only present to a limited extent into November. A mode of large Stage I and II sagittae, the 'B' mode, appeared in the 1966 samples when oblique tows were included. The 'B' mode was present throughout the 1968 program, because of the more extensive vertical sampling. The newly hatched S. elegans only became conspicuous as a well-defined modal group, the 'C' mode, in September. The difficulty in delimiting the 'B' and 'C' modes earlier in the summer was due to the under-sampling of the smallest size-classes by the #0 mesh. The larger individuals which had hatched during the current year added onto the tail of the mode of the previous year's brood. By

September, the current year-class had grown sufficiently to produce a distinct, though unrepresentative, mode.

An increase in the size of individuals comprising the 'B' and 'C' modal classes was evident throughout the sampling period, with the exception of chaetognaths caught on 17 November, 1966. The November specimens showed no size increase in the immature 'B' and 'C' modal class. This indicated a period of retarded growth rate extending through the winter months. This slowdown in growth rate was also seen in the two series of icebreaker samples. The modes for March, 1967 were not very much different from the November, 1966 'B' and 'C' modes, or for that matter from the late October modes. This was also true for the modes of April, 1968, which, although belonging to a different brood than the one above, exhibited the same modal size. Growth in 1968 resumed after April and before June 19, possibly coincident with the local spring phytoplankton-zooplankton bloom. Between 17 April and 19 June the current year's spawning group grew to the mature modal size of 30 mm and matured from Stage II to Stage III.

Two regression lines, based on the modal sizes for those dates when the two modes were clearly distinguishable, were calculated (Fig. 18). The 'winter-growth' period was excluded from the calculations. The origin of the 'X' axis was placed at 1 June. No regression was attempted for the 'A' mode as it was obvious that

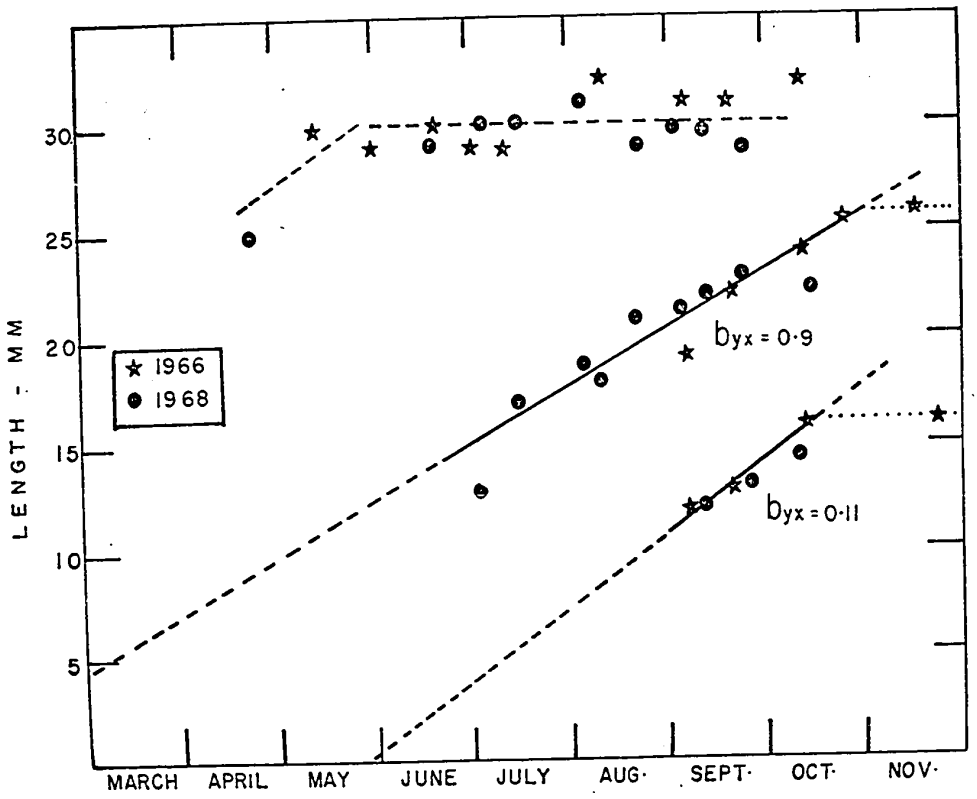


Fig. 18. The growth rate of Sagitta elegans. The lower line represents the current brood of S. elegans, the middle line the one year-olds, and the upper line the breeding group. Dashed lines are extrapolations of the fitted lines and the dotted lines the estimated onset of 'overwintering'.

the regression coefficient or slope would not differ from 0, i.e. no overall growth was taking place in the spawning group since the larger animals were spawning and dying as the smaller animals continued to grow. The regression coefficients for the 'B' and 'C' modes were 0.09 and 0.11 respectively. The equations for the two regression lines were:

B mode $Y= 11.94 + 0.09X$
C mode $Y= 0.85 + 0.11X$

The points lay very close to the calculated line and the slopes of the two lines, which represented the broods' growth rates, were very nearly parallel.

Back-calculating the regression of the current year's brood to length = 0 gave the last week in May as the approximate modal spawning period. To be more realistic, time of hatching was also calculated from the line. Newly hatched S. elegans are about 3 mm long (Huntsman and Reid 1921). This was found to be late June. Some bias can be expected because of exclusion of the smaller size classes due to our large mesh size. Taking this into account, the modal spawning period took place later in the summer, probably around the end of July. The decline in the frequency of the breeding mode'A' through the summer also indicated the end of July as the middle of the breeding period.

VII. Vertical Distribution of Sagitta elegans

VII. A. Historical Review

VII. A.1. Bathymetric Distribution

Sagitta elegans is a creature of the surface waters of the northern oceans. Alvarino (1964) listed it among the epiplanktonic chaetognaths; occurring in the upper 150 meters. The picture of its vertical distribution behaviour is by no means clear, as should become evident from the discussion below. The main facts are that the species is distributed in the upper water layers, generally in the top 150 meters, that larger sized animals are found deeper than smaller ones, that individuals undergo a diurnal vertical migration, and that individuals have been found concentrated near the sea floor.

Records sometimes have been obtained from waters to 1000 meters (Kramp 1939; Fraser 1952; Østvedt 1955; Vinogradov 1955). Most records, however, indicate that the species is limited to the upper 150 meters. Some discrepancies may have arisen from the use of non-closing nets (Table 9). Østvedt, however, used closing nets and obtained specimens from 600 meters.

Huntsman and Reid (1921), using closing meter plankton nets, obtained S. elegans at all depths down to 175 meters, but found greatest concentrations between 75 and 125 meters. Catch numbers dropped off below 125 meters.

Kramp (1939) listed the species as scarce in the upper 25 meters off the Greenland coast, but abundant at a depth of 50 meters.

Clarke, Pierce, and Bumpus (1943) encountered variations in the vertical distribution on Georges Bank from cruise to cruise. In September the majority were below 25 meters in the day and above 25 meters at night. Similar tendencies were found in the spring, but in June they found greater concentrations from 25 meters to 75 meters during the night than during the day. They concluded that vertical distribution and diurnal migration changed according to season and in relation to the size and maturity of the animals.

The difficulty in defining the vertical distribution of a species, or for that matter, the species' range, is that we are dealing with distribution as though it were a static phenomenon. Depth distribution is determined by the interplay of causal factors acting on the organism. The vertical distribution of the individual is the resultant of environmental variables acting on changing

biological factors. The sum of the responses of the individuals makes up the vertical distribution of the species. Therefore, the description of the vertical range of the species is predictive and depends on the determination of the responses of the animals to environmental factors during different stages of its life.

Russell's study (1933b) was one of the most thorough examinations of vertical distribution done on this species. His animals were caught in oblique tows with a non-closing 2-meter stramin net. Shallow catches were subtracted from successively deeper catches to determine concentrations at a given depth. He presented data for the Plymouth population from April to September and concluded that vertical distribution is correlated with light. The population moved deeper from April to June; then in July, August and September the population moved higher in the water column, into more brightly lit waters.

Russell recognized the difficulties in interpreting his data to construct a picture of the vertical distribution patterns relevant to the biology of the species. He noted that the studies were limited to "average-sized full-grown individuals" since animals less than 7 to 8 mm were excluded by the stramin mesh (a proportion of the animals larger than 8 mm were probably under-sampled). This is especially significant since the modal size of

his Stage III individuals ranges from about 12 mm for the September brood to a maximum size of 19 mm for the May brood. Therefore, a considerable proportion of the population was either excluded from the study or undersampled. In addition the distribution studies were done by grouping all of the size ranges in the population, although he noted that young chaetognaths tended to be higher in the water column than older animals.

He concluded that the early spring brood lived in the upper waters in the daytime. The brood succeeding this one took up residence in deeper water, while the next brood or broods in July and August, appeared to be less light-sensitive and were concentrated nearer the surface. Offspring of this brood left the surface waters and kept near the bottom until February, when they matured and rose higher in the water column. This latter finding was based on a comparison of oblique and hyperbenthic hauls. Russell had found S. elegans in relatively large numbers off the bottom all year round, but the hyperbenthic catches were not included in the vertical distribution calculations because these catches were done during different years.

In Inner Oslofjord, Jakobsen (1971) caught larger animals at increasingly greater depths and concluded that the largest animals have a daytime optimum depth of 85-90 meters and that

most of these individuals occur between 60 and 120 meters.

VII. A.2. Ontogenetic Descent

It has long been recognized that some species of chaetognaths undergo an ontogenetic descent. The older, more mature individuals generally are found deeper than the younger. Fowler (1905) first described this phenomenon in Eukrohnia hamata. Huntsman (1919), Huntsman and Reid (1921), Bigelow (1926), Meek (1928), Russell (1931, 1933b), Kramp (1939), McLaren (1969), and Jakobsen (1971) all mentioned that young S. elegans were distributed in more superficial water than the adults. David (1955) found the same to be true for S. gazellae in the Antarctic and Alvarino (1964) reported the same type of behaviour in S. scrippsae, S. gazellae, S. zetesios, S. minima, S. planctonis, S. macrocephala, and E. fowleri.

The size stratification with depth of S. elegans in the Bay of Fundy was studied by Huntsman and Reid (1921). Catches of animals taken in successive 25-meter hauls were counted and measured. Their figures showed a definite size increase with depth, with a considerable overlap. For example, at one station the catch at 25 to 50 meters ranged from 14 to 19 mm, the catch between 50 and 75 meters was 18 to 26 mm, between 75 and 100 meters

the animals were 19 to 33 mm, between 100 to 150 meters they ranged between 24 and 37 mm, and between 150 and 172 meters they were from 22 to 34 mm long. Unfortunately, no examination of maturity stages was done. They also found some seasonal differences in stratification. In August, smaller animals were nearer the surface than in September and October. They suggested that the difference was due to local weather conditions; September and October being sunnier then August. It was impossible to say whether this was a seasonal trend or a "local" effect, due to the limited time range of their data.

Jakobsen (1971) found a good correlation between vertical distribution and length in Oslofjord. He measured animals caught between 0-20, 20-50, 50-100, and 100-164 meters. Although animals from 1 mm to 18 mm were caught at 0-20 meters during the daytime, the percent of each size-class caught at this depth declined with increasing size; 99.2% of the 1-2 mm animals were caught here, 28% of the 10 mm class, 9.6% of the 15, and 1.1% of the 18. The inverse was true of animals caught at depths greater than 50 meters; nearly 0% of the 1-5 mm, 28% of the 10 mm, 58.6% of the 15 mm, and 90.7% of the 18 mm size classes were caught at these depths. 92.7% of the 18-28 mm animals were caught deeper than 50 meters. He found no evidence that the optimum depth of a given size S. elegans varied seasonally and concluded that apparent seasonal migrations

were simply the result of growth and "length dependent vertical distribution".

On the other hand Clarke, Pierce and Bumpus (1943) concluded that on Georges Bank "in most cases both large and small specimens were represented in the same relative proportions at the various depths at each station."

Although the land-locked population of S. elegans that McLaren (1969) studied in Ogac Lake was limited to the upper 30 meters by anaerobic conditions at greater depths, he found that there was an ascent of newly-hatched young followed by a descent of older individuals at the "onset of sexual differentiation". He concluded that "differences between developmental stages may be just as great as differences between species; it is not possible to generalize about diurnal, seasonal or geographic differences in depth of a species from studies of all stages combined or of a single stage, although there are many such studies in the literature".

VII. A.3. Hyperbenthic Distribution

It has long been recognized that a hyperbenthic distribution plays some role in the biology of Sagitta elegans. Hunts-

man's account (1919) was probably the earliest to appear in the literature. He used a young-fish trawl in the Bay of Islands, Newfoundland over various depth bottoms and caught "an abundance of large individuals". At a station 110 meters deep he caught specimens from 23 to 43 mm long; from a depth of 270 meters the catch measured between 21 and 52 mm, while plankton hauls as deep as 70 meters only caught specimens up to 16 mm.

Russell (1933b) did a series of hyperbenthic hauls off Plymouth. Unfortunately the material was examined before it was realized that the Channel chaetognaths included two species, S. elegans and S. setosa, so that his data did not distinguish between the two species. An investigation of annual variations in abundance from oblique hauls alone led to the conclusion that the number of chaetognaths declined over the winter months; comparisons with hyperbenthic net results indicated no winter population decline; rather the chaetognaths settled lower in the water column during the winter months. He caught large numbers of chaetognaths off the bottom throughout the year; usually in numbers exceeding the oblique catches.

Clarke et al. (1943) mentioned having fitted stramin nets with rollers to obtain oblique hauls from the bottom to the surface, but included no data on hyperbenthic distribution in their study.

Bossanyi (1957) caught S. elegans in his closing hyperbenthic net in 5 - 6 fathom and 13 - 15 fathom waters in Blyth Bay and Cambois Bay, whereas Colman and Segrove (1955) fishing with hyperbenthic apparatus in Robin Hood's Bay at a depth of 2 feet did not mention S. elegans among their catch.

Deevey (1952) mentioned catching S. elegans in abundance off the bottom in Block Island Sound. Beyer (1958) occasionally caught the species in great abundance in his closing bottom net in Oslofjord. He concluded that hyperbenthically distributed plankters should "be considered functional members of the soft bottom animal community whilst they remain in the vicinity of the soft bottom".

Jakobsen (1971) used hyperbenthically caught animals in his analysis of the life history in Oslofjord. S. elegans occurred regularly in large numbers in the toboggan net, often in contrast with vertical Nansen hauls. The hyperbenthic animals generally were larger than 15 mm (maturation takes place at about 18 mm). Large immature animals which exhibited "subnormal maturing of the ovaries" were caught at the innermost station in 1962 and the abnormality was correlated with low oxygen concentration; an oxygen concentration of 0.96 mg/l was recorded at 95 meters in January. During August 1968 no S. elegans were caught above the

bottom at this station. It was suggested that this was due to a general impoverishment of zooplankton in Inner Oslofjord in recent years, possibly an effect of "toxic substances". Beyer (1958) had asked if concentrations of zooplankton near the seafloor might not be due to poor condition of the animals. Jakobsen compared the feeding frequency of hyperbenthic S. elegans to that of animals caught in plankton nets, found no significant difference, and concluded that hyperbenthic distribution "is not due to bad condition".

McLaren (1969) also noted what may be another instance of hyperbenthic habit. In the outer basin of Ogac Lake he found older over-wintered animals concentrated near the bottom at 18 meters, but in the inner basin they were found dispersed throughout the water column down to anaerobic depth (35 meters).

VII. A.4. Vertical Distribution as a Causal Factor in Life History

VII. A.4.a. Proximate Causes of Vertical Distribution

Most authors have agreed that temperature and salinity were not important causal factors of vertical distribution behaviour. Huntsman and Reid (1921) found the species vertically stratified in size and numbers, as mentioned above, in an environment with no temperature or salinity stratification.

Their conclusion was that light was the determinant of depth. The same conclusion was reached by Russell (1933b) for the population in the unstratified waters of the English Channel. Russell estimated the light intensity at different depths throughout his sampling period and found good correlation with the changes in vertical distribution of the population. He concluded that Sagitta avoided light intensities greater than 20 kilo metre-candles (1 metre-candle = 1 lux) during spring and early summer, but in late summer large numbers were caught at intensities as great as 50 kilo metre-candles. No attempt was made to relate this response to light to the different broods or to the different size ranges within the population.

VII. A.4.b. The Relationship Between Vertical Distribution and Fecundity

Although temperature is not a causal factor of depth distribution, it does determine the length of the life cycle, size of the chaetognath at maturity, and, since ovary length and egg number increase logarithmically with relation to body size, fecundity (see Section VI.A.2).

Several different authors have come to the conclusion that there is an inverse causal relationship between size and

temperature in Sagitta elegans. This conclusion was reached by some authors (Huntsman 1919; Clarke et al. 1943) solely on examination of a single brood of one population. From the above discussion of size stratification with depth, it follows that in thermally stratified waters one would catch the larger chaetognaths in the deeper, colder water, producing what would look like an inverse temperature-growth relationship. Russell (1932a), however, was able to study a population in which several broods were produced annually. He found a considerable difference in the average adult size of the different broods. The average adult size for the May brood was about 20 mm, for June about 14 mm, for July about 13 mm, for September about 10 mm, for February about 12 mm and for the April-May brood about 16 mm. He plotted the average adult size for each of these broods on the same time base with what he estimated to be the growth temperature and found a reciprocal relationship.

The most dramatic example of the relation between adult size and temperature was in the Ogac Lake population studied by McLaren (1969). In the lake, at a temperature of 5^{o}, adults were about 14 mm; outside, in Frobisher Bay, at a temperature of 0^{o}, the average was about 37 mm.

McLaren (1966) looked at the relationship between mean

length of mature S. elegans from different areas and the estimated mean temperature during their development. He found that the expected inverse length-temperature relation fell on separate curves; one based on values from the Canadian Arctic and the other based on populations from British waters (Fig. 19). From this separation he concluded that there were two genotypes which differed in their ecophenotypic responses to temperature. The difficulty in this type of study is in determining the average growth temperature, since, as we have seen, the species will go through a considerable temperature range in thermally stratified waters, excluding considerations of diurnal vertical migration, due to the ontogenetic descent. McLaren's separation of the S. elegans stocks into two genotypes was based on two points, which swung the curves apart; the undersized Ogac Lake population and a population of large individuals caught near the Faröes. If we ignore these two points a single curve can be drawn whose middle values would fall through an area where we would expect to find the "temperatures of growth; length at maturity" points for the Gulf of Maine and Georges Bank population (the Gulf of Maine and Georges Bank populations were not included in the study); but that would still leave the Ogac and Faröe points to be explained.

Sameoto (1971), in fact, replotted the relation excluding the arctic population points and the point from the Faröe Islands,

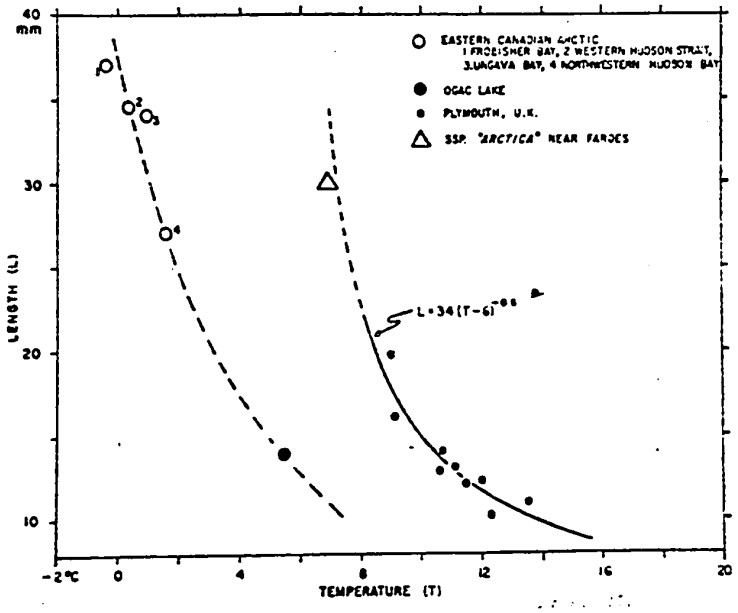


Fig. 19. "The relationship between mean (length) of samples of mature Sagitta elegans and estimated mean temperature during their development." (From McLaren 1966)

while adding points from St. Margaret's Bay and Bedford Basin and obtained a single curve.

VII. A.5. Diurnal Vertical Migration

Russell (1931) studied the diurnal vertical behaviour of Sagitta elegans and found that it varied with the different size ranges within the population; the younger individuals appeared at the surface in the evening before the older, while the older ones left first. He considered that the older individuals were more sensitive to light. Variations in behaviour at different dates were explained by differences in water transparency. Bigelow and Sears (1939) did not find a type of vertical migration in this species comparable to that in Calanus finmarchicus; they observed a great variability which probably indicated that more factors than light were involved.

Lacroix and Morisset (1962) looked at the influence of the thermocline on diurnal vertical migration off Grande-Rivière. They split the population into three size classes (3 - 11.5 mm; 12 - 20.5 mm; 21.0 - 35.5 mm) and examined the migrations of the classes on two dates in September; one day when a thermocline was present and one day after the structure had broken down. No essential difference in the vertical migration patterns were found

in the first two size classes. The larger size class stayed longer at the greatest depths and was found in the superficial waters only on the day when the thermocline was present. The thermocline was not a definite barrier to migration for any size class; but the larger size animals appeared in the surface waters in much smaller numbers than the younger.

McLaren's (1969) Ogac population showed vertical migrations only in Stage I and II animals; Stage III animals remained at depth.

VII. B. Vertical Distribution of *Sagitta elegans* in the Gulf of St. Lawrence

VII. B.1. Bathymetric Distribution

The actual numbers of *Sagitta elegans* caught during the 1966 and 1968 season were of limited use, since most of the samples were taken by unmetered nets. The plankton nets used during the 1968 season had no flow meters until the last three cruises, due to a series of logistic mishaps, including a postal strike. An attempt was made to hold the plankton tows to a uniform ten minutes throughout the season. Filtration values from flowmeters available at the end of the season, however, ranged between 44.3 m^3 and 265.4 m^3. The average filtration value for

the plankton samples taken on the 24 hour cruise on 19 - 20 September was 153±43 m^3. Although the variance was large, the mean was representative, since it was greater than 2.5 times the standard deviation (Stanley 1963).

During the day the density of S. elegans increased rapidly with depth. With a few exceptions mid-water samples at 25, 50, and 75 meters contained very few sagittae. Catches at 25 meters ranged from 0 to 125; at 50 meters from 0 to 238; at 75 meters from 6 to 233. Samples taken at 100 meters ranged from 25 to 1153, while the numbers caught by the Macer net at the deepest station (119 meters) ranged from 138 to 2650.

There seemed to be an order of magnitude of difference in the concentrations of S. elegans in the daytime between the more superficial depths, 25, 50, and 75 meters, and 100 meters and off the bottom at 119 meters (Fig. 20). The values plotted on Figure 20 are from the cruises when flowmeter readings for the midwater-plankton tows were available. The total-catch numbers, however, also reflected these order of magnitude differences between 25, 50, and 75 meters, 100 meters and the bottom. The catches in the 25 meter and 50 meter nets increased into August and September, perhaps reflecting the increase in mean length in the current year's brood to a size large enough for the #0 mesh net to catch them.

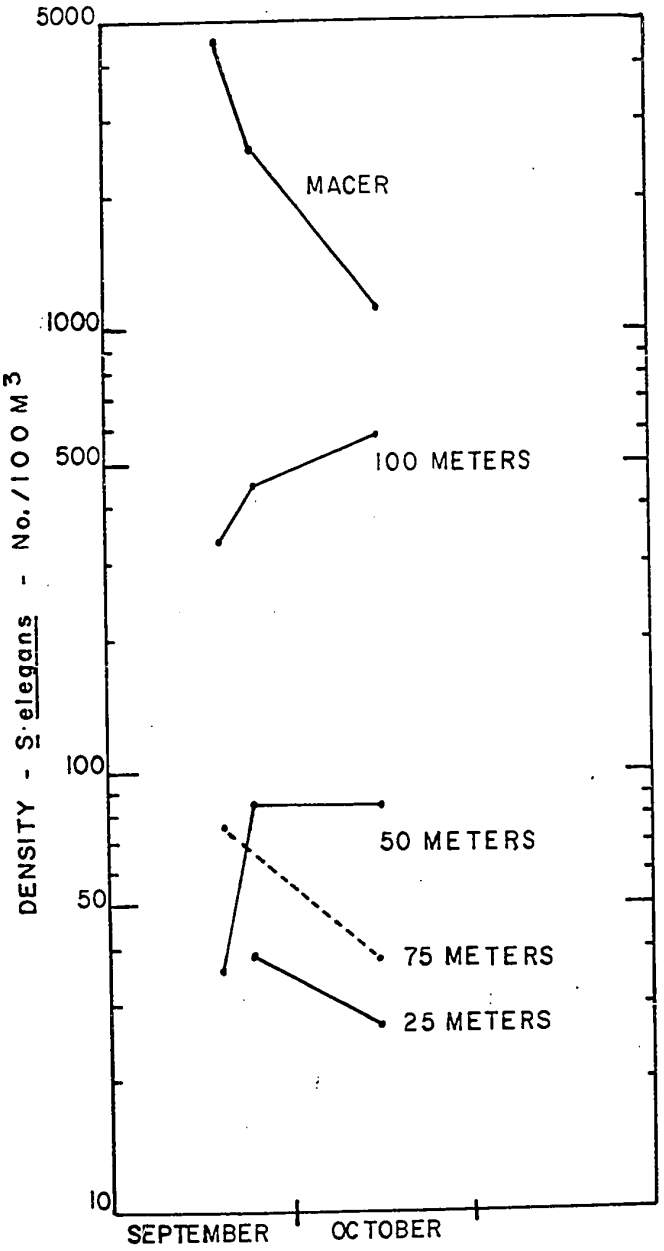


Fig. 20. Densities of Sagitta elegans at Station HP 112M in the Autumn of 1968. 'Macer' refers to collections taken with the hyperbenthic apparatus just off the sea floor (119 meters).

The largest hyperbenthic catches were obtained in September and October in both 1966 and 1968. In 1966, large numbers of S. elegans were caught in the hyperbenthic trawl in May and early June; the catch size declined through late June and fell to almost zero in the beginning of July, increased again in August and through September and in October finally returned to the high numbers caught in June. The same pattern was seen in the Macer samples in 1968 (Table 10), especially for Station HP 112M. The sampling season in 1968 did not start as early as in 1966, so it was impossible to confirm the spring highs. In 1968, the number caught hyperbenthically increased at Station HP 112M throughout the summer. This trend was not seen as clearly at the other transect stations (Table 10). The lowest densities of hyperbenthic S. elegans, however, were caught in the beginning of July at all the stations.

During the day a large proportion of the population was just off the bottom or quite near to the bottom. Figure 21 shows the distribution of S. elegans through the water column along the length of the transect for 24 September, 1968. At the two deep stations the population was concentrated near the bottom; at the shallower stations approximately the same densities were obtained off the bottom, but mid-water catches at the same depths were at least an order of magnitude less. This indicated schooling

TABLE 10. Density of hyperbenthic S. elegans in 1968 - chaetognaths / 100 m^3

Depth (M)	HP 23 / 54	HP 24 / 75	HP 112 / 110	HP 112M / 119
DATE				
5 July	267	145	366	114
16 July	103	571	---	---
23 July	---	---	2211	207
5 Aug.	370	480	539	192
13 Aug.	---	---	---	855
22 Aug.	7571	850	2222	816
26 Aug.	---	---	---	223
3 Sept.	---	527	719	2382
11 Sept.	845	1540	542	217
19 Sept.	---	---	---	4594
24 Sept.	1914	540	1349	2637
15 Oct.	---	---	---	1113

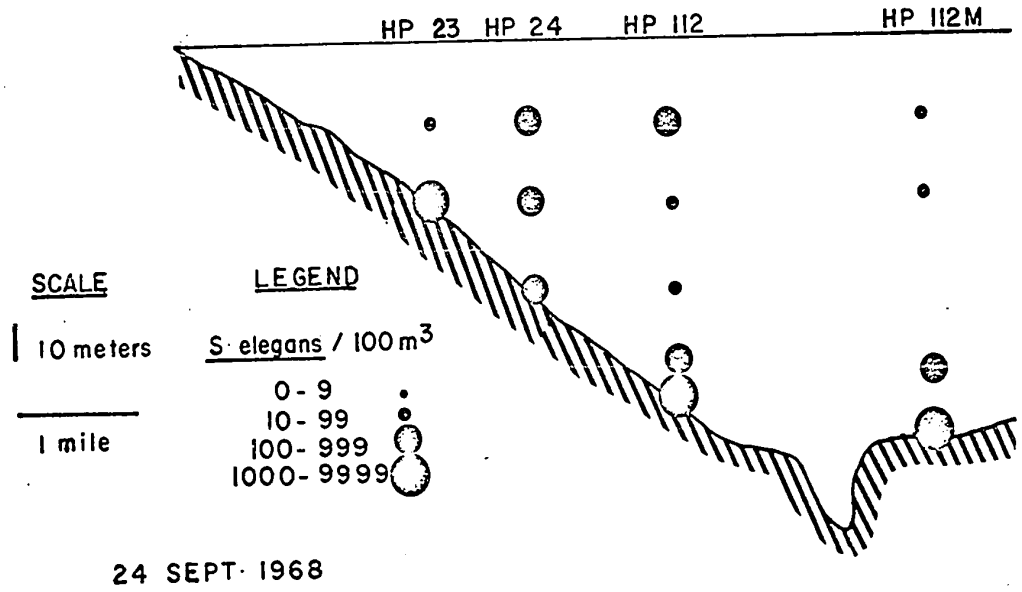


Fig. 21. The distribution of Sagitta elegans off Grande-Rivière on 24 September 1968.

adjacent to the bottom. This was in fact born out by the catch numbers throughout the 1968 season. Table 11 shows the catch of hyperbenthic S. elegans as a percentage of the total catch through the water column at each station in 1968. At the shallower stations nearly 100% of the chaetognaths were caught hyperbenthically, whereas at the deeper station the percentages varied from 18.0% to 82.1% of the total catch. About 90% of the S. elegans, however, were caught at 100 meters and deeper during the day at Station HP 112M (Table 12). No seasonal changes in the hyperbenthically distributed S. elegans as a percentage of the total catch through the water column were noticed; the percentages remained consistently high throughout the sampling period.

VII. B.2. Diurnal Vertical Migration

Vertical migration studies were conducted at Station 112M on four dates during the 1968 sampling program (Fig. 22). Chaetognath density values were only available for one of the dates, 19-20 September. The percentage of the catch at the different depths derived from the density values were superimposed on the percentage as a function of the catch numbers for this date (Fig. 22). The percentage of the catch at the different depths based on simple catch numbers and on the chaetognath densities showed a generally good match. The basic pattern of deep

TABLE 11. Percentage of the total catch of S. elegans at each station caught in the hyperbenthic net during the day, 1968.

DATE	HP 23	HP 24	HP 112	HP 112M
5 July	97.8	29.3	82.1	76.5
5 Aug.	100	97.9	39.3	44.0
13 Aug.	---	---	---	58.4
22 Aug.	100	90.6	67.4	71.6
26 Aug.	---	---	---	50.6
3 Sept.	92.1	96.2	36.6	70.1
11 Sept.	87.6	98.4	32.7	33.1
19 Sept.	---	---	---	70.8
24 Sept.	94.3	31.1	42.7	70.6
15 Oct.	---	---	---	18.0

TABLE 12. Percentage of the total catch of S. elegans caught between the given depth and the bottom during the day at Station HP 112M, 1968.

Depth (M)	Bottom 118	100	75	50
DATE				
5 Aug.	44.0	87.8	91.9	91.9
13 Aug.	58.4	88.0	93.0	93.5
22 Aug.	71.6	98.5	98.8	99.9
26 Aug.	50.6	97.2	98.7	99.6
3 Sept.	70.1	98.5	99.8	99.9
11 Sept.	33.1	57.3	62.5	79.8
19 Sept.	70.8	93.3	97.2	99.7
24 Sept.	70.6	93.8	---	---
15 Oct.	18.0	89.5	93.2	98.9

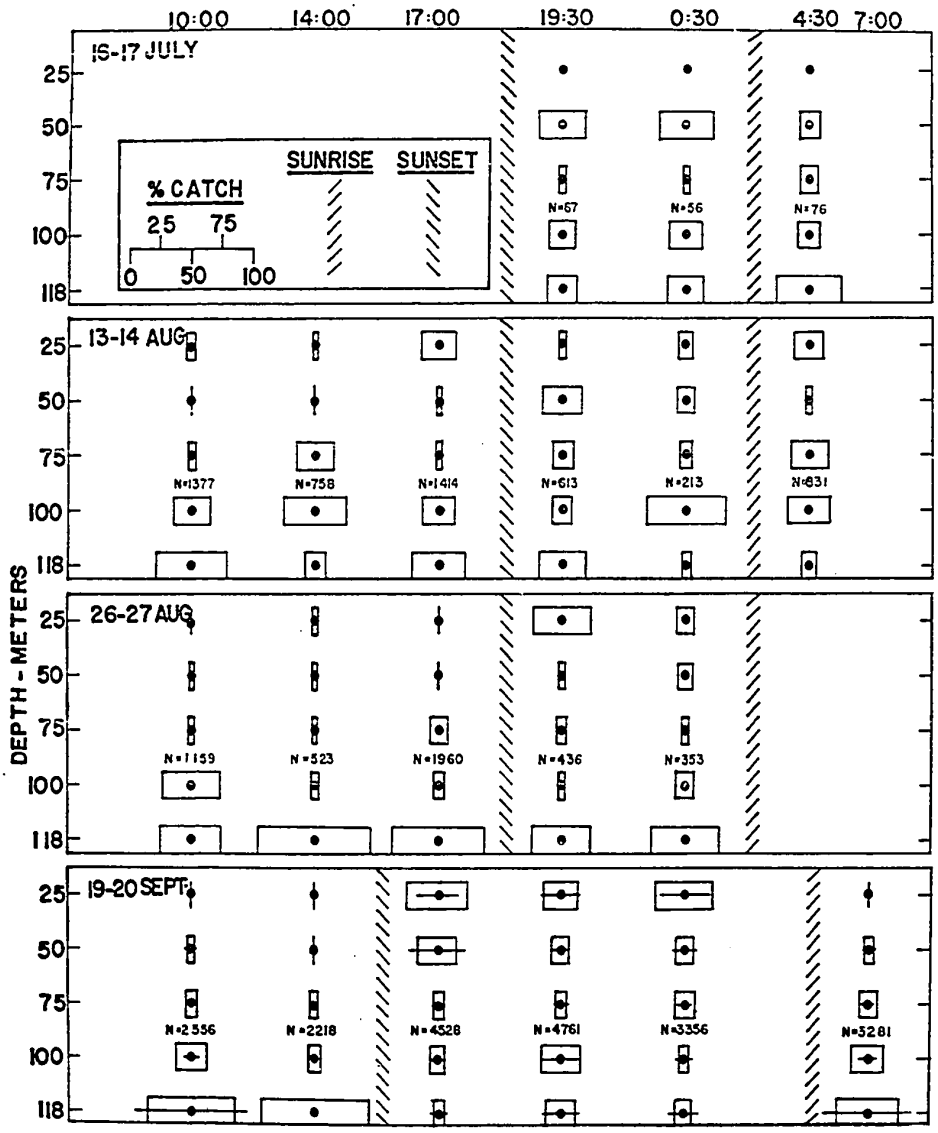


Fig. 22. Diurnal vertical migration of Sagitta elegans at Station HP 112M in 1968. The boxes represent % of the total catch through the water column based on catch numbers; the lines for 19-20 September are % of the total catch based on chaetognath density values (using metered nets). A dot by itself indicates no chaetognaths caught in the sample.

distribution during the day, migration of large numbers into the surface waters following sunset, random dispersal during the middle of the night, pre-dawn rise to the surface, and post-dawn return to the daytime pattern of deep distribution can be seen from both sets of data. However, the relative distribution of the numbers through the water column for any of the sampling times varied considerably between the two representations. Values based on chaetognath densities showed a greater tendency toward random dispersal during the night and smaller predawn surface migration than did those based on the catch numbers.

A considerably greater percentage of the population remained hyperbenthically distributed during the night in July and August than in September. This may have been due to the population change among hyperbenthic animals between the summer and fall. (Hyperbenthic animals in mid-summer were principally two year-old mature animals, whereas in the fall the increase in numbers of hyperbenthic animals was due to the one year-old 'B' mode animals taking up deep distribution; see Section VII.B.4.)

VII. B.3. The Relation Between Size and Vertical Distribution

Throughout the summer months a very wide size-range of *Sagitta elegans* was present in the water column. Those present

from June to October covered the entire size-range for the species in these waters; from newly hatched young to recently spent adults (see Section VI.B.2).

The catch from the icebreakers in late winter ranged from 12 to 32 mm for March 1967 and from 10 to 36 mm for April 1968 (Fig. 17). Since these collections were made with #6 mesh nets towed through the entire water column at different locations in the Gulf, these ranges were probably representative of the population present in the Gulf. In the April 1968 samples the size distribution of animals caught at Cabot Strait, in the central Gulf, and off Anticosti Island coincided with the catch at Station HP 112, suggesting that the life cycle for this species is uniform throughout the Gulf of St. Lawrence. The number caught in March 1967 was too small to make a similar comparison, but the size range and the shape of the distribution were quite similar to the 1968 samples.

There was no indication of spawning taking place as early as April. Only the two year-old, maturing 'A' mode individuals, which were still at Stage II, and the younger size group, spawned in the previous year, were present until the first spawning took place. Thereafter, the entire size range for the species was represented until the Stage III animals or 'A' class

had spawned and died. After the major spawning period, growth continued, but the recruitment of newly hatched individuals progressively declined resulting in a gradual decrease in the smallest size-ranges through the fall and then the discontinuous distribution pattern that we found at the end of the winter.

The pattern of continuous size distribution, from newly hatched to spent animals, through the summer months was found only when samples from different depths were combined. The individuals caught at a particular depth had a relatively tight size range (Fig. 23). The size range at successive depths overlapped; but size generally increased with depth. The size at 25 and 50 meters and at 100 and 119 meters was consistent, while the animals caught at 75 meters were more variable. Those caught at 25 meters averaged about 11 mm; animals caught at 50 meters tended to be larger, but not very much so. Animals which were appreciably larger than usual were caught at 50 meters on 16 July. With some exceptions few mature sagittae were caught above 75 meters. At 100 meters and deeper, during the early part of the summer, the population generally consisted of mature Stage III animals. By 5 August larger immatures had replaced the mature animals at 100 meters.

Stage II and Stage III made up only a small proportion of

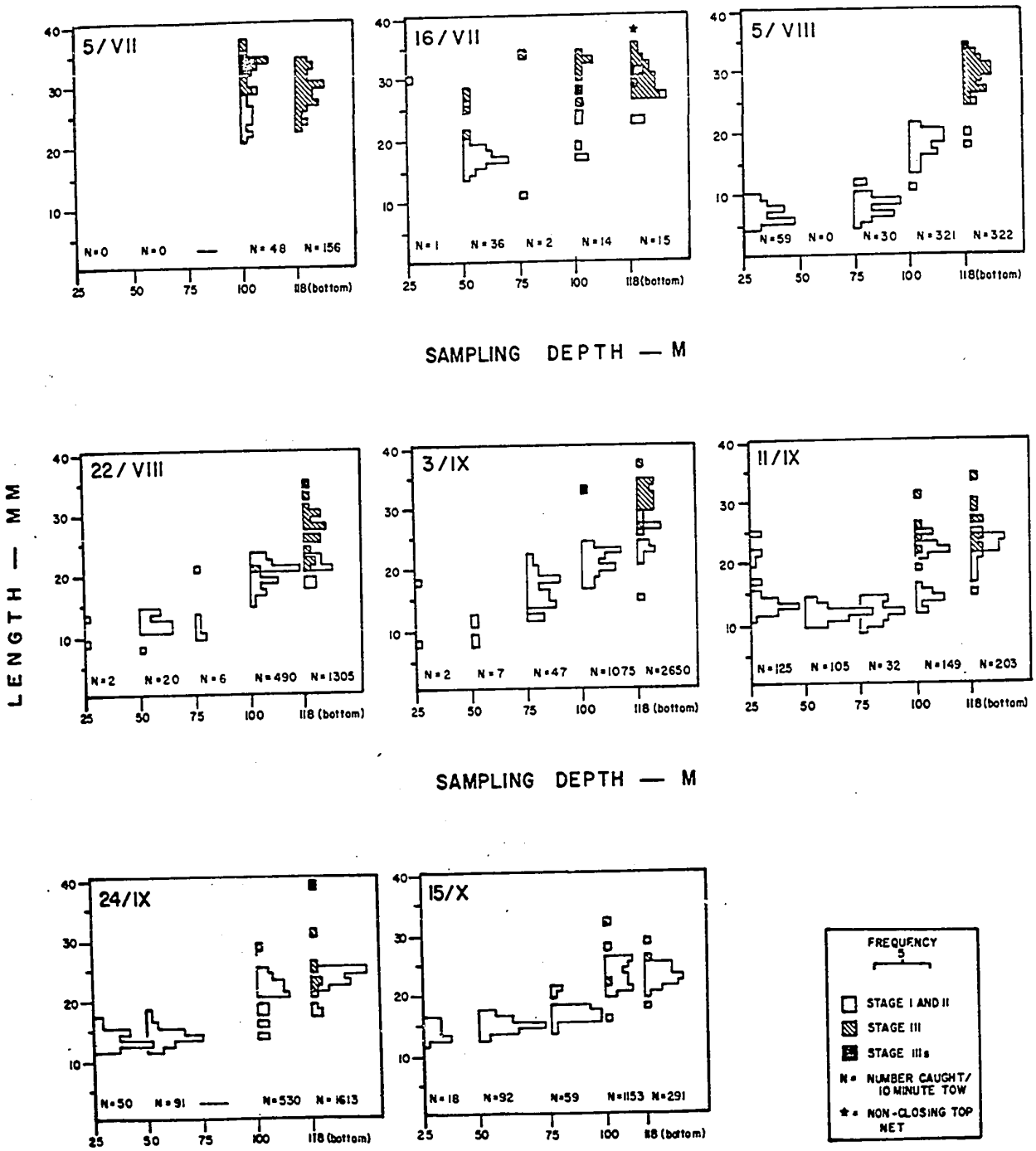


Fig. 23. The size distribution of Sagitta elegans with depth at Station HP 112M in 1968.

the daytime catch above 75 meters (Fig. 24). In these waters development to Stage II occurs at about 18 mm to 20 mm. Maturation to Stage III is not dependent on a threshold size, but takes place through the entire 'B' mode during a brief period in the spring. In the fall, the chaetognaths that are to make up the following summer's breeders are relatively large Stage II individuals; they over-winter with very little additional growth and mature to Stage III rapidly in the spring (Fig. 17). This transformation seems to affect all individuals in the spawning class at the same time, even those as small as 23 mm. This rapid change from Stage II to Stage III combined with the static threshold of transition from Stage I to Stage II was probably the reason for Stage II S. elegans composing only a relatively low proportion of the total population during the summer and fall.

In early July a substantial part of the catch at 50 meters was made up of Stage III, but Stage I and II animals made up progressively higher percentages of the catch through the summer. This was true for the deeper waters as well; at 75, 100 and depths greater than 100 meters the catch became progressively weighted toward Stage I and II S. elegans.

The Stage III animals were concentrated in the deepest waters. In the beginning of July Stage III made up a large

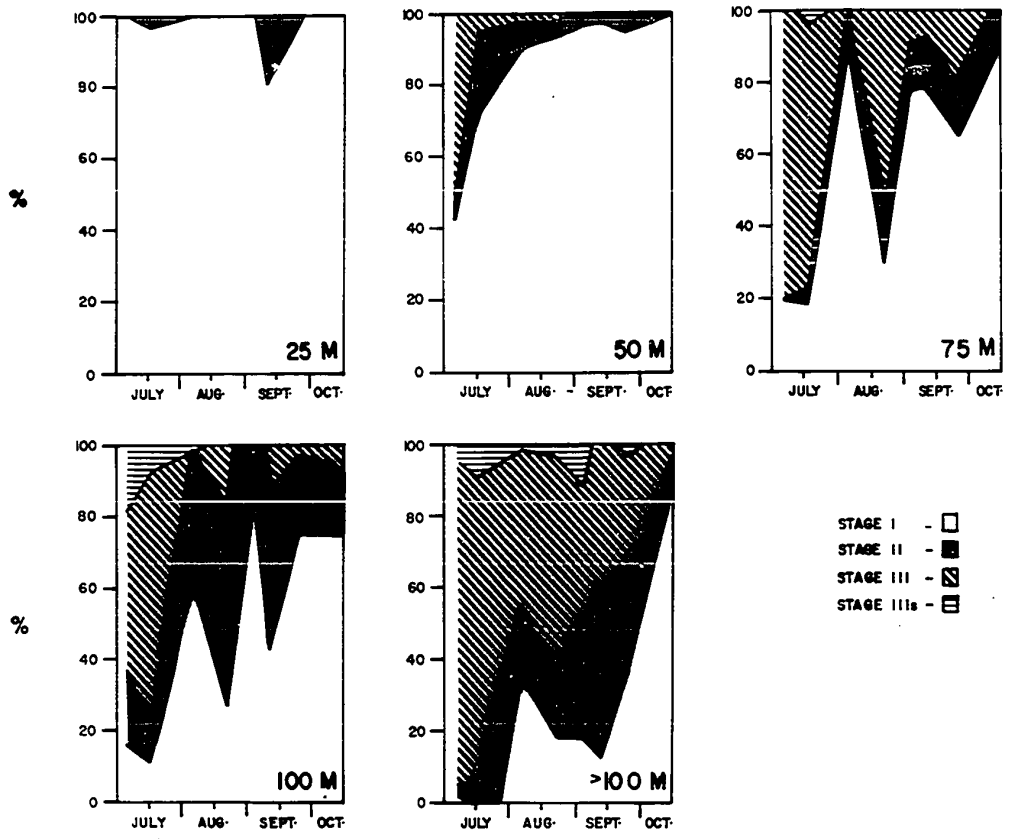


Fig. 24. The depth distribution of Sagitta elegans maturity stages in 1968; all stations.

proportion of the catch from 75 meters down to the bottom, but as the summer progressed Stage III was replaced continuously by immature animals, until late in the summer when the only remaining stronghold of Stage III was just above the deepest bottoms. As Stage III continued to breed and die, and the larger Stage I and II animals settled gradually lower in the water column, the part of the population that was at Stage III made up less and less of the population at all depths, including those greater than 100 meters.

Large chaetognaths having no seminal vesicles, a clear tail coelom, and long ovaries with no enlarged ova were sometimes caught. These individuals have been designated as Stage IIIs (see Section III.B.1). The Stage IIIs animals were caught almost exclusively at depths of 100 meters and below, but generally made up less than 3% of the catch even at these depths. In July some Stage IIIs specimens were caught at 100 meters, but thereafter they were only encountered hyperbenthically at Stations 112 and 112M, i.e. below 100 meters. The proportion of Stage IIIs animals was relatively constant below 100 meters through July and August, but declined in September. The vertical distribution and the pattern of abundance, as well as the extremely large size and the narrow size-range of Stage IIIs specimens (Fig. 17) was what would be expected if this stage represented spent animals.

An ontogenetic descent took place during the end of August and into September (Fig. 23 and 24). The total catch numbers progressively increased at the lower depths during this time; the mature Stage III portion of the population had nearly finished their spawning and had mostly died. The increase in the density of animals at depths greater than 100 meters in the fall (Table 10) was the result of the larger Stage I and II assuming a hyperbenthic distribution. By the end of September in both 1966 and 1968 large Stage I and Stage II had almost completely replaced the breeding Stage III animals in the deeper parts of the water column.

VII. B.4. The Relationship Between Size and Hyperbenthic Distribution

Hyperbenthic samples were collected above 54, 75, 110, and 119 meter bottoms in 1968. A 30-chaetognath aliquot was measured from each of the samples.

Nearly the full size range of Sagitta elegans has been recovered, at one time or another, in the hyperbenthic nets (Fig. 25). Individuals smaller than 12 mm, however, were rarely found in these hyperbenthic collections. This might have been due to the smaller individuals not being distributed over bottoms as deep as 50 meters or to the loss of the small chaetognaths by the relatively large size mesh. Since the size ranges recovered by

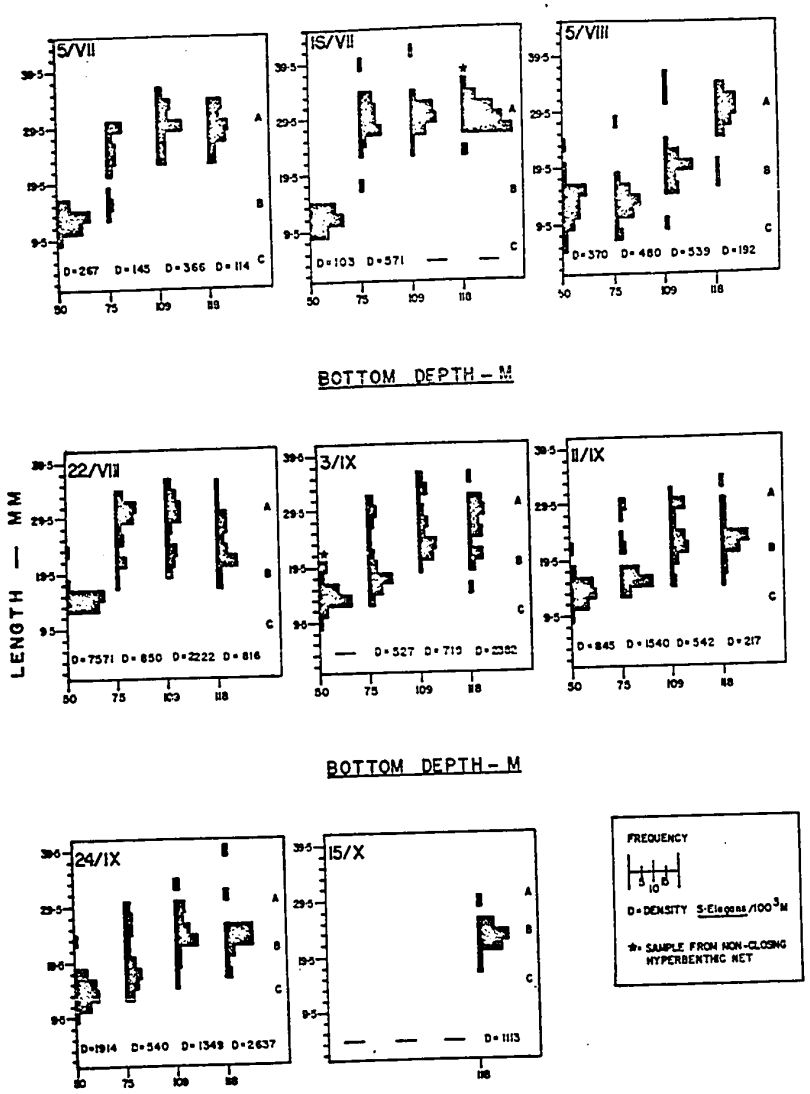


Fig. 25. The size distribution of hyperbenthic Sagitta elegans over different depth bottoms in 1968. Lengths in 2 mm size-classes. The letters 'A', 'B', and 'C' refer to the position of the three age modes.

the hyperbenthic nets reflected the range of mid-water collections for the same date (Fig. 23) it is probable that the latter was the reason.

At the deepest stations (HP 112 and HP 112M) the hyperbenthic catch consisted almost entirely of the mature breeders until early August when a second group composed of immatures ('B' mode) appeared. In the 5 August 1968 sample, the catch from Station HP 112M was almost entirely the large, breeding chaetognaths of the 'A' mode, while that from Station 112 was the one year-old 'B' mode. As the season progressed the size range at these stations decreased, presumably as a result of the death of 'A' mode individuals. The catch of younger chaetognaths at these stations showed an increase in the modal size with time.

The size range over the 50-meter bottom remained remarkably constant during the midsummer. The modal length of animals at this depth remained at about 14 mm from 5 July to 24 September (range from 11 to 16 mm). Figure 25 notes the position of the three calculated class modes for each date alongside the graph. Although the length of animals above the 50-meter bottom remained relatively constant through the mid-summer, the modal size of the current year's crop increased. The 'C' mode did not make up any portion of the catch at 50 meters on 5 July, but it began to be

caught in the hyperbenthic nets by 5 August. The 'B' mode of one year-olds made up the catch at 50 meters before 5 August. As considerable overlap was seen in the size ranges caught over the progressively deeper bottoms, the three age classes were undoubtedly mixed at all levels, mid-water and hyperbenthic.

The chaetognaths distributed above intermediate depth bottoms (75 m) were extremely variable. In the early summer these belonged mainly to the breeding group. The catch in early July consisted of a mixture of the 'A' and 'B' modal groups, but in mid-July the size distribution was grouped about the calculated 'A' mode while in early August it was grouped about the 'B' or 'C' mode. Thereafter, the distribution ranged through at least two of the size modes. This size distribution over 75 meters appeared bimodal; early in the summer the larger group belonged to the breeding class, and these were replaced through the summer by the one year-olds. The smaller group, however, retained a "modal" constancy, similar to that at 50 meters; it ranged from 14 to 18 mm, or slightly larger than the range at 50 meters.

The cause of hyperbenthic distribution still remains a question. To test whether this distribution simply was due to a combination of vertical distribution behaviour and local bottom topography, i.e. chaetognaths coming into contact with the sea-

floor at depths where they ordinarily would have been distributed in mid-water, hyperbenthic samples and mid-water plankton samples taken at the same depths, but at different stations (see Fig. 4) were compared (Fig. 26). The sizes of animals caught above 50 and 75 meter bottoms were compared to the sizes of those at the same depths from mid-water. The sizes of the planktonic animals were the sum of all chaetognaths in the measured aliquots caught at that depth on the date; the 50 meter plankton samples came from Stations HP 24, HP 112, and HP 112M, while samples for the 75 meter histograms were collected at Stations HP 112 and HP 112M.

At 50 meters very little variation in size distribution between the planktonic and hyperbenthic animals was seen from late August to late September. In July, however, the planktonic animals were considerably larger than the hyperbenthic.

It was difficult to compare planktonic and hyperbenthic catches at 75 meters due to the large variability in size at this depth and to the complete absence of catches in the plankton nets at this depth during July. In August hyperbenthic and planktonic animals had a very similar size range. In September the hyperbenthic catch contained some animals well above the planktonic size range. Since the percentage of these large hyperbenthic animals was so small and the sizes at this depth were so variable,

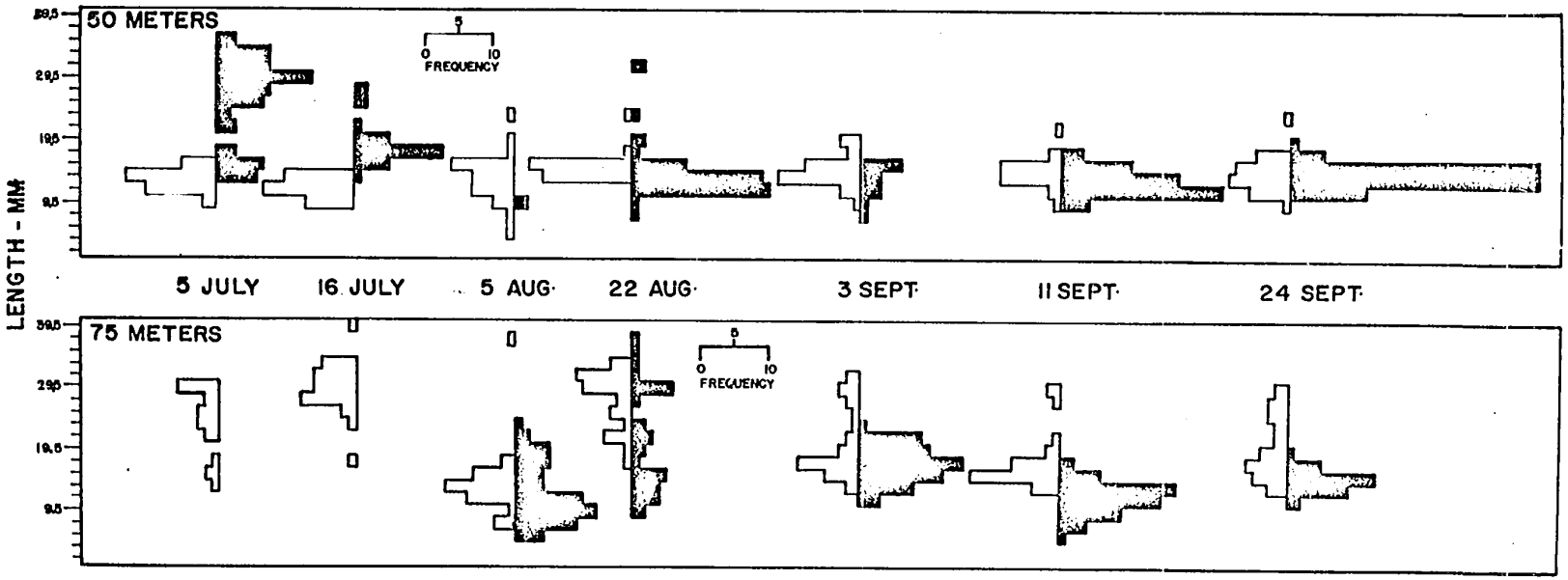


Fig. 26. Comparison of the size of Sagitta elegans distributed hyperbenthically and planktonically at the same depths. White area: hyperbenthic animals. Black area: planktonic animals. Lengths in 2 mm size-classes.

it is difficult to tell just how meaningful their presence in the hyperbenthic samples was.

VII. C. Allometric Relationship Between Body Length and Ovary Length

VII. C.1. Historical Review

Several studies on the relationship between size of the organism and length of the ovaries have been done on Sagitta elegans and data are available on these two dimensions over a considerable part of the species' range. Russell (1932a) calculated the average ovary length of a range of "mature" Stage III individuals, and determined the ratios between body length and ovary length. The relation was nearly isogonic (maintaining a constant ratio between the sizes,or a log-log slope=1) between 10 and 14 mm, while smaller and larger animals had a heterogonic (constantly changing ratio between the two variables) slope.

Dunbar (1940) related ovary size to body length in his West Greenland S. elegans. The averages of ovary lengths lay on a straight line when plotted against body length on a log-log grid and had a heterogonic relation with body length. The relation followed the "allometric" equation (Huxley 1932)

$$Y = bX^{a}$$

or in logarithmic form

$$\log y = \log b + a \log x$$

where y and x are the dimensions of the body and organ and a and b are constants. The equation is a simple description of the relation between two dimensions or organs when they grow in such a way as to maintain the ratio between their geometric growth rates approximately constant over a considerable time. This relation held for individuals between 22 and 43 mm. The smaller animals were not included in the plot, but the data for these animals hinted at a change in the relation during the life of the individual; an early isogonic relation changing into a heterogonic slope in the older animals.

McLaren (1963, 1966) used data from Russell and Dunbar to determine the fecundity of S. elegans. He (1963) attempted to find a relation between fecundity and body length, based on data from the Greenland and the Plymouth populations, and data from populations in Ogac Lake and Ungava Bay. He plotted a line through maximum ovary lengths in each population to determine fully mature ovary size, and then related ovary length to egg number; indirectly relating"fecundity" to body length. In the 1966 paper he directly related egg number to body length, by stripping eggs from S. elegans. He included animals from over a much wider range than in the earlier paper and again plotted the line through the maximal

points, to cover eggs the specimens may have shed. The egg estimates from the latter paper were considerably higher than in the former. He concluded that egg production was the same function of adult size in populations with different generation length and that fecundity was dependent on the temperature of growth, since the colder the water temperature the larger the adult size and the larger the adult size the more eggs produced.

VII. B.2. Ovary Studies on the Gulf of St. Lawrence Population

Ovary measurements were routinely made in 1966 to determine the effect of parasitism on maturation and reproduction. Measurements were also taken from animals caught in April 1968, since this was the earliest date in the year for which data was available. Failure of sexual development or retardation is often mentioned as a consequence of parasitism; Russell (1932a) mentioned the failure of ovary development in Plymouth *S. elegans* which were infested with nematodes or trematodes. The papers discussed above were based on measurements from a single date or on samples from several dates combined. Studies were done on the Gulf population to determine whether the ovary length-body length relation varied with time in the same size-class.

It should be noted here that the results of allometric

studies of this sort, which are derived from measurement of an assortment of animals from different sampling dates, are not expressions of growth (Simpson, Roe and Lewontin 1960). True determination of allometric growth is obtained from measurements taken from single animals whose growth is followed over a time interval. By basing growth studies on measurements taken from natural populations, which cannot be replaced and collected again, we make the unwarranted assumption that larger individuals are older individuals. At the present time, however, it is impossible to obtain laboratory confirmation of the kind of studies done here, and therefore these allometric size relations will have to be considered as growth approximations.

From Table 13 it can be seen that there was a changing relationship between body length and ovary length with time. In spring and early summer, the ovary length-body length relation of chaetognaths larger than 20 mm generally conformed to the allometric equation; the points lay close about a line drawn on a double logarithmic grid (Fig. 27). Animals smaller than 18-20 mm were generally at Stage I and showed little ovary development. By mid-summer, when three age groups were present, two ovary length-body length relations were seen in the sagittae larger than 20 mm (Table 13); one from the mature two year-olds and the other from the larger one year-olds. The same size-class had quite

TABLE 13. Annual change of ovary length - body length ratio of S. elegans population off the Gaspé coast.

Body Length (mm)	Ratio: ovary length * / body length					
	13/5/66	1/6/66	1/7/66	11/8/66	12/10/66	17/4/66
13						0.077
14						0.086
15						---
16						0.075
17				0.071		0.100
18				0.067	0.067	0.094
19				0.063	0.063	0.079
20			0.080	0.065	0.070	0.100
21				0.071	0.062	0.119
22			0.123	0.073	0.077	0.118
23	0.165		0.074	---	0.070	0.148
24	0.167		0.108	---	0.083	0.150
25	0.184	0.208	0.196	---	0.076	0.144
26	0.177	0.215	0.219	0.127	0.081	0.185
27	0.185	0.211	0.237	0.107	0.085	0.185
28	0.204	0.239	0.236	0.193	0.086	0.193
29	0.210	0.272	0.266	0.228	0.083	0.231
30	0.223	0.260	0.263	0.253	---	0.243
31	0.232	0.293	0.281	0.271	---	0.245
32	0.234	0.281	0.281	0.269	0.303	0.228
33	0.249	0.297	0.272	0.300	0.373	0.218
34	0.250	0.315	0.271	0.271	0.250	0.277
35	0.251	0.337	0.266	0.274	---	0.269
36	0.272	0.339	---	0.308	0.283	0.369
37	0.281	0.387	---	0.322	---	---
38	0.295	---	---	0.340	---	---
39	0.287					
40	0.288					

* (See Appendix 3 for table of the mean ovary lengths.)

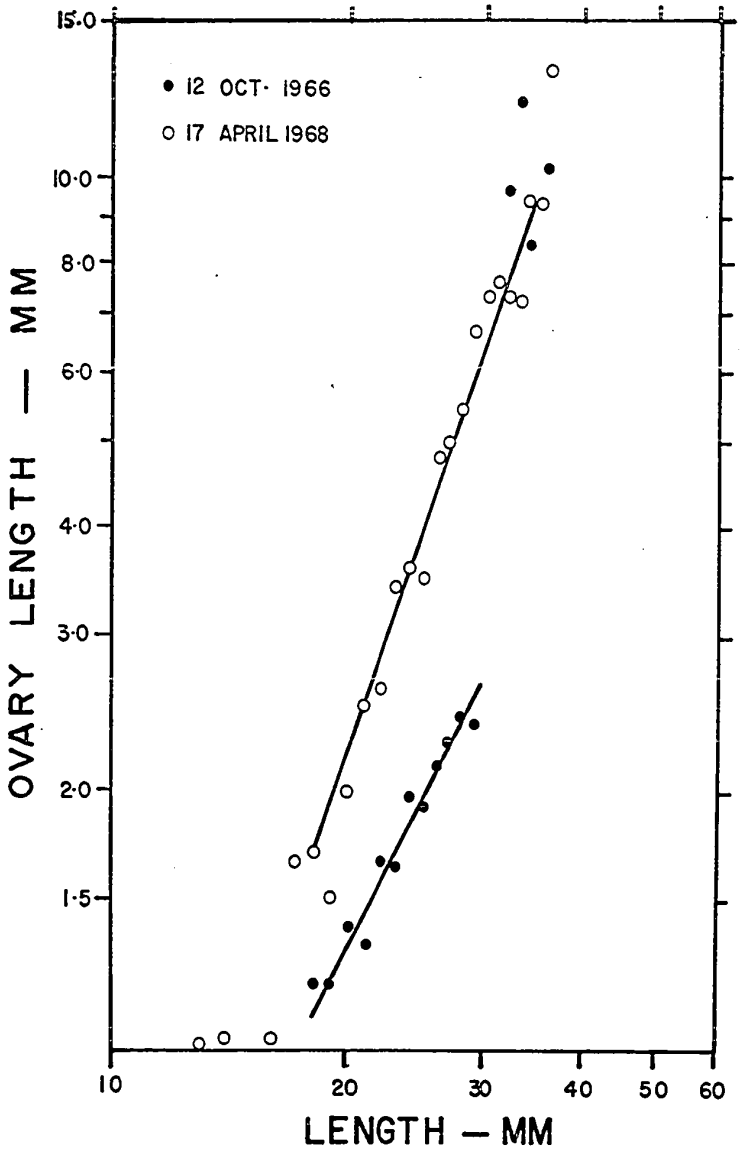


Fig. 27. The relationship between body length and ovary length of Gulf of St. Lawrence Sagitta elegans. The two lines represent extremes in a changing relationship.

different average ovary lengths in the spring and in the fall; for example on 12 October the 27 to 29 mm S. elegans had an average ovary length of 2.3 mm, which was the average ovary length of 20 mm animals in the spring.

Figure 27 shows the ovary-body length relation of animals in mid-October and mid-April. Lines were plotted for these two dates because they presented the two relations most clearly. The October sample was composed almost entirely of large individuals with little ovary development, while the line for April shows the population after most of the ovary growth was completed and prior to a "fall-off" in the relationship due to spawning. At the end of each of the lines there is a scatter of individuals from the other date. These represent large mature individuals which had not yet spawned by October and small two year-olds or one year-olds which showed little ovary development in the spring.

The average size of the ovaries for all size-classes was lowest in April and May; they showed some increase in size until about July and then had a slight decline. This is shown in Table 13, where the Gulf of St. Lawrence ovary-body length relation was expressed as a ratio. It was not clear how significant was the variation in the ovary sizes of the larger individuals during the sampling period. In mid-summer the ratios for any one size-class were quite similar. The ratios showed a trend which could be

interpreted as representing an increase in the average ovary length prior to and in the early part of the breeding period, followed by the general decline of the ratio in the late summer after the more mature individuals of each size-class have completed spawning and died. The ratios for the largest individuals for each date probably were not representative, since the averages of ovary length for these size groups generally were based on one or two animals. The number of animals in each of the size-classes averaged for the ratios was approximately equal to the frequency for that size-class and date shown in Figure 17 (approximately, because ovary lengths were not determined for animals with broken ovaries and in which ovaries could not be seen).

The two different slopes in Figure 27 probably represent two separate metabolic phases. At first body growth took place with very little development of the ovaries, or testes for that matter; this was represented by an isogonic slope. This was followed by accelerated growth of the gonads during the winter of the second year, prior to sexual maturation. In the Gulf of St. Lawrence the change in metabolic phase was not determined by size or age but seemed to be correlated with season, taking place by April.

Reeve (1970) conducted laboratory growth studies on S.

hispida and found evidence for a two-phase growth process; initial emphasis on body length followed by an acceleration in the ovary growth rate. S. hispida grew rapidly to about 7.5 mm, when the body growth rate decreased and the length curve began to approach an asympote. The ovaries began to show evidence of small eggs by 7.6 mm. He concluded that "by the time animals reach a size at which appreciable numbers of large eggs are visible in the ovaries, their growth rate is beginning to fall off".

Table 14 compares the ovary length-body length relationship for Sagitta elegans populations from Plymouth, Greenland and the Gulf of St. Lawrence. In the Plymouth population the animals were considerably smaller than in the other two populations and had smaller ovaries. The proportions of ovaries to body length, however, differed among these populations. Dunbar did not include the maturity stages of the Greenland animals, but in animals from Ungava Bay he showed (1962) the mature breeding mode at about 35 mm. If we took this as the breeding size and looked at the proportions of only the larger Greenland animals, the proportions of the animals in the Greenland population and the Gulf of St. Lawrence population were nearly identical and differed considerably from the Plymouth animals. The ratio for the 'A' mode of Gulf of St. Lawrence animals (29 mm) was about 0.240, while those of the largest animals from Greenland were 0.292 and 0.237.

TABLE 14. Comparison of ovary length - body length ratio of S. elegans in the Atlantic part of its range.

Body Length (mm)	Ratio: ovary length / body length		
	Plymouth (Russell 1932a)	Greenland (Dunbar 1940)	Gulf of St. Lawrence 17/4/68
9.0	0.061		
9.5	0.075		
10.0	0.101		
10.5	0.113		
11.0	0.104		
11.5	0.096		
12.0	0.113		
12.5	0.097		
13.0	0.100		0.077
13.5	0.110		---
14.0	0.111	0.031	0.086
14.5	0.112		---
15.0	0.130	0.025	---
15.5	0.143		---
16.0	0.139	0.050	0.075
16.5	0.167		
17.0	0.188	0.040	0.100
17.5	0.168		
18	---	0.031	0.094
19	0.194	0.047	0.079
20	0.193	0.041	0.100
21		---	0.119
22		0.052	0.118
23		---	0.148
24		0.059	0.150
25		0.063	0.144
26		0.063	0.185
27		0.070	0.185
28		0.074	0.193
29		0.090	0.231
30		0.103	0.243
31		0.107	0.245
32		0.114	0.228
33		0.126	0.218
34		0.122	0.277
35		0.136	0.269
36		0.212	0.369
37		---	
38		---	
39		0.292	
40		---	
41		---	
42		---	
43		0.237	

The Plymouth breeders had a ratio of only 0.193. Dunbar (1941) stated that in the two year-old "A" group from the eastern Canadian Arctic he found no good correlation between ovary development and the size of the animals; the ovaries varied from small eggs to near spent. The extreme slope in the relationship he found between the ovaries and body length of the larger Greenland animals was probably due to only a few mature animals having been caught. The average ovary length for the 35 mm class was 4.76 mm, for the 37 mm class it was 7.85 mm, while for the 39 mm class it was 11.4 mm.

VII. E. Discussion

Chaetognaths play an important role in the bioenergetics of the world's oceans. Reeve (1970) examined 11 macrozooplankton studies and concluded that the biomass of chaetognaths is probably 30% of that of copepods. Grice and Hart (1962) found the chaetognaths the second most abundant zooplankton group in the American Atlantic shelf and slope waters, based both on displacement volumes and catch numbers.

Sameoto (1972) noted that the biomass of Sagitta elegans in St. Margaret's Bay exceeded that of copepods in winter and early spring. He calculated that the chaetognath consumes 0.7-1.1% of the total energy produced annually by copepods in the Bay.

Although it wasn't an important copepod predator when considering total annual production, it had a great impact on the zooplankton community during winter and spring. Lacroix (1968) found S. elegans in 82% of all his catches in the Baie des Chaleurs; and in 100% of the deeper catches. In 1968, when we took samples at relatively close intervals through the water column off Grande-Riviere, 94.6% of the samples contained S. elegans. Of 241 samples only 9 samples at 25 meters and 4 samples at 75 meters did not contain this species.

Different types of organisms vary considerably in their life history patterns, due to a diversity of adaptations for dividing limited resources between the individuals' growth and survival and their reproductive task (Gadgil and Bossert, 1970). The strategies are the result of trying to maximize the spawn and their probability of success, while ensuring that mature animals will survive to produce the young. The diverse strategies taken by organisms determine the different population patterns. Cole (1954) drew the distinction between semelparous organisms (breeding once per lifetime) and iteroparous organisms (breeding more than once per lifetime). Chaetognaths belong to the former group and as a result should have no overlapping age groups in any homogeneous population; that is, animals mature, spawn (which is the climax of their life; here one can really feel teleology in the von Bertalanffy

sense) and die. This life strategy results in a maximum of two size-age modes at any instant in a population.

This is the pattern found for S. elegans populations in most areas except in the Arctic (Dunbar 1940, 1941, 1962). Dunbar found three modal groups in the Arctic during mid-summer and concluded that the species had a two-year life cycle there. Since S. elegans produced young in successive years there must have been two more or less separated breeding groups, which were at least potentially reproductively isolated.

Three modal groups were also found during the summer in the Gulf of St. Lawrence, indicating a biennial life history there the same as in the Arctic. At first glance this is surprising, since Redfield and Beale (1940) and Sherman and Schaner (1968) have substantiated that the S. elegans population in the nearly adjacent Gulf of Maine breeds annually and Zo (personal communication) has found two broods per year in Bedford Basin, Nova Scotia as has Sameoto (1971) in his subpopulations from St. Margaret's Bay. The water mass structure in these water bodies, however, are completely different. Just looking at the temperature structure (since generation length in this species has been correlated with environmental temperature), in the Gulf of Maine during the summer temperatures at 50 meters ranged from $3^{o}C$ in the Eastern Channel to

almost 9°C in the Eastern Basin, while the temperature at 100 meters ranged between a low of 4°C in the Western Basin and a high of 7°C in the Eastern Basin (Redfield and Beale 1940). In the Gulf of St. Lawrence at 50 meters temperatures ranged between 0°C in April to 9°C in July (Fig. 8). At 100 meters, the temperatures remained below 1°C throughout the spring and summer, but climbed to about 2°C in mid-fall after the decay of the thermocline. Temperatures below 75 meters remained stable at 2°C and less throughout the summer and except for the fall warming of the lower depths, we could say throughout the year. Temperatures between at least 75 meters and the bottom in our sampling area, were roughly comparable to temperatures in the Arctic. The temperature range is very similar to that recorded for Disko Bay, Greenland by Dunbar (1941); "the temperature range, between 10 and 100 meters, was from 0.16° to 2.55°C".

Russell (1932a) determined that the average length of adult S. elegans off Plymouth was inversely proportional to environmental temperature as was the generation length. The lower the temperature, the longer the generation time and the larger the average length of the adults. Russell's temperature/body length relation was confirmed by McLaren (1963, 1966).

McLaren (1963) also raised the question of the effect of

food on growth and fecundity. He concluded that at least for the Plymouth population "the relationship between generation length and mean crop of zooplankton is consistent with the suggestion that the effect of temperature on development rate is masked by the effect of food. On the other hand, food fails to account for the residual scatter in the length - temperature relation". Reeve's (1970) experiments on Sagitta hispida showed that growth increased with food at low food concentrations, but a ceiling was quickly reached at which additional food produced no further increase in the growth rate. Starved animals showed a loss in length! On the other hand, the percentage of animals with mature eggs increased in proportion to increases in food concentration. This suggests that body length is a function of temperature given an adequate food threshold, but that maturation of ova is a function of food abundance.

In the Gulf of St. Lawrence S. elegans was found to have a long spawning period, beginning early in June and continuing into September. The newly hatched young grew to about 15 mm by the end of their first summer and had a decreased growth rate over the winter. By the end of their second summer they averaged 24 mm and had little ovary development. The growth rate decreased again over the winter. Sometime in the early spring of their second year, perhaps stimulated by the increased food intake during the spring

phytoplankton-zooplankton bloom, there was a metabolic shift and gonadal growth was emphasized over somatic. There was a slight increase in body length during this period, bringing the modal size up to about 28 - 30 mm, but growth of ovaries accelerated very rapidly; 29 mm individuals averaged 2.4 mm ovaries in mid-October, but by mid-April 29 mm sagittae had 6.7 mm ovaries. Maturation from Stage II to III, which amounts to development of the ova, took place between April and June. If we followed the ovary development through the life of a chaetognath, we would find the acceleration in ovary development taking place between April and May of the "second" year (Table 15). The ovaries developed through the entire year class at the same time.

TABLE 15. Timing of ovary development (based on averaged measurements for populations in 1966 & 1968).

Date	Approx. Modal Class (mm)	Mean Ovary Length (mm)
June	12	<1
July	15	<1
August	18	1.2
October	24	2.0
April	25	3.6
May	30	6.7
June	28	6.7
July	29	7.7

The modal length of the mature chaetognaths compares well with the modal size of mature S. elegans caught in Hudson Bay (Dunbar 1962). McLaren (1966) plotted the mean length of mature S. elegans from Frobisher Bay, western Hudson Strait, Ungava Bay, and northwestern Hudson Bay as 37, 35, 34, and 28 mm respectively.

Sagitta elegans settle progressively lower in the water column with increasing maturity. This phenomenon, termed an "ontogenetic descent" by McLaren (1969), seems to be part of the behavior of many chaetognath species. Within any one S. elegans population, larger animals are found at increasingly greater depths, but in comparing different populations we find differences in the sizes of animals at equivalent depths. In mid-summer at the height of the spawning period in the Gulf of St. Lawrence, animals at 119 meters average about 30 mm and are at Stage III. In Oslofjord (Jakobsen 1971), where S. elegans mature at 18 mm, larger individuals are also distributed at proportionately greater depths, but animals at 104 meters average about 21 mm during the mid-summer spawning period. In these two populations, where the analysis of size-range and vertical distribution have been carried out, animals at the same stage of maturity but quite different sizes are found at approximately the same depth. Therefore, since size at maturity and age at maturity (i.e. length of the life cycle) vary through the species' range, changes in vertical distribution are maturity

dependent rather than size dependent. Animals probably become increasingly sensitive to light with increasing maturity.

In the Gulf of St. Lawrence the relation between size and depth was not orderly; considerable size overlap occurred through successive depths. Only a small fraction of Stage II and III animals (>18 mm) were found above 75 meters during the day. Since the temperature at 75 meters and deeper was less than $2^{o}C$ throughout the year, with the exception of the late fall, this descent placed the animals during the part of their lives that they were sexually developing in a temperature environment similar to that of the Arctic. During the winter the entire water column was isothermal about $0^{o}C$. Therefore, the total time spent in waters above 2^{o} in the two years needed to complete development and spawn was probably no more than 6 to 8 months.

If growth is inversely proportional to temperature and depth distribution becomes deeper with length, then the vertical temperature structure of the area that the population occupies or passes through will determine the size at maturity and, since the Chaetognatha are semelparous, length of the cycle; and that in turn is at least partly responsible for the level of fecundity and production.

Studies which are limited in their sampling to the surface waters probably under-represent the larger and more mature size ranges of chaetognaths and are not reliable for life history studies. Since there is a size stratification with depth, any study of the biology of S. elegans and probably other chaetognath species should include samples down to the deepest depth in the range. If this is not done it follows that there will be bias against the more mature individuals.

From reports in the literature, a hyperbenthic distribution seems to be a general feature in the biology of S. elegans, at least in boreal waters. It would be very interesting to know if this phenomenon occurs in the sub-arctic populations. S. elegans were caught in all hyperbenthic samples. The individuals caught in these samples at the deepest station, i.e. the deepest sampling depth, were consistently the largest individuals found on each sampling day. Samples early in the summer from these stations contained only Stage III, but by the middle of August Stage II, 'B' mode animals became dominant in these samples, indicating a progressive settlement in the water column of the succeeding year's breeders. By October these samples contained almost exclusively the Stage II animals. Shallower hyperbenthic samples contained correspondingly smaller chaetognaths. Plankton samples and hyperbenthic samples collected at the same depths contained the same

sized chaetognaths, indicating that hyperbenthic distribution was the result of animals attempting to take up a depth level but running into the bottom. This was seen most clearly in the hyperbenthic samples collected at 50 meters, where the size range of chaetognaths remained constant through the summer of 1968, while the animals were actually growing. This suggests that animals over this bottom were constantly being replaced. The changes in catch density confirmed this. There was a rapid increase in the density above the 50-meter bottom when the size range was coincident with the 'C' mode (Fig. 25), i.e. the size mode of the current year's brood. The large concentrations of chaetognaths caught hyperbenthically were probably the result of a mass of chaetognaths, which would normally be distributed over a considerable depth range settling against the bottom interface.

This hyperbenthic distribution, which is now being recognized as both a specialized planktonic niche (Beyer 1958) and a normal part of the lives of a number of planktonic organisms, presents a means for interactions in planktonic and benthic communities and expands the possible food webs and energy pathways. A static interface environment presents special problems for planktonic animals to cope with and it would be interesting to discover if there are differences in adaptation between oceanic plankton and neritic species; to allow the latter group to deal effectively

with this environment, which may otherwise be stressful to an animal adapted to an entirely fluid environment.

One general problem of planktonic animals is the maintenance of a breeding stock of the animals within its range. A drifting population would normally be swept from a limited range by water movements. Various schemes have been proposed to account for the maintenance of a species or population within its range, but none of the schemes explains the way that animals with long life cycles are maintained. Neritic animals which have an "ontogenetic descent" would be able to retain breeding stocks in hollows and bottom topographic irregularities. Therefore, animals having hyperbenthic distribution in their mature stages have a distinct advantage in being retained within their normal range than do long-lived animals without this distribution. It is possible that ontogenetic descent and hyperbenthic distribution have been selected for in long-lived neritic species for this reason.

VIII. The Relationship Between *Sagitta elegans* and its Parasites

VIII. A. Introduction

Recent trends in marine parasitological research have expanded the traditional morphological and life history approaches to include studies on host-parasite interactions. These studies have pointed out the importance of environmental factors, such as the zoogeographic distribution of hosts and parasites, the hosts' age, behaviour, and food preferences, as well as the general parameters of the external environment, in determining the numbers and kinds of parasites carried by a host. Reciprocally, they have shown that host specificity, which was frequently assumed to be due to phylogenetic adaptations of the host-parasite complex, often was actually a result of environmental factors (Shulman 1954; Arai 1967). V. A. Dogiel and his associates in the Soviet Union have been particularly active in applying these approaches to marine fauna.

Most of the marine studies on ecological host-parasite relations have concentrated on fish populations. Polyanski (1955) studied the effects of the hosts' age and mode of life, i.e. whether the species was pelagic or benthic, on the parasite fauna

of Barents Sea fishes. Noble (1957) investigated seasonal variations in some marine fishes and their protozoa. Noble, King and Jacobs (1963) examined the seasonal variations and the relationships between the parasites on fish gills. Llewellyn (1962) studied the population dynamics of monogenetic trematodes on the horse mackerel, Trachurus trachurus, and Scott (1969) examined the population dynamics of hemiurid trematodes in the Atlantic argentine Argentina silus. Meskal (1967) studied seasonal variations of the trematodes infecting cod.

Many of these ecoparasitological studies have been done on parasites whose complex life cycles involve a succession of invertebrate hosts. Virtually no information exists on the host-parasite relations of these vectors, although some studies have been done on relations between digenetic trematodes and their molluscan hosts (for example, Bowers and James (1967) examined the seasonal and age dynamics of Meiogymnophallus minutus metacercariae in the cockle, Cardium edule). No studies of this type have been done for marine planktonic vectors which serve as intermediate hosts for many of the more common marine helminths.

VIII. B. Results

A large sub-sample from the open-net hyperbenthic

collections taken on each sampling day in 1965 and 1966 were examined for parasites. In 1968, the thirty-chaetognath aliquot from each closing net sample and a 200-chaetognath subsample collected at Station HP 112 by the non-closing hyperbenthic net mounted on top of the Macer apparatus were examined. In all, about 9400 of the Sagitta elegans caught in 1965, 1966, and 1968 were examined for parasites. Five types of parasites were found: Hemiurus levinseni, Derogenes varicus, Metaphrya sagittae, Scolex pleuronectis and Contracaecum type larvae. The latter two were extremely rare: each was found only twice. Hemiurus levinseni was found in 451 of the chaetognaths, D. varicus in 18, and M. sagittae in 45. Infestations by single individuals was the rule for the helminths, with the exception of H. levinseni, which was found in multiples of up to six trematodes per host in the autumn. Metaphrya sagittae generally packed the host's main body coelom with dense clusters of large cells. Infestations of less than fifty cells were rarely seen. The ciliates were too densely packed and too numerous to count, but the average intensity of infestation was estimated at over 100 cells per host.

All of the parasites were found in the hosts' body coelom. They were dispersed randomly throughout the coelom; no preference for any particular region was noticed. Lebour (1917a) noted finding D. varicus and Opechona bacillaris generally near

the ovary in S. bipunctata (?). In the few non-fixed infected chaetognaths which were examined here, the parasites moved actively about in the coelom. Since the chaetognaths and their parasites were subjected to mechanical buffeting as well as extreme and rapid change in light and temperature during capture, it was not possible to be certain if there was a preferred site within the coelom, in the undisturbed animals. Hemiurid trematodes have been reported emerging from copepods (Pratt 1898; Lebour 1923; Sewell 1951). After catching free H. communis, and Acartia with emerging H. communis in her plankton nets, Lebour suggested that these parasites emerged after they grew too large and killed the host. The shock of being caught in a plankton net, however, may duplicate that of being eaten by a predator and serve as a stimulus for emergence activity in these metacercariae. None of the chaetognath parasites were seen emerging from the host, but the active movements might be "emergence" behaviour stimulated by the mechanical shock. In any event, it was not possible to determine the normal degree of activity or location of these parasites.

VIII. B.1. Seasonal Variations in Parasitism

Hemiurus levinseni was the only parasite which had an undoubted seasonal cycle in the S. elegans population. Among the other parasites, only Metaphrya was found in sufficient numbers and

regularity to even hint at possible seasonal fluctuations.

Chaetognaths infected with H. levinseni were found on every sampling day, except for one in midsummer, when the total number of S. elegans caught was less than fifty. The incidence during the sampling period varied between 0% in midsummer and 16% in the autumn (Fig. 28). There seemed to be two periods of infestation, one in the spring and a much greater one in the autumn. The incidence decreased from the spring to the early summer and then began a gradual increase which rose precipitously during September-October and declined in late October and November. The most distinguishing feature of the cycle is the abrupt increase in the autumn, when the incidence repeatedly rose during each of the years sampled from about 3.5% to 10 - 16% in less than a month. In 1965 the percentage of the S. elegans population parasitized by H. levinseni rose from 1.63% to 11.22% in seven days. The timing of the increase varied to a small extent over the three years; in 1965 it took place in mid-September, while in both 1966 and 1968 it took place from late September to early October. There was also some variation in the maximum found in different years. In 1965, 15.99% of the S. elegans were infested, in 1966 it was 9.34%, while in 1968 the maximum was 14.72%.

The incidence of S. elegans infested by M. sagittae

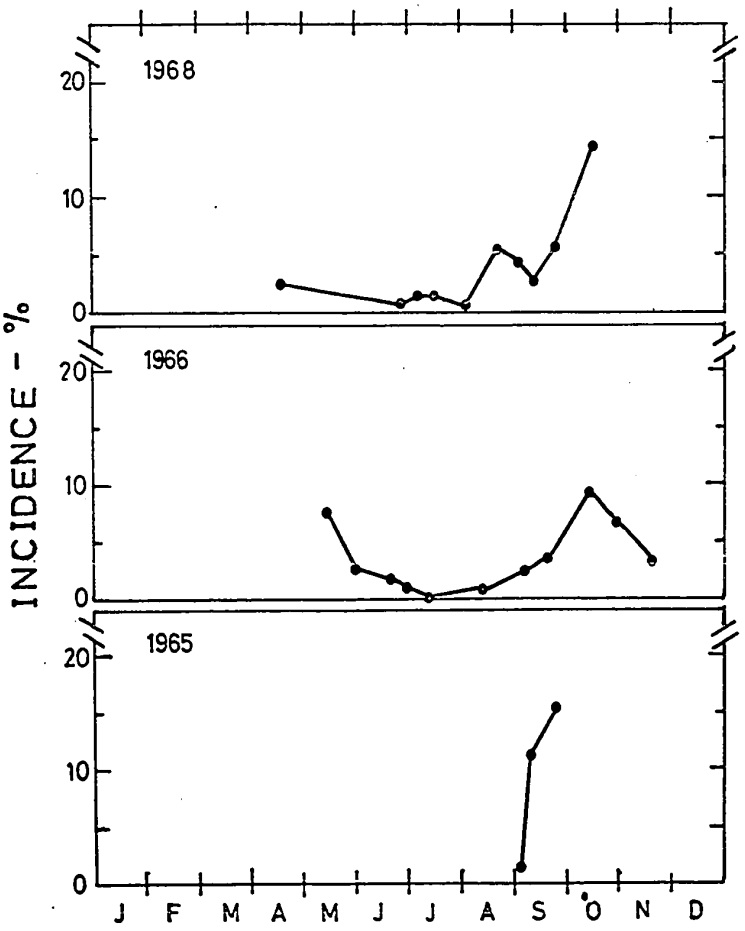


Fig. 28. Seasonal variations in the incidence of Hemiurus levinseni infesting Sagitta elegans.

remained low; generally less than 1% of the S. elegans population was infested by the ciliates at any time. Slight variations in numbers of parasitized chaetognaths were noticed through 1966 and 1968 (Table 16), with the peak period in June and no ciliates seen late in the year. Because of the small numbers of infected S. elegans found on any one day, it was not clear how meaningful were these variations.

Derogenes varicus was found in the chaetognaths only occasionally (Table 17). The largest numbers of this trematode were seen in June, both in 1966 and 1968, but numbers were never great enough to detect changes in the levels of parasitism. The highest incidence found was 1.12%.

VIII. B.2. Seasonal Changes in the Intensity of Infestation by Hemiurus levinseni

The chaetognaths were most frequently parasitized by single H. levinseni, but as many as six trematodes were found in one S. elegans. The average intensity of infestation for the entire S. elegans population was 0.05 H. levinseni per host. This is quite low compared to the burden of hemiurids carried by the definitive hosts; cod have averaged 134.0 H. communis and 4.0 D. varicus (Meskal 1967), while Argentina silus have harboured 5.8

TABLE 16. Seasonal variations in incidence of Metaphrya sagittae.

	1965		1966		1968	
	(%)	Number of Hosts Examined	(%)	Number of Hosts Examined	(%)	Number of Hosts Examined
April	----	------	----	-----	0.96	(209)
May	----	------	0.0	(217)	----	-----
June	----	------	2.60	(461)	1.12	(269)
July	----	------	0.66	(153)	0.90	(893)
August	----	------	0.32	(619)	0.41	(974)
September	0.20	(1500)	0.64	(941)	0.17	(1182)
October	----	------	0.63	(755)	0.0	(333)
November	----	------	0.0	(354)	----	------

TABLE 17. Seasonal variations in incidence of Derogenes varicus

	1965		1966		1968	
	(%)	Number of Hosts Examined	(%)	Number of Hosts Examined	(%)	Number of Hosts Examined
April	----	------	----	-----	0.96	(209)
May	----	------	0.0	(217)	----	-----
June	----	------	0.22	(461)	1.12	(269)
July	----	------	0.0	(153)	0.34	(893)
August	----	------	0.16	(619)	0.0	(974)
September	0.40	(1500)	0.11	(941)	0.0	(1182)
October	----	------	0.0	(755)	0.30	(333)
November	----	------	0.0	(354)	----	------

H. levinseni and 1.3 D. varicus (Scott 1969) per host.

All of the H. levinseni infestations consisted of single parasites throughout the sampling period until the autumn increase in incidence (Table 18), at which time multiple infestations appeared. No multiple infestations were found in May or June, at the time of the lesser incidence peak. The increase in the proportion of infected chaetognaths with multiple infestations roughly parallels the increase in overall incidence in the host population, but the asymptote for the intensity was reached slightly in advance of the maximum incidence. In 1965 the maximum intensity was effectively reached on 10 September, while the incidence continued to increase until 24 September; similarly, in 1966, the intensity peak was effectively reached by 20 September while the incidence maximum was reached on 12 October. High proportions of infested S. elegans also harboured multiple infestations in August and September 1968 when the population incidence was relatively low. During two sampling dates in September 1968 no multiple infestations were found.

VIII. B.3. The Size-Age Dynamics of Parasitized Sagitta elegans

The samples for all dates in 1966 and 1968 were combined

TABLE 18. Seasonal changes in the intensity of H. levinseni infestations.

Date	% infested S.elegans with multiple infestations	% of parasitized S.elegans with different burdens of H.levinseni				
		Number of H. levinseni				
		2	3	4	5	6
1965						
3 Sept.	0.0%					
10 Sept.	24.6%	21.8%	1.4%	0.0%	1.4%	0.0%
24 Sept.	25.4%	18.6%	2.0%	1.0%	3.0%	1.0%
1966						
Prior to 6 Sept.	0.0%					
6 Sept.	7.2%	7.2%	0.0%	0.0%	0.0%	0.0%
20 Sept.	21.4%	14.3%	7.2%	0.0%	0.0%	0.0%
12 Oct.	15.0%	15.0%	0.0%	0.0%	0.0%	0.0%
26 Oct.	22.7%	18.2%	4.5%	0.0%	0.0%	0.0%
17 Nov.	0.0%					
1968						
Prior to 22 Aug.	0.0%					
22 Aug.	15.4%	7.7%	3.8%	0.0%	3.8%	0.0%
3 Sept.	0.0%					
11 Sept.	21.4%	21.4%	0.0%	0.0%	0.0%	0.0%
24 Sept.	0.0%					
15 Oct.	38.8%	24.5%	8.1%	2.0%	4.0%	0.0%

to determine how the infestations of H. levinseni and M. sagittae varied with the chaetognaths' size (age) (Fig. 29). The larger size-classes were the most heavily infested by both parasites.

Very few H. levinseni were found in the smaller chaetognaths; only 1% of the 16 - 20 mm S. elegans were infested. The higher rates of infestation began in hosts larger than 21 mm. The animals in the mature modal class, 26 - 30 mm, were the most parasitized but there were only slight differences between the rates of infestation of the largest size-classes. The percent of infestation of all animals 21 to 40 mm long, which represented nearly all the Stage II and Stage III animals, was almost constant. None of the animals in the two largest size-classes, 41 - 45 mm and 46 - 50 mm, were infested by the trematode. The drop of parasitism in these size-classes, however, may not have been significant, since only 10 chaetognaths larger than 40 mm were caught.

On the other hand, the chaetognaths infected with M. sagittae comprised only a small proportion of the size-classes smaller than 36 - 40 mm. An extremely high proportion of the largest S. elegans were infected by this ciliate. About 6.5% of the chaetognaths 36 - 40 mm long and 44.5% of the animals 41 - 45 mm long were infected by M. sagittae.

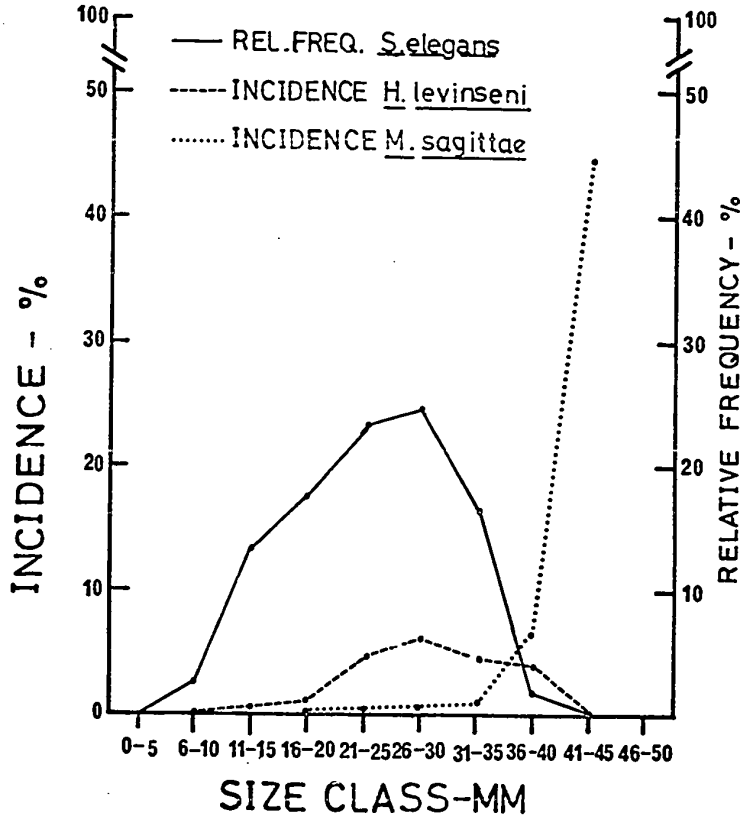


Fig. 29. Relationship between the size of Sagitta elegans and infestation by Hemiurus levinseni and Metaphrya sagittae.

Figure 30 shows the percentage of each of the size-classes which were parasitized by H. levinseni on each sampling date in 1965, 1966, and 1968. Three lines representing the three year-classes (the currently spawning animals and their young, and the alternate generation of one year-old chaetognaths) were laid over the graph so that the dynamics of parasitism could be traced through the host's life cycle as well as seasonally through the population. (See Section VI.B.2 for the discussion of the host's life cycle and the calculations of the modal size-classes for each of the year-classes).

During the first year of its two-year cycle S. elegans was rarely parasitized by H. levinseni. The only infestations which took place among the newly spawned generation, during both 1966 and 1968, occurred in mid-October, about the same time as the massive decline in infestations.

All of the larger size-classes of S. elegans, consisting of the Stage II and Stage III animals, became infected on approximately the same date in the fall, but the largest size-classes (26 - 30 mm and 31 - 35 mm) reached the high levels of infestation several weeks earlier than the smaller. The early high incidence in the former group, which was for the most part the late-spawning portion of the mature Stage III two year-old S. elegans, tended to

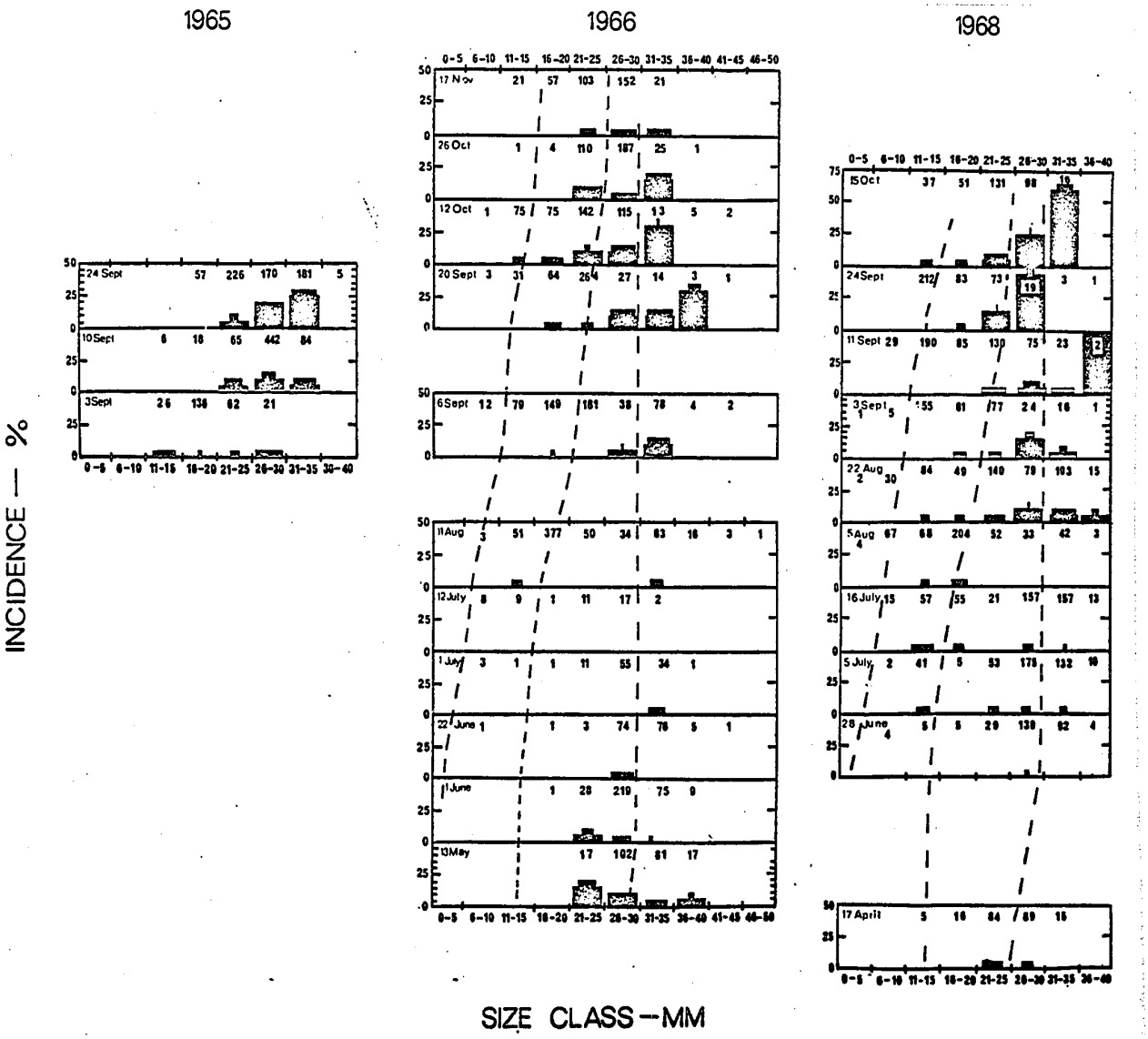


Fig. 30. Seasonal dynamics of the infestation of Hemiurus levinseni in Sagitta elegans. The broken lines trace the growth of the three S. elegans age-groups through the sampling periods. The numbers record the number of S. elegans examined from each size-class. To represent incidences ranging from 1/10 % to 100% here and in Fig. 31, the vertical scale increases by 5% units, while an horizontal scale (see Fig. 31) records single percent units and less.

be hidden in the overall incidence figures for the S. elegans population for these dates, due to the relatively small proportion of the total chaetognath population that these size-classes represented in the fall. For example, on the 20 September 1966, when the overall incidence of H. levinseni was 3.44%, 14.8% of the 26 - 40 mm chaetognaths were infested. Generally, the larger the size-class, the higher was the incidence and the earlier the higher levels of parasitism (above 10%) were reached.

In 1965, by September 3, H. levinseni infected all size-classes from 11 - 15 mm through 26 - 30 mm. No animals larger than 30 mm were caught in these samples. 29.3% of the 31 - 35 mm, 20.0% of the 26 - 30 mm, and 6.6% of the 21 - 25 mm animals were infested by 24 September. Higher proportions of the smaller size-classes may have become infested at a later date, as happened in 1966 and 1968, but the time series was too short to determine if this occurred.

In 1966, infestation of the large size-classes occurred by 6 September; by 20 September all of the size-classes from 16 - 20 mm through 36 - 40 mm had infected individuals. High levels of infestation (14.1%) were found among the 31 - 35 mm animals on 6 September; comparable levels (14.8%) occurred among the 26 - 30 mm animals on 20 September; and the maximum (11.3%) infestation in the

21 - 25 mm chaetognaths was only reached on 12 October. The maximum infestation of the 16 - 20 mm animals (4.0%) was also reached on this date. Parasitism began to fall in all the size-classes from the 26th of October and by 17 November only low levels of parasitism (5%) were found in the three largest size-classes present.

The onset of parasitism took place earlier in 1968. By 22 August, when 5.2% of the entire S. elegans catch were found with H. levinseni, all the size-classes from 11 - 15 mm through 36 - 40 mm had infected individuals. Thereafter the level of parasitism in the whole population declined and only passed the incidence found on 22 August one month later, on 24 September: only 2.6% of the catch were parasitized on 11 September. Over 10% of the 26 - 30 mm class were infected from 22 August to 15 October, the end of the series, except for 11 September, when the incidence dropped to 8%. The change in incidence among the 31 - 35 mm animals during the same period was erratic, probably due to the low numbers of these larger animals left in the population at this late date. On 15 October, however, 10 of the 16 chaetognaths of this class were parasitized by H. levinseni. About 10% of the 26 - 30 mm and 31 - 35 mm chaetognaths were infected by 22 August. Comparable levels of infestation among the 21 - 25 mm animals were only reached on 24 September. The highest incidence in the 16 - 20 mm animals, 2.5%, was reached

on 3 September.

The high level of parasitism declines during the winter. The rate of this decline appears to be a question. Animals collected at the end of winter, on 17 April, had a relatively low incidence, which suggested a fall-off in the autumn or through the winter months. In the 1966 series a definite and rapid decrease in incidence was seen during the end of October and into mid-November (Fig. 28 and 30), when the sampling was terminated. In the 1968 series, however, there was no evidence for a decline in the incidence on 15 October, the last sampling date. This could be expected if the timing of the H. levinseni "epidemic" was similar to that of 1966, when the maximum incidence was reached about 12 October; evidence for a decline was found only on 26 October in 1966. Additional samples collected in mid-winter would be necessary to clarify the rate of fall-off.

During the spring, both in 1966 and 1968, the highest incidence occurred in the 21 - 25 mm class. There is some question as to whether there actually is a spring period of infection or if the relatively high levels of infestation found in the spring were simply a carry-over from the fall. The incidences in May and June 1966 for all the infected size-classes were higher than found in November (Fig. 30), and there was a regular fall-off in parasitism

between mid-May and early June, similar to that found late in the fall. The incidence of the infected size classes dropped considerably between 13 May and 1 June 1966. If there was a regular spring period of infestation it probably took place between mid-April and mid-May, since the levels of parasitism found on 17 April 1968 were marginal.

In terms of the life cycle of these Sagitta elegans, parasitism effectively did not begin until the animals' second fall, when the chaetognaths had reached a length of at least 20 mm and were at Stage II. High levels of parasitism probably did not persist after the fall; either the parasitized animals were subjected to a high mortality or the life span of H. levinseni in the chaetognaths was very short. After over-wintering, the then mature two year-old Sagitta were reinfected in the spring. During the summer spawning period the probability of becoming infected by H. levinseni was low. The small proportion of mature Stage III S. elegans which lived into the fall was again subjected to another period of parasitism. The timing of parasitism of these older animals was earlier than for the Stage II's and the probability of infestation at this time was higher than when the animals were younger.

No clear seasonal patterns emerged for Metaphrya sagittae,

when the animals infected by the ciliates were broken down by size-class through time (Fig. 31). The few infected smaller Sagitta occurred in the first year modal size-classes. In 1966, the infected 1+ year-old specimens were found almost exclusively in the fall; only one infected 1+ year-old was found in 1968. Infections in the mature modal classes seemed to occur around the spawning period in mid-summer. Infections in the largest size-classes (36 - 40 mm and 41 - 45 mm), in which infestation by M. sagittae was the rule rather than the exception, were scattered throughout the summer and fall months.

VIII. B.4. The Effects of the Parasites on the Development of the Host's Ovaries

In 1965, 1966, and 1968 studies on the effects of parasitism on the development of the host's ovaries were done. Hosts may react to parasitism at all levels: from the chemical (immunological) and physico-chemical (tissue damage and inflammations) to the population (castration and enhanced mortality). Ideal parasites, which have had a long history with a host during which mutual adaptations presumably have taken place, should have little obvious adverse effects on the host. Some reaction is bound to occur, especially with coelomic parasites, which must penetrate the host to gain entrance to the blind cavity, but the

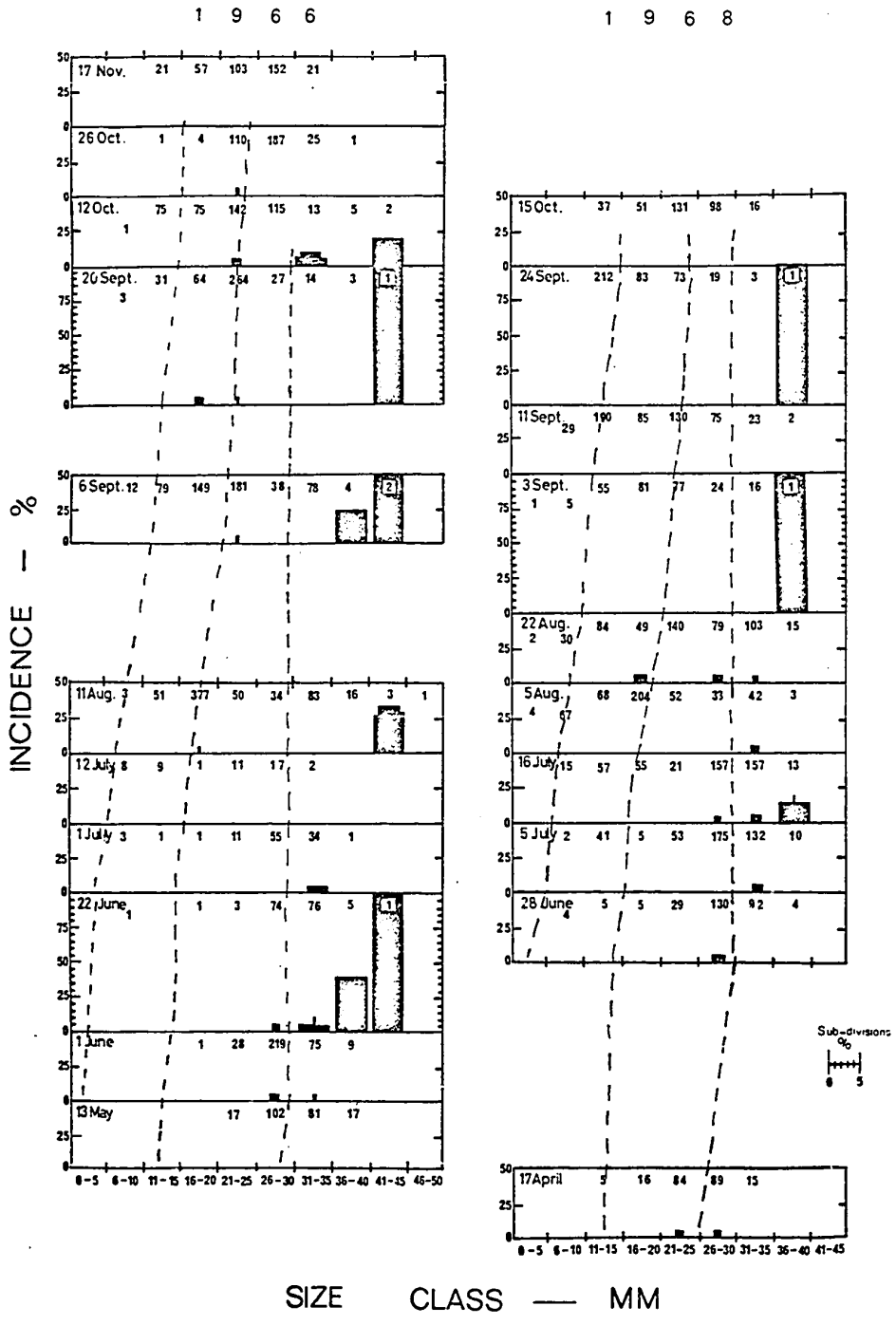


Fig. 31. Seasonal dynamics of infestation of Metaphrya sagittae in Sagitta elegans. Data from 1965 was not included as measurements of infected animals were not taken prior to staining.

effect may be local or short-term. In dealing with a natural host population in which it is impossible to follow the history of any given infestation, a good, measurable indicator of damage is required. The effect of the parasite on the host population must be expressed in reproductive terms. Damage to the population's reproductive potential is a function of change in fecundity and/or the mortality rate. If damage is local and rapidly healed, as it seems is the case with most digenetic trematodes if the intensity is low (Dawes 1956), mortality is probably not enhanced and fecundity not affected significantly.

It has been shown that there were two stages to the development of S. elegans (Section VII.C.2): the somatic growth period and the gonadal development period; and that the allometric relation between body length and ovary length, as determined from the natural population, varied with time. The possible effect of H. levinseni and M. sagittae on the development of the hosts' ovaries was examined by comparing the allometric relation between the hosts' body size and ovary length in the entire population and in the portion of the population infested with the two parasites (Fig. 32 and 33).

In Figure 27 lines were drawn through the mean ovary length of each 1 mm size class of S. elegans from two dates which

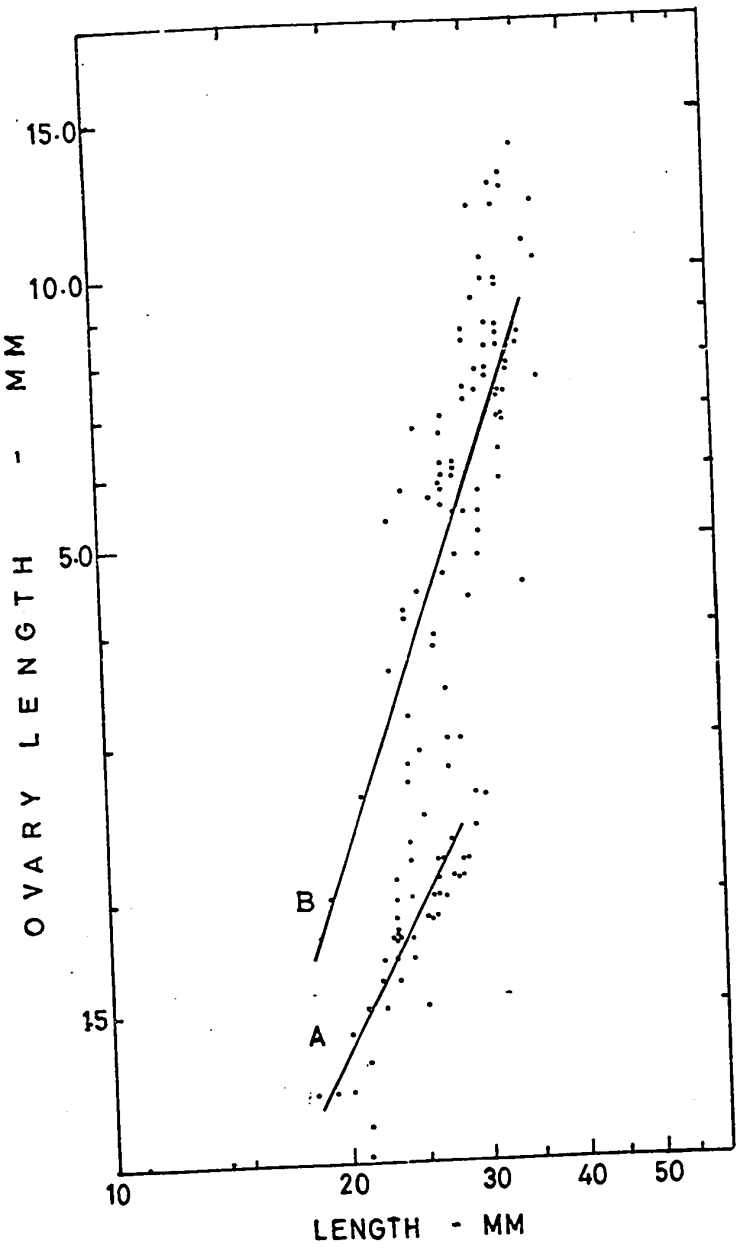


Fig. 32. Body length-ovary length relationship in Sagitta elegans infested by Hemiurus levinseni compared to non-infested hosts. Line A represents the non-infested S. elegans population in the autumn state; line B the population in the spring condition. Dots indicates the lengths of infested individuals.

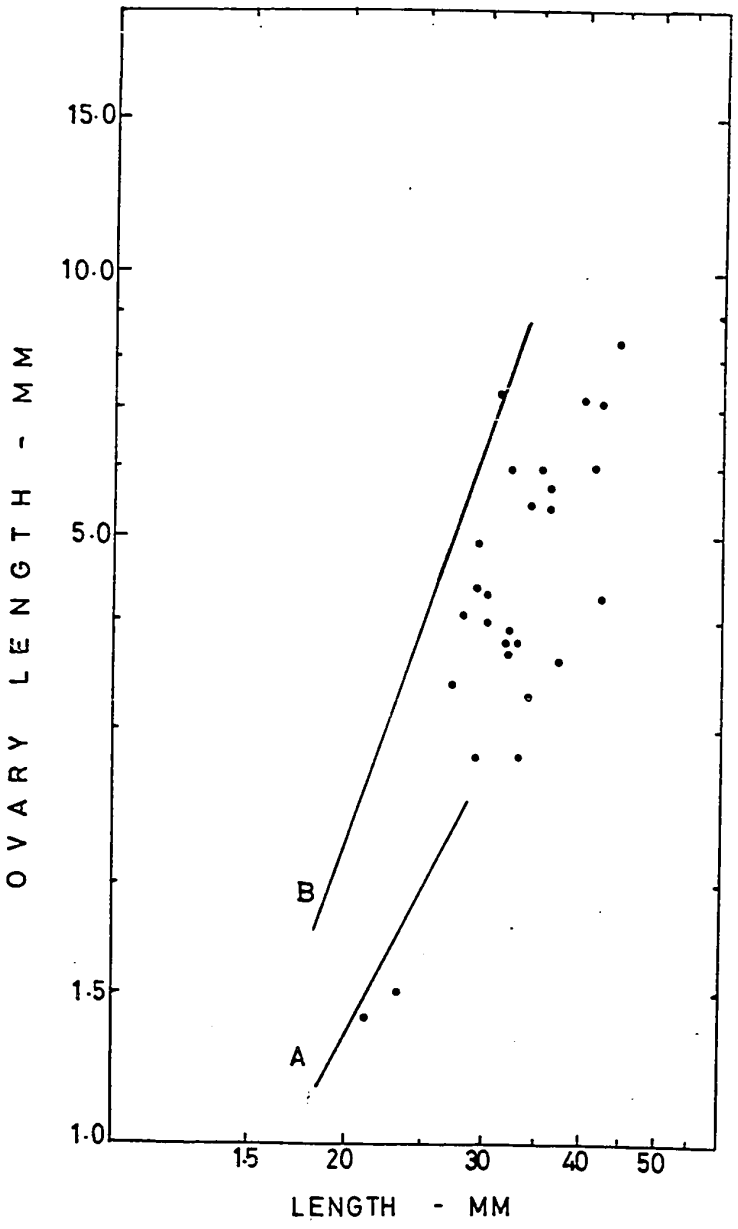


Fig. 33. Body length-ovary length relationship of Sagitta elegans infested by Metaphrya sagittae. Line A represents the non-infested S. elegans population in the autumn state; line B the population in the spring condition. Dots indicate the lengths of infested animals.

represented the population's allometric extremes. These two lines are used as reference "points" for the extremes of normal ovary-length body-length in Figures 32 and 33. The relationship represented by line A (12 October, 1966) occurred after nearly all the mature animals had spawned and died, leaving a population composed of immature S. elegans, some of which were near maximum size but had not undergone final sexual development. Line B, (17 April, 1968) on the other hand, was drawn through points for the mature population prior to the beginning of the spawning period. Points for the early and mid-summer length - ovary lengths lay closely about line B. As the summer spawning period progressed, the proportion of large mature two year-olds decreased while that of large immature one year-olds increased, and the form of the curve switched progressively to line A. The animals making the line A relation undergo rapid ovary development in early spring, re-establishing the line B relation.

The proportions of ovary length to body length of the S. elegans infected by H. levinseni conformed closely to those of the non-infected chaetognaths (Fig. 32). Some of the ovary lengths of the infected chaetognaths appeared proportionately larger than those of the non-infected (B-line). The B line, however, was drawn through the averaged ovary lengths for the population in the early spring, whereas the infected animals came from samples collected

through the entire sampling periods in 1965, 1966 and 1968. Since ovary length continued to increase more rapidly than body length into mid-summer (Table 13) and most of the points for the infested S. elegans were from the fall, the ovary lengths of normal S. elegans would be proportionately larger than in the spring. In any event, the important point was that H. levinseni either because it was a well-adapted parasite or because it had a short life span in S. elegans, produced no apparent effect on ovary development. No aberrant forms of testis or ovary development were noticed in these chaetognaths. They appeared morphologically identical to the non-infected Sagitta. Some mechanical damage by these coelomic parasites was to be expected, but no punctures or recently healed wounds on the digestive tract or body wall were seen.

On the other hand, nearly all the individuals infested by the ciliates had an abnormal appearance, both in general morphology and in the male and female gonads. The animals were large and flacid and more similar in appearance to S. maxima, which tends to be rather limp when fixed, than to the relative state of rigidity of fixed S. elegans. The body appeared swollen. The appearance of the tail coelom was variable: in some animals the sperm was fragmented into discrete packets of cells rather than in the dense granular arrangement in the normal larger chaetognaths; the largest animals, both the Stage IIIs (see Fig.

17 and Section III.B.1 for a description of Stage IIIs) and those infected by ciliates, had transparent tail coeloms filled with a clear yellow fluid and showed no evidence of cells or spermatozoa.

The ovary lengths of almost all chaetognaths infested by M. sagittae were much shorter than averaged lengths of uninfected animals (Fig. 33). None of these chaetognaths had developed ova; all of the ova were uniformly small and as a result the ovaries were 2.5 to 3.5 times thinner than those of the non-infested Stage III animals. An extremely high proportion of the largest size-classes of S. elegans were either infested with ciliates or had the same type of gonads as these animals.

VIII. C. Discussion

Sagitta elegans can only be considered as a potentially important host for two of the five parasites found. Hemiurus levinseni metacercariae and Metaphrya sagittae were found in sufficient numbers and regularity to be considered as usual parasites, tied in non-casual ways to the biology of the host.

M. sagittae occurred in less than 1% of the total S. elegans population. While the younger chaetognaths were only rarely infected, 45% of the largest size-class (41 - 45 mm)

harboured the parasites. Hosts infected by this parasite are so characteristically swollen and flacid in appearance that the infected animals can be recognized without microscopic examination. S. elegans infested with ciliates have a spent appearance and it is a possibility that M. sagittae infects the host during or after spawning. The size range of the infected animals and the similarity in condition to the spent Stage IIIs S. elegans suggests that the gonadal aberrations may not be an effect of the ciliates, but that the ciliates may infect the animals post spawning.

On the other hand, the animals infected by H. levinseni had the characteristics of normal, healthy chaetognaths at the state of maturity appropriate to their length. Although this trematode was constantly present in the chaetognath population, it went through a seasonal cycle of abundance, with numbers rising in the spring and declining in the summer months and then rising abruptly in August or September into October and then declining again. The sagittae first became infested during their second fall, after they were one year-old and were at Stage II. The level of infestation attained by the population declined in the late fall and through the winter months, either due to increased mortality of the infected animals or to the rejection of the parasite. During the early spring there was another period of heavy infestation, followed by another rapid decline. The mature

S. elegans, during their second year, spawned through the summer and fall months and died immediately on spawning. The members of this age class which were still alive in the following autumn became infected earlier than the young Stage II animals and sustained a higher incidence of infestation.

A low diversity of parasites seems to be characteristic of plankters and planktophagous fishes. The further up the food chain the greater is the potential for having a diverse parasitic fauna. Thus piscivorous pelagic fishes, such as salmon, have a greater diversity of parasites than planktophages such as the herring. Margolis (1963) found about 40 species of marine parasites which were mainly helminths in the sockeye salmon, whereas Polyanski (1955) found only nine species of parasites in the herring. As a result of his extensive survey of the parasites of the Barents Sea fishes Polyanski concluded "the parasite complex of planktophagous fish is in general depauperate in species and of low incidence and intensity of infestation". The principal helminths which have most successfully adapted to a pelagic life belong to one family of digenetic trematode, the Hemiuridae, one order of cestode, the Tetraphyllidea, and the anisakid nematodes. The same seems true for nektonic and planktonic hosts alike. With the exception of a variable protozoan fauna (Jepps 1937a; Sewell 1951), the parasites found in marine holoplankters are limited to

the same three groups of helminths.

Noble (1957) suggested that catholicity of food habits may lead to high parasite diversity and conversely a diet restricted to one or two prey species may limit the diversity of those parasites dependent on the food chain for transmission. The low diversity of parasites in S. elegans may well be the result of a restricted diet. Chaetognaths feed almost exclusively on smaller crustacea, notably on copepods, and rarely on larval fish and other chaetognaths. Only copepods and their nauplii and a rare chaetognath or two were seen in the gut of the S. elegans examined here.

Both of these factors play decisive roles in determining the parasite fauna. Parasites adapted for pelagic life represent the universe of potential infectors, to some of which the host is exposed, depending on its diet. Few groups of marine helminths are adapted to pelagic hosts compared to the rich helminth fauna of benthic fishes and crustacea (Polyanski 1955; Uspenskaya 1960). This may simply be due to the difficulties in colonizing an extensive three-dimensional environment by parasites with complex life cycles.

Some parasites have evolved seasonal cycles, which

synchronize the parasite to the complex of interactions of several different hosts and the environment. Annual cycles are a fundamental fact in the biology of organisms. There are obvious advantages in doing the right thing at the right time; being synchronized to a predictable changing environment, to other members of a population, and to your prey. It is not surprising that when seasonality in parasites has been looked for it has been found. Parasites do not have the obvious seasonally linked problems of sexual synchrony, or insuring abundant food for their progeny, but they are tied to the seasonal responses of the host species and must ensure that their infective stages have a high probability of success. There is an advantage in timing the production of infective stages to avoid production or release when the intended host has migrated out of the range of the intermediate host. Alternatively, seasonal presence of a migratory host may be responsible for annual changes in abundance of larval parasites in their intermediate host, as Bowers and James (1967) found when they correlated seasonal variations of Meiogymnophallus minutus metacercariae in cockles with changes in the population density of the migratory definitive host, the oystercatcher.

Meskal (1967) found seasonal fluctuations in the populations of Hemiurus communis and Derogenes varicus from Norwegian Sea cod. No H. levinseni or any other trematodes were found in

the cod stomachs. The timing of the seasonal variations for both the hemiurid species was remarkably similar to that of H. levinseni in S. elegans. "For H. communis there is a sharp continuous fall in population from May through June and July. The load remains at almost the same level in August, and rises in September and October to reach a maximum in November." There was a decline through the winter and a local rise in February, which declined rapidly. The first juvenile parasites were seen in September, suggesting that this was the start of a period of heavy exposure to cercariae. Polyanski's results (1955) may be interpreted as evidence of a similar cycle for H. levinseni and D. varicus in Barents Sea gadoids. He found higher incidence in summer than in winter eod yearlings. Grouping all age classes, he found only a slight decline in the incidence from summer to winter, but in the haddock the incidence of H. levinseni and D. varicus declined from 30% and 20% respectively to 0%.

Variations of a parasite in an intermediate host, such as S. elegans, are the resultant of changes in exposure to the infective agent (input) and the loss of the parasite due to the parasite's life span or to the immunity responses of the host or to increased host mortality. The increase of H. levinseni in S. elegans in the fall was partly due to a behavioural (distributional) change which occurred in a part of the host population at this time

and, probably, to an increased exposure to H. levinseni cercariae. Stage III (two year-old) S. elegans underwent no significant change in their vertical distribution at the time of the fall increase in incidence. These animals have had a hyperbenthic distribution since the previous fall. The one year-old S. elegans took up hyperbenthic distribution coincident with their infestation by H. levinseni. The source of the cercariae is unknown, but, following the pattern of nearly all aquatic digenetic trematodes, the first intermediate host is probably a benthic mollusc. If cercarial emergence were constant through the summer and fall, the Stage III Sagitta would have been expected to maintain a constant level of infestation and the Stage II animals would have become heavily parasitized following their ontogenetic descent and the taking up of a hyperbenthic distribution. Since the Stage III chaetognaths also have a periodic maximum incidence in the fall, the seasonal change was probably due to a change in the abundance of the infective agent.

The fall increase in H. levinseni takes place at a time of dramatic change in the relatively stable environment of the intermediate cold-water layer in the Gulf (Fig. 6 and 7). During the fall the temperature of this layer, which had been uniform between 0^{o} and $1^{o}C$ throughout the late winter and summer, began to increase due to surface cooling and the mixing of the warmer surface waters

and the colder waters below the thermocline.

Cercariae emerging from benthic molluscs would have difficulty in becoming dispersed in the upper part of the water column. Chances of infecting an intermediate host are better closer to the sea floor. Tschubrik (1952) found a cystophorous cercaria in Natica clausa from the Barents Sea which had a tail appendage with protrusable feather-like extensions, which were unfolded following upward swimming, to retard the rate of sinking. Even with this type of adaptation for planktonic dispersal, the probability of infecting an intermediate host is better closer to the bottom. The vertical and the horizontal range of a minute nonfeeding cercaria must be quite limited. Heavy metacercarial infestation in a planktonic intermediate host can only take place where the ranges of the first intermediate host and the transport host are coincident.

To attain levels of parasitism of over 10% in an intermediate host with a population as large as S. elegans requires the release of an immense number of cercariae. Certainly the concentration of potential hosts close to the point of release would be an advantage to the parasite. The mature S. elegans would be exposed immediately to the cercariae and Stage II animals would become exposed upon assumption of a hyperbenthic distribution.

The cod was found to be the most important definitive host of H. levinseni in the Barents Sea (Polyanski 1955; Table 19). Although comparable knowledge of the bionomics of the definitive hosts in the Gulf of St. Lawrence is lacking, the same is probably true here. In the Gulf, Heller (1949) found H. levinseni only in cod. During this study I found the trematode in several mackerel, in a juvenile four-bearded ling, and in abundance in all of the cod dissected for experimental infestation studies. Scott (1969) found it in 100% of the smaller argentine, Argentina silus, off the Nova Scotia shelf. The incidence varied with this host's length; 100% of the 19 cm fish were infected and 0% of the 34 cm animals (Fig. 34). The cod in the Gulf have seasonal migratory behaviour, the timing of which is reminiscent of the timing of the seasonal increases of H. levinseni in S. elegans and of hemiurids in Norwegian cod stocks.

Jean (1964) showed that the cod off northern New Brunswick were below the cold-water layer in April and began moving into the surface waters in May. In summer they were most abundant in the cold-water layer at about 100 meters. Jean suggested that "a deeper thermocline concentrates cod near bottom at some seasons, or in some years". During one of our cruises, in mid-September 1968, massive shoals of cod were seen on the depth recorder in the area of Stations HP 112-112M. The deep thermocline at this

TABLE 19. The bionomics of the definitive hosts of *Hemiurus levinseni* in the Barents Sea (from Polyanski 1955)

	Incidence (%)	Number of fish examined	Intensity	Most usual intensity
Clupea harengus	1.9	54	1	---
Pollachius pollachius	+	3	1	---
P. virens	10.0	40	1-4	---
Melanogrammus aeglefinus	14.1	99	1-16	1-2
Gadus morhua morhua	48.6	140	1-150	1-10
Sebastes marinus	6.7	15	1	---
Gynnacanthus tricuspis	6.7	15	1	---
Myoxocephalus scorpius	11.3	133	1-2	---
Artediellus europeus	+	19	---	---
Cyclopterus lumpus	6.7	15	22	---
Liparis liparis	+	7	---	---

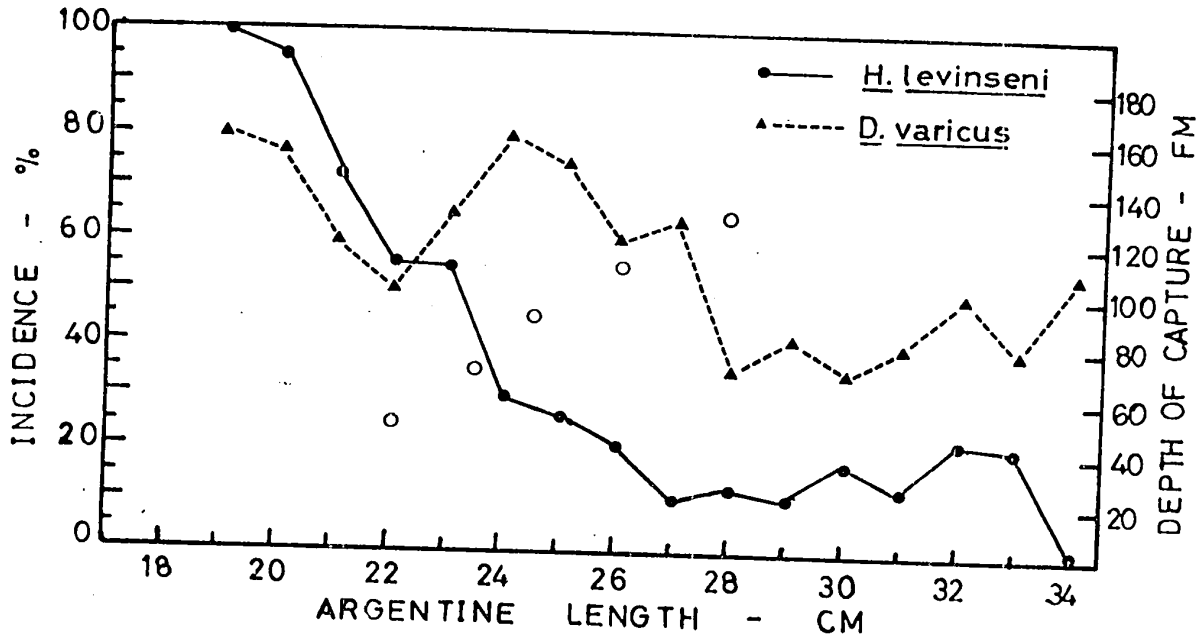


Fig. 34. The relation between size and infestation by Hemiurus levinseni and Derogenes varicus and size and vertical distribution in the Atlantic argentine, Argentina silus. The former relation from Scott (1969) and the latter from Emery and McCracken (1966).

time of year may have concentrated cod in the depression where these stations were located. During the winter they migrated to greater depths and were "concentrated in 130 - 180 meters along the western slope of the Laurentian Channel at bottom temperatures of 1^{o} to 3^{o}C".

If the first intermediate host of H. levinseni was limited in distribution to the surface layer or the cold intermediate layer, then the seasonal distribution of cod would place it out of the range of the infective agent during the winter months. S. elegans is limited to the upper and intermediate water masses. There is some rather indirect evidence for similar distributional limits for the first intermediate host. The incidence of H. levinseni in the argentine was inversely proportional to the fish's size (Fig. 34) and the mean length of the fish increased with depth (Emery and McCracken 1966). The fish with highest incidence were distributed between 55 and 90 meters, which was the approximate depth of the cold water-layer in the Gulf. Of course, the data for A. silus were from the Scotia shelf and the decline in H. levinseni with the hosts' size may have been due to some other size (age) dependent behavioural change, but the decline might well be due to decreased exposure to plankton infected with H. levinseni. It was interesting to note that A. silus feeds mainly on chaetognaths and larger planktonic crustacea (Emery and McCracken 1966). As argued

above, infected plankton were probably a local phenomenon dependent on the immediate presence of infected and cercarial releasing molluscs.

Information on the life span of marine hemiurids in their definitive hosts has recently become available. The life span of different species of trematodes is quite variable. Margolis and Boyce (1969) found experimentally that Lecithaster gibbosus in salmon lived less than 9 months and Tubulovesicula lindbergi could live longer than 31 months. L. gibbosus showed a gradual decline in intensity and incidence during the 9 months. Meskal (1967) suggested that the life span of H. communis and D. varicus in cod was about 8 months, with a maximum of up to 15 months. Scott (1969) estimated that Lecithophyllum botryophorum had a life span of 8 to 10 months in the argentine. The rapid decline of H. levinseni in S. elegans from October to November certainly suggested that infestation here was a local phenomena. It is unknown how long this trematode lives in cod, but the rapid decline with size in A. silus suggests a limited life span in the definitive host. Nothing at all is known of the life span of marine hemiurids in their molluscan first intermediate hosts.

The seasonal cycle of H. levinseni in S. elegans, then, may be due to the infested cod reentering the upper waters and the

range of the first intermediate host in the spring; thus reinfesting this host. The low incidence in mature hyperbenthic chaetognaths through the summer months suggests that cercarial release by the first intermediate host is at a low level during this time. A release of large numbers of cercariae in the fall prior to the departure of cod or other important migratory definitive hosts from the waters where the ranges of the first intermediate, transport and definitive hosts are coincident, might be stimulated by autumnal environmental changes, such as the increase in bottom temperatures. Any two year-old, Stage III S. elegans still present would be immediately exposed to the cercariae due to their hyperbenthic distribution. The one year-old Stage II chaetognaths would become infected as they take up a hyperbenthic distribution. The massive settlement of one year-old S. elegans just above the bottom at a time when the seasonal release of H. levinseni cercariae is taking place may be responsible for the high autumnal incidence in the host population.

IX. Summary and Conclusions

1. Planktonic and hyperbenthic samples were collected off Grande-Rivière in September 1965, from May to November 1966, and from April to October 1968. A series of stations over progressively deeper bottoms was sampled in 1966 and 1968. The 1968 program was designed to permit comparison of animals caught in mid-water and just above the bottom.

2. A beam trawl, mounting plankton nets on the beam, was used for collecting animals in the vicinity of the bottom in 1965 and 1966. An opening and closing hyperbenthic sledge, scaled-up and modified from a design by C. T. Macer, was constructed and used in 1968.

3. Sagitta elegans from these samples were counted and examined for parasites; the body and ovary lengths were measured and the stage of maturity was determined. Parasites were removed from their hosts, stained, identified, and measured.

4. Sagitta elegans at the mouth of the Baie des Chaleurs has a biennial life-cycle, with spawning occurring from June to late September. The newly hatched young grow to an average size of 15 mm by the end of the first summer and have a decreased growth rate over the winter. By the second fall they average 26 mm, but have

little ovary development. After another over-wintering period there is a slight increase in the average size and full maturation takes place at about 30 mm.

5. Ovary development takes place through the entire year-class during the early spring of the second year. The relationship between ovary growth and body growth is not uniform throughout the life cycle; little ovary growth is seen prior to the second spring. Animals 27 - 29 mm long have an average ovary length of 2 - 3 mm in the fall and 5.7 - 7.9 mm by the following June. There appear to be two growth phases: a somatic followed by a gonadal.

6. The pattern of vertical distribution is related closely to the life cycle. Animals settle progressively lower in the water column with increasing maturity. Individuals at a given depth in the daytime have a relatively tight size-range.

7. Animals born the previous year begin to settle to the greater depths toward the end of August and into September. The daytime population in waters deeper than 75 meters thins out through the summer as the mature animals spawn and die, but the chaetognath densities at the deepest level increase in the late summer and fall as the 1+ year-old animals descend.

8. Hyperbenthic distribution seems to be caused by maturity-dependent vertical distribution and the proximity of the bottom at depths that a given size range of chaetognaths are "trying" to assume. Nearly the full size range of the species in these waters were caught hyperbenthically at various depths.

9. Large numbers of S. elegans migrate into the surface waters following sunset, disperse throughout the water column during the middle of the night, and return to the surface waters at dawn. A considerable portion of the population remains just off the bottom through the night at the deepest depths sampled.

10. Since the length of the life cycle and the fecundity are inversely proportional to the temperature of growth, and animals take up deeper distribution with increasing age, the thermal structure of the water column in which the population is resident will determine both the life cycle and the fecundity.

11. Studies limited to daytime sampling of the surface waters, i.e. depths less than 75 - 100 meters, may under-represent or omit the larger, more mature animals in the population.

12. A mechanism was proposed whereby hyperbenthic distribution and local bottom irregularities help to maintain a breeding population within the species' range.

13. S. elegans in the Gulf of St. Lawrence has a parasite fauna characterized by low diversity. Only for Metaphrya sagittae and Hemiurus levinseni can it be considered a potentially important host. 4.8% of all chaetognaths examined harboured the trematode; the intensity of infestation varied from 1 to 6 trematodes per host, but multiple infestations were the exception. 0.48% of the hosts were infected with M. sagittae, with intensities varying from about 40 ciliates per host to several hundred. D. varicus was found in 0.13% and both S. pleuronectis and Contracaecum type larva were found in 0.02% of the hosts; no multiple infestations were found for these three parasites.

14. New definitive host records for H. levinseni were established in Scomber scombrus and young four-bearded rockling, Enchelyopus cimbrus. The size range of this parasite in its chaetognath host varied from 0.98 x 0.49 mm to 0.30 x 0.10 mm. The maximum size was somewhat smaller than has been reported for non-planktoniferous definitive hosts, but was similar to the sizes found in the planktoniferous fishes mentioned above, suggesting that the life cycle may go from plankton to planktoniferous fish to piscivorous fish, with egg production occurring at any of these stages.

15. Progenecity is size dependent in Sagitta H. levinseni. No worms smaller than 0.5 mm were found with eggs, but above this

threshold the proportion of animals with eggs increased with size. The number of eggs in utero increased rapidly with size.

16. The incidence of H. levinseni varied between 0% in mid-summer and 16% in the autumn. The overall incidence seems to increase in the spring and then decline through the summer. It rises abruptly in August or September, continues rising into October, and then declines. Multiple infestations appear in the fall, during the period of rapid increase.

17. The high levels of infestation by H. levinseni only occur in hosts larger than 21 mm. Nearly all size-classes composed of Stage II and Stage III animals had the same overall levels of infestation. The timing of the onset of high levels of parasitism in the fall varied with size; the larger size-classes became infested before the smaller. Parasitism falls in all size-classes at the same time in the autumn.

18. Examining the changes in incidence during the two year life of the host in these waters, we find that very few animals are parasitized by H. levinseni before their second autumn. The first major onset of parasitism occurs at this time, when the 1+ year-olds undergo ontogenetic descent and take up a hyperbenthic distribution above the deeper bottoms. The incidence drops during

late fall and increases the following spring, followed by another decline during the summer. The mature Stage III animals from this brood which survive into the fall become infested earlier than the subpopulation of 1+ year-old animals.

19. A highly speculative theory explaining the seasonal cycle of H. levinseni was attempted: The unknown benthic first intermediate host releases vast quantities of cercariae in the autumn, prior to the winter migration of cod (the cod hypothetically was taken to be the most important definitive host of this parasite) into deeper waters and out of the range of the chaetognath and the first intermediate host. The release of cercariae at this time of year might be timed to the small increase in the temperature of the cold intermediate layer. Mature S. elegans, which are distributed hyperbenthically off the deeper bottoms, become heavily infected at this time and 1+ year-olds become exposed to the parasite on settling lower in the water column. The incidence drops over the winter either due to a short life span of the parasite in this host or to increased mortality of the infected animals. Chaetognaths again become infected in the spring following the return of the cod to these waters.

20. No obvious effects of parasitism by H. levinseni were seen. Infested animals possessed the characteristics of "normal", healthy chaetognaths at a state of maturity appropriate to their size.

21. Metaphrya sagittae, a holotrichous ciliate of uncertain taxonomic status, was recorded for the first time parasitizing S. elegans. This is also the first record from the western Atlantic and from arctic waters (the Barents Sea). The shape and size of the ciliates varied between hosts.

22. Metaphrya sagittae generally infested less than 1% of the host population at any time. The highest incidence found was 2.6%, but no definite seasonal cycle was seen. Animals at the limits of their size range in these waters were heavily infested. While only a small proportion of animals smaller than 36 mm were infested, levels of infestation in animals larger than 39 mm rose rapidly with size; 6.5% of the 36 - 40 mm and 44.5% of the 41 - 45 mm hosts were infected.

23. Animals infected by M. sagittae had an overall abnormal appearance; the body was flacid and swollen. In some the sperm in the tail coelom appeared "fragmented", while in the others the tail coelom contained only a clear yellow fluid. Ovaries were considerably shorter than normal for the host's body size and had no developed ova. The size range of these hosts and the appearance of their gonads is similar to that of non-infected animals which were considered spent, suggesting that M. sagittae may infest chaetognaths during or following spawning. If this is so the

deteriorated gonadal condition may not be caused by this parasite.

24. Derogenes varicus was found in the coelom of S. elegans from the Gulf of St. Lawrence. Progenetic hemiurid trematodes, which may have been D. varicus also were found in specimens from Godthaab Fjord and the Barents Sea.

25. A number of D. varicus were seen in intensely red-coloured Calanus finmarchicus. They had a very narrow size range; being slightly smaller than the smallest worms found in S. elegans. The size-range in S. elegans varied between this and the size of mature D. varicus recovered from fishes.

26. Some of the D. varicus from S. elegans were progenetic, but no egg-producing worms were seen in C. finmarchicus. The number of eggs in utero was proportional to the worm's size.

27. Two Scolex pleuronectis-type tetraphyllidean cestode larvae were found in S. elegans from the Gulf. Chaetognaths appear to be infrequent hosts of cestodes.

28. High incidences of nematodes have been reported in chaetognath populations, but only two Contracaecum-type larvae were seen in the nearly 10,000 S. elegans examined.

29. It was suggested that the low diversity of parasites of S. elegans may be due to the limited variety of its prey and to a difficulty of parasitic organisms with complex life cycles (i.e. cycles which involve transfer between several different types of hosts) in colonizing an extensive three-dimensional environment.

APPENDIX I

Surface and Bottom Temperatures 1966 and 1968

I. 1966 Surface Temperatures

Date	Surface Temperature (°C)				
	Station HP 23	Station HP 24 *			Station HP 112
		40 fm	45 fm	50 fm	
3 June	6.8	---	---	7.6	6.4
12 July	---	---	13.9	---	13.8
6 Aug.	---	---	---	---	13.7
11 Aug.	15.3	---	---	---	15.5
6 Sept.	13.1	14.8	---	14.4	13.9
20 Sept.	11.4	11.3	---	11.2	11.5
12 Oct.	7.4	---	7.2	---	7.2
18 Oct.	6.3	---	6.6	---	6.5
26 Oct.	---	---	---	---	5.8

II. 1966 Bottom Temperatures

Date	Bottom Temperature (°C)				
	Station HP 23	Station HP 24 *			Station HP 112
		40 fm	45 fm	50 fm	
3 June	-0.25	---	---	-0.19	-0.05
12 July	---	---	-0.08	---	-0.08
6 Aug.	---	---	---	---	0.06
11 Aug.	0.87	---	0.28	---	0.32
6 Sept.	2.01	0.05	---	0.41	0.38
20 Sept.	9.70	1.74	---	0.83	0.43
12 Oct.	3.19	---	0.87	---	0.66
18 Oct.	2.08	---	0.67	---	0.62
26 Oct.	---	---	---	---	0.62

* See Section III.A; 40 fm = 73 meters, 45 fm = 82.5 meters
50 fm = 91.5 meters.

I. 1968 Surface Temperatures and Salinities

Date	Stations							
	HP 23		HP 24		HP 112		HP 112M	
	T °C	S‰	T °C	S‰	T °C	S‰	T °C	S‰
19 June	--	--	--	--	10.8	28.60	10.0	28.78
28 June	11.1	28.39	11.3	28.37	11.7	28.44	10.6	28.34
5 July	14.4	28.23	13.3	28.19	13.5	28.08	13.4	28.11
8 July	--	--	--	--	--	--	13.9	28.01
16 July	14.8	27.28	15.3	27.51	16.9	27.62	16.1	27.34
30 July	--	--	--	--	--	--	15.4	28.46
5 Aug.	15.5	28.50	15.0	28.17	16.2	28.37	15.1	28.60
13 Aug.	--	--	--	--	--	--	14.3	28.58
22 Aug.	12.3	29.31	12.5	29.17	11.8	29.21	11.5	19.25
26 Aug.	--	--	--	--	--	--	13.6	29.15
3 Sept.	13.3	29.39	9.7	28.93	9.5	28.67	10.1	29.68
11 Sept.	10.8	29.84	13.0	29.19	15.9	29.26	15.1	29.37
19 Sept.	--	--	--	--	--	--	12.0	30.80
24 Sept.	12.9	29.79	13.5	29.71	13.0	29.94	11.7	30.12
15 Oct.	--	--	--	--	10.4	29.46	10.4	29.38

II. 1968 Bottom Temperatures and Salinities

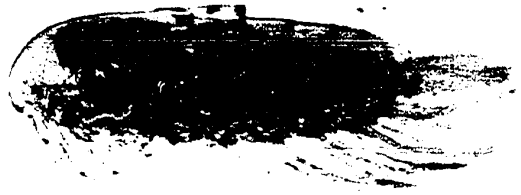
	Bottom Depth (M)							
	55 (Sta.HP 23)		75 (Sta.HP 24)		110 (Sta.HP 112)		119 (Sta.HP 112M)	
Date	T °C	S‰	T °C	S‰	T °C	S‰	T °C	S‰
19 June	--	--	--	--	0.22	32.81	0.22	32.06
28 June	0.96	31.81	0.23	32.72	0.22	32.95	0.13	32.80
5 July	5.48	30.32	0.49	32.52	0.42	32.65	0.15	32.83
8 July	--	--	--	--	--	--	0.17	32.60
16 July	1.42	32.20	0.49	32.56	0.10	32.75	0.14	32.78
30 July	--	--	--	--	--	--	0.30	32.76
5 Aug.	2.24	31.80	0.78	32.38	0.24	32.69	0.22	32.69
13 Aug.	--	--	--	--	--	--	0.42	32.70
22 Aug.	2.48	31.45	0.40	32.62	0.46	32.74	0.16	32.51
26 Aug.	--	--	--	--	--	--	0.55	33.03
3 Sept.	3.05	31.81	--	--	0.81	32.34	0.63	32.95
11 Sept.	2.72	31.96	1.04	32.19	0.51	32.24	0.47	32.82
19 Sept.	--	--	--	--	--	--	0.49	33.03
24 Sept.	3.70	31.74	0.72	32.49	0.48	32.72	0.41	32.69
15 Oct.	--	--	--	--	0.74	32.09	0.40	32.20

APPENDIX II

Some Helminth Parasites of *Calanus finmarchicus* in the Gulf of St. Lawrence

While sorting plankton collections for chaetognaths some vividly red *Calanus finmarchicus* were noticed. Microscopic examination of these specimens showed them to be parasitized. These parasitized copepods could be recognized in a dish of plankton without the aid of a microscope. The colour was due to pigment, which seemed to be concentrated on the inner surface of the cuticle. The infected animals maintained their transparency. The colour in the fixed animals faded on exposure to sunlight.

Two different parasites were found; single metacercaria of *Derogenes varicus* (Fig. 9c) and tetraphyllidean larvae with four pronounced bothridia (Fig. 35). Both parasites occurred in the hosts' haemocoel. The cestode was always present in massive numbers in each host, generally greater than 100. 80.4% of the copepods infested by *D. varicus* were copepodite V, 11.8% were adult females, and 7.8% were copepodite IV. All of the copepods infested by the tetraphyllideans were adult females.



a

b

Fig. 35. Larval tetraphyllidean cestodes from Calanus finmarchicus.

a. Infected C. finmarchicus

b. One of the larval tetraphyllidean cestodes removed from the host.

APPENDIX III

Values for the Relationship Between Body Length and Mean Ovary Length of Gulf of St. Lawrence *Sagitta elegans*

Body Length (mm)	Mean Ovary Length (mm)					
	13/5/66	1/6/66	1/7/66	11/8/66	12/10/66	17/4/68
13						1.0
14						1.2
15						
16						1.2
17				1.2		1.7
18				1.2	1.2	1.7
19				1.2	1.2	1.5
20			1.6	1.3	1.4	2.0
21				1.5	1.3	2.5
22			2.7	1.6	1.7	2.6
23	3.8		1.7		1.6	3.4
24	4.0		3.6		2.0	3.6
25	4.6	5.2	4.9		1.9	3.6
26	4.6	5.6	5.7	3.3	2.1	4.8
27	5.0	5.7	6.4	2.9	2.3	5.0
28	5.7	6.7	6.6	5.4	2.4	5.4
29	6.1	7.9	7.7	6.6	2.4	6.7
30	6.7	7.8	7.9	7.6		7.3
31	7.2	8.8	8.7	8.4		7.6
32	7.5	9.0	9.0	8.6	9.7	7.3
33	8.2	9.8	9.0	9.9	12.3	7.2
34	8.5	10.7	9.2	9.2	8.5	9.4
35	8.8	11.8	9.3	9.6		9.4
36	9.8	12.2		11.1	10.2	13.3
37	10.4	14.3		11.9		
38	11.2			12.9		
39	11.2					
40	11.5					

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