

Canadian Technical Report of  
Fisheries and Aquatic Sciences 940

June 1980

A GUIDE TO THE MARINE FLORA AND FAUNA OF THE BAY OF FUNDY:  
POLYCHAETE LARVAE FROM PASSAMAQUODDY BAY

by

T. C. Lacalli

Biology Department  
University of Saskatchewan  
Saskatoon, Saskatchewan

This is the one hundred and twenty-fifth Technical Report from  
the Biological Station, St. Andrews, N.B.

## PREFACE

This Technical Report is part of a series originating at the St. Andrews Biological Station entitled "Guide to the Marine Flora and Fauna of the Bay of Fundy." The series will consist of original and/or adapted, illustrated manuals on the identification, distribution and general biology of the estuarine and marine animals and plants occurring within the Bay of Fundy.

The series is a continuation and expansion of "A Preliminary Guide to the Littoral and Sublittoral Marine Invertebrates of Passamaquoddy Bay" and is produced under the auspices of Fisheries and Environmental Sciences to assist in environmental studies concerning the Bay of Fundy. The guide is being prepared in collaboration with systematics specialists and the manuals will be based as much as possible on recent revisionary systematics research. Each manual, concerning a major taxon, will include an introduction, illustrated glossary of terms, illustrated keys, alphabetic checklist and available information on distribution, habitat, life-history related biology, and references to the major literature on the group.

The series is intended for use by students and researchers wishing to identify marine organisms found in the Bay of Fundy. They are written as much as possible so that persons without a systematic background may use them, and with the hope they will serve as a guide to additional information concerning a taxon. Since the Bay of Fundy has a wide range of physical habitats and therefore organisms, these manuals will be useful for organism identification throughout the Maritimes and may, in some cases, replace or expand the old series "Canadian Atlantic Fauna." In general this series will be complementary to Natural History Series in progress at the National Museum of Natural Sciences, Ottawa.

Whenever possible representative specimens dealt with in the manuals will be deposited in the reference collection of the Identification Center at the Biological Station, St. Andrews. Researchers in the Bay of Fundy are requested to donate to this collection series of specimens they believe should be available for future examination and reference.

M. J. Dadswell  
Head, Identification Center  
Fisheries and Environmental Sciences

© Minister of Supply and Services Canada 1980  
Cat. No. 97-6/940 ISSN 0706-6457

Correct citation for this publication:

Lacalli, T. C. 1980. A guide to the marine flora and fauna of the Bay of Fundy: Polychaete larvae from Passamaquoddy Bay. Can. Tech. Rep. Fish. Aquat. Sci. 940, iv + 27 p.

iii  
TABLE OF CONTENTS

	Page
Abstract . . . . .	iv
Introduction . . . . .	1
Abbreviations used in the figures . . . . .	2
Characteristic polychaete larval types . . . . .	3
Larval descriptions by species . . . . .	9
Arabellidae . . . . .	9
<i>Arabella iricolor</i> . . . . .	9
Capitellidae . . . . .	9
<i>Capitella capitata</i> . . . . .	9
<i>Heteromastus filiformis</i> . . . . .	10
Dorvilleidae . . . . .	11
<i>Dorvillea caecus</i> . . . . .	11
Glyceridae . . . . .	11
<i>Glycera dibranchiata</i> . . . . .	11
Lumbrineridae . . . . .	12
<i>Lumbrineris fragilis</i> . . . . .	12
<i>Ninoe nigripes</i> . . . . .	12
Maldanidae . . . . .	13
<i>Clymenella torquata</i> . . . . .	13
Nephtyidae . . . . .	14
<i>Nephtys incisa</i> . . . . .	14
<i>Nephtys caeca</i> . . . . .	15
<i>Aglaophamus neotenus</i> . . . . .	15
Nereidae . . . . .	16
<i>Nereis virens</i> . . . . .	16
<i>Nereis pelagica</i> . . . . .	16
Orbiniidae . . . . .	16
<i>Naineris quadricuspida</i> . . . . .	16
Oweniidae . . . . .	17
<i>Myriochele heeri</i> . . . . .	17
Pectinariidae (Amphictenidae) . . . . .	17
<i>Pectinaria granulata</i> . . . . .	17
Phyllodocidae . . . . .	18
<i>Phyllodoce maculata</i> . . . . .	18
<i>Phyllodoce mucosa</i> . . . . .	19
<i>Eteone longa</i> . . . . .	20
Polynoidae . . . . .	21
<i>Lepidonotus squamatus</i> . . . . .	21
<i>Harmothoe imbricata</i> . . . . .	22
Serpulidae . . . . .	23
<i>Spirorbis spirillum</i> . . . . .	23
Sigalionidae . . . . .	23
<i>Pholoe minuta</i> . . . . .	23
Spionidae . . . . .	24
<i>Prionospio steenstrupi</i> . . . . .	25
Syllidae . . . . .	25
<i>Autolytus</i> sp. . . . .	25
Acknowledgments . . . . .	26
References . . . . .	26

## ABSTRACT

Lacalli, T. C. 1980. A guide to the marine flora and fauna of the Bay of Fundy: Polychaete larvae from Passamaquoddy Bay. Can. Tech. Rep. Fish. Aquat. Sci. 940, iv + 27 p.

This guide comprises (1) a brief survey of the general characteristics of the larvae of nine polychaete families commonly encountered in zooplankton in Canadian Atlantic waters and (2) a series of illustrated descriptions of the eggs and larvae of 30 species of polychaetes from Passamaquoddy Bay representing 17 families. Notes are included for most species on habitat, spawning times, larval behavior and the relevant literature.

Key words: Eggs, larvae, biology, spawning, development, Polychaeta, Passamaquoddy Bay, Bay of Fundy

## RÉSUMÉ

Lacalli, T. C. 1980. A guide to the marine flora and fauna of the Bay of Fundy: Polychaete larvae from Passamaquoddy Bay. Can. Tech. Rep. Fish. Aquat. Sci. 940, iv + 27 p.

Le guide comprend, premièrement, un bref survol des caractéristiques générales des larves de neuf familles de polychètes courantes parmi le zooplancton des eaux de l'Atlantique canadien et, deuxièmement, une série de descriptions illustrées des oeufs et des larves de 30 espèces de polychètes de la baie Passamaquoddy, qui représentent 17 familles. Pour la plupart des espèces, on trouve des notes concernant l'habitat, les périodes de reproduction, le comportement des larves et les publications sur le sujet.

# INTRODUCTION

In comparative studies of marine invertebrate larvae it is often desirable to work with larvae taken directly from the plankton since a range of stages of a number of species can be collected from plankton in far less time and with less effort than would be required to raise the same larvae from eggs and sperm. There is, however, the problem of identifying the larvae when they are collected in this fashion. This publication is a compilation of observations made while attempting to identify polychaete larvae from Passamaquoddy Bay (Fig. 1), an inlet of the Bay of Fundy in New Brunswick, while the author was engaged in a comparative study of the development of the annelid nervous system. It was not difficult to identify all of the more conspicuous planktonic polychaete larvae found in Passamaquoddy Bay to species with reasonable certainty, and these are dealt with in the following pages. The figures are all drawn from specimens collected from the Bay.

The author found Passamaquoddy Bay to be a good place to obtain identifiable polychaete larvae for three reasons. First, the polychaete fauna, and indeed the fauna in general, is arctic-boreal and very similar to the extensively studied fauna of northern Europe. Therefore, although there are no published studies on polychaete larvae from Canadian Atlantic waters, a large literature is available on the development of European species which are very similar to those found in Passamaquoddy Bay. Papers by Thorsen (1946), Rasmussen (1956, 1973), Hannerz (1956), and Cazaux (1968, 1969, 1972) are particularly useful sources for descriptions of the larvae and accounts of the European literature. Blake (1975) describes some related forms from the Pacific coast.

Second, Passamaquoddy Bay has a relatively uniform substratum that is either mud or some combination of rock and mud. As a result, the polychaete fauna comprises few species and, once identification of a particular larva has been made to genus, there are few remaining choices to be made

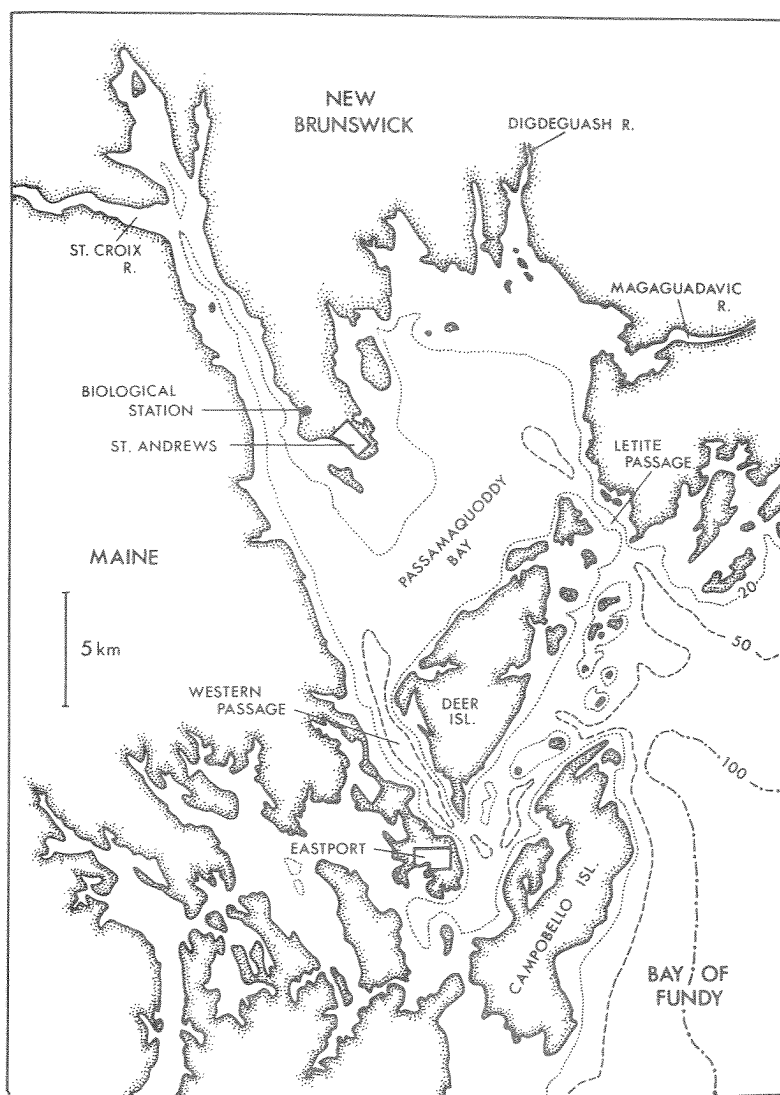


Fig. 1. Map of Passamaquoddy Bay.

ABBREVIATIONS USED IN THE FIGURES

to determine it to species. In addition, Passamaquoddy Bay communicates with the Bay of Fundy through narrow channels so that exchange of water is relatively restricted. Ketchum and Keen (1953) calculate a flushing time of between 8 and 15 d for Passamaquoddy Bay depending on season. This minimizes the chance of finding larvae in the plankton belonging to species not found in Passamaquoddy Bay itself. In fact, all the larvae found in any numbers in the plankton could be ascribed to benthic species common in the Bay.

Third, Passamaquoddy Bay has been the site of fisheries and tidal power investigations based at the Biological Station on Brandy Cove since early in this century. There is a considerable literature on hydrography and productivity of the area, and the Station is itself a convenient and pleasant place to work.

Although this study is primarily based on live material, it is the author's intent that it should be of some use in identifying preserved larvae, particularly the advanced stages encountered in zooplankton surveys. Except for very young stages, it is usually possible to identify polychaete larvae to family quite easily. For larvae too young to possess setae, identification is based on general body form, location and number of eyes, ciliary bands, and auxiliary ciliary structures such as sensory tufts. The advanced, setigerous stages develop a larger number of distinctive morphological features such as cirri, tentacles, palps, parapodia and setae. In principle, identification of advanced stages to genus and species should be possible on the basis of such features, but in most cases we lack sufficient information to do so. In dealing with live larvae, as in the present study, it is easier in practice to rely on differences in color and pigmentation when distinguishing species since this can be done both with setigerous and non-setigerous stages. In preserved material, unfortunately, larval colors are either altered or disappear, and the less conspicuous ciliary structures are difficult to see. There are therefore limits to the usefulness of this guide in dealing with preserved specimens.

This guide is not arranged in the form of a conventional key. In part this reflects the incomplete state of our knowledge of polychaete larval structure. It is also difficult in general to construct a key for larvae because different diagnostic features are important at each stage. A separate key would be required for each stage with an additional guide for determining the stage. The more manageable solution adopted here is to summarize the general distinguishing features for the larvae of the more important families and to provide, in a separate section, more detailed accounts of the particular species likely to be encountered. It is hoped that in this form the guide will be sufficiently useful to facilitate future studies of the strictly morphological features of taxonomic significance upon which a conventional identification key might be based.

A	- antenna
AC	- anal cirri
AK	- akrotoch
AP	- apical tuft
C	- chorion or egg membrane
CH	- chromatophore
DC	- dorsal cirri
E	- eye
ET	- elytra
F	- food debris
FO	- frontal organ
G	- gelatinous egg capsule
J	- jaws
MT	- meniscotroch
NT	- neurotroch
OB	- oral brush
OC	- oral cilia
OL	- oral lobes
P	- palps
PH	- pharynx or pharyngeal bulb
PL	- paleae
PPR	- parapodial rudiments
PR	- prostomium
PS	- provisional setae
PT	- prototroch
S	- setae
SP	- surface pigmentation
SS	- setal sacs
ST	- stomach
T	- tube
TC	- tentacular cirri
TR	- developing trunk rudiment
TT	- telotroch
V	- vesicles
YK	- yolk

COLORS OF TISSUE OR SURFACE PIGMENTATION

B	- dark blue
BL	- black
BN	- brown
BNS	- brown spots
GS	- green spots
R	- red
Y	- yellow

# CHARACTERISTIC POLYCHAETE LARVAL TYPES

The basic polychaete larva is the trochophore (Fig. 2) which appears in modified forms in the various polychaete families. In some (spionids) the trochophore is suppressed in favor of a more worm-like larva. In others (phyllodocids, polynoids, nephtyids, pectinariids, glycerids) a long-lived planktotrophic trochophore stage is retained, and segmentation appears (metatrochophore stage) and becomes functional (nectochaete stage) only as settlement and metamorphosis approach. The trochophore is usually suppressed in species with lecithotrophic larvae (nereids, lumbrinerids, maldanids), but some trochophore features (e.g. ciliation) may be retained. The arrangement of external ciliation shown in Fig. 2 is found in *Polygordius* larvae and serpulid trochophores, but is modified in all the larval forms considered here. The prototroch, the chief organ of motility, frequently includes at least one band of compound cilia in the larger planktotrophic trochophores along with one or more bands of smaller, simple cilia. Fig. 2 shows the prototroch in schematic fashion only; in most cases in which both compound and simple cilia occur the prototroch has been drawn in the figures as a double row of cilia. The planktotrophic forms considered here have a neurotroch in most cases, but lack the metatroch. The telotroch may also be absent (polynoids, *Phyllodoce*) or appear only late in development. The apical tuft is frequently absent or is lost during development, but in many larvae other apical ciliary structures appear: sensory tufts (phyllodocids), comb-like rows of cilia (polynoids), or spines composed of long immobile cilia (syllids, spionids). Oral ciliation can be extremely elaborate (polynoids, pectinariids) or be reduced to a single row of ciliated cells at the mouth (phyllodocids).

Beyond the details of ciliation there are features of general appearance which make it relatively easy to distinguish the trochophore and metatrochophore stages of the families dealt with here. Polynoid and sigalionid trochophores are characterized by a small, relatively flat episphere; the larvae have the shape of an inverted cone. Phyllodocid trochophores have a relatively large episphere so that the prototroch girdles the larva

around its middle. Nephtyid trochophores are less distinctive and more variable in shape. The episphere is relatively large and often dome-shaped and the trunk, when well developed, is a uniform cylinder. Pectinariid trochophores always have an elaborate buccal apparatus.

A detailed consideration of larval setae is beyond the scope of this study, but some representative examples are shown in Fig. 3. The larval descriptions given here do not categorize the setae except to general type: simple, compound or hooked setae. This is sufficient to assist in identifying larvae to family. Setal type is a relatively consistent feature within each family. Thus polynoids, nephtyids, pectinariids, spionids and capitellids have simple setae, including hooks in the last two families listed, while sigalionids, nereids and phyllodocids have compound setae.

Larval color can be a useful identifying feature, and a note is required on coloration. In all cases, the colors mentioned in this study are as seen in live larvae by reflected light. This accounts for their distinctiveness and brilliance. Larval color is much less noticeable using other means of illumination. In general, the colors noted here agree extremely well with what is described for the same or related species from European waters. Thus, the yellow chromatophores described for *Phyllodoce mucosa* from France were distinctive features of the same species in Passamaquoddy Bay, and *Capitella capitata* larvae collected had the same dark blue pigment in the posterior gut noted in larvae from Denmark. A distinction should probably be made between two different types of larval colors. First, there are colors arising from the accumulation of specific pigments; examples include pigmentation of the episphere in *Lepidonotus* (black), the gut in *Phyllodoce* (green), chromatophores in *Phyllodoce mucosa* (yellow) and the gut of *Nephtys incisa* and *Capitella* (blue or dark blue). These colors seem to be fairly constant features of a particular species and can be more or less counted on to be present. Other colors, such as the color of the stomach and associated droplets in *Harmothoe* and *Nephtys* (green and yellow), appear to be due to food storage products and so are less likely to be a constant feature of every specimen.

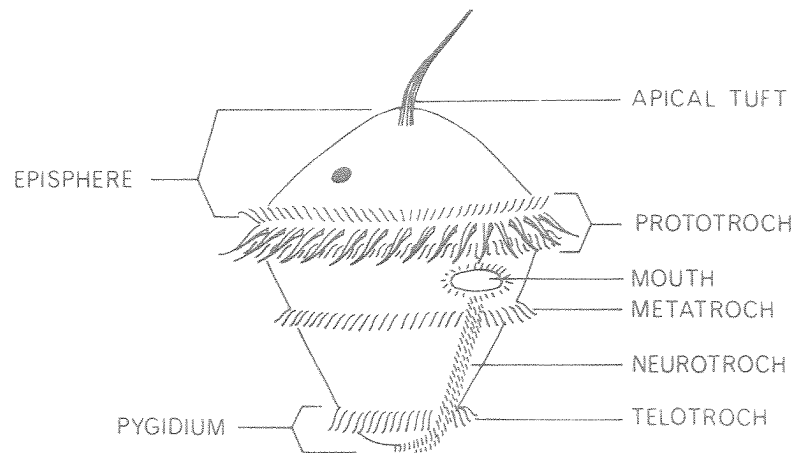


Fig. 2. External ciliation of an idealized planktonic trochophore.

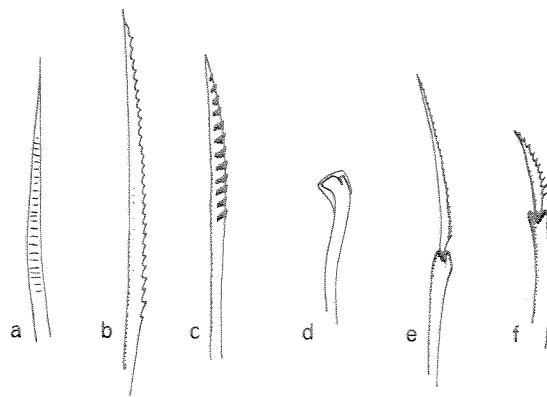


Fig. 3. Representative types of setae, all drawn from larvae. Simple setae from (a) a nephtyid and (b, c) a polynoid; (d) a hook from a capitellid; compound setae from (e) a phyllodocid and (f) a nereid.



# POLYNOIDAE

Trochophores are shaped like an inverted cone with the prototroch girdling the broadest point. The episphere forms a shallow dome which may be quite flat in some species, and the posterior part of the body tapers quite sharply. A number of inconspicuous comb-like ciliary bands known as akrotrichs are found in the apical region. These vary in number and location in different species. Up to three pairs of eyes are present depending on stage. A thick, heavily ciliated lip surrounds the mouth, and a characteristic brush of long, immobile cilia flanks the mouth on the left side (shown in Fig. 65, 66 and 73). The telotroch is absent.

Nectochaetes show the characteristics of the adult developed to varying degrees depending on stage. These include the antennae, palps, tentacular cirri, dorsal cirri and elytra. The setae are simple and are frequently serrated or may have rows of small spines.

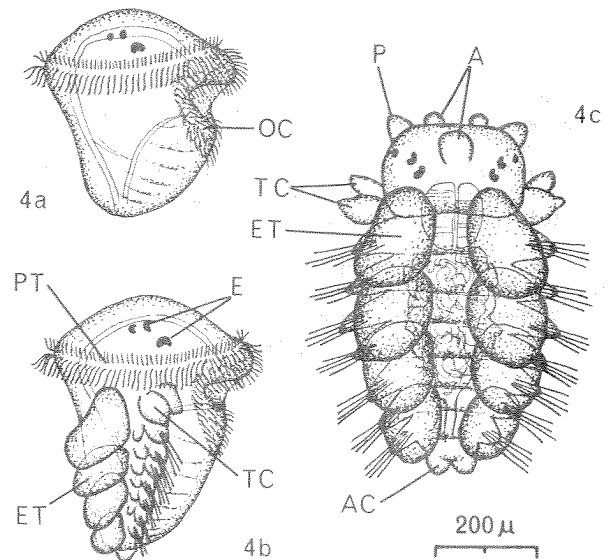


Fig. 4. Polynoid larvae  
4a. early metatrochophore  
4b. advanced metatrochophore  
4c. early nectochaete

# SIGALIONIDAE

Trochophores and nectochaetes are quite similar in general appearance to polynoid larvae, but the corresponding stages are smaller. The elytra are more poorly developed at metamorphosis, and the setae are compound rather than simple.

# NEPHTYIDAE

Trochophores have a dome-shaped episphere and a cylindrical, untapered trunk region. The episphere lacks ciliary structures, but has a single conspicuous pair of eyes. The larvae may be very brightly colored, and the colors appear to be species-specific in most cases. Prototroch and telotroch are well developed, but only the young stages have a neurotroch.

The nectochaetes have nine or ten segments of equal width bearing simple, capillary setae. As metamorphosis progresses, the prostomium, at first rounded, becomes more angular and the eyes are shifted to a more posterior position. A single anal cirrus may be visible.

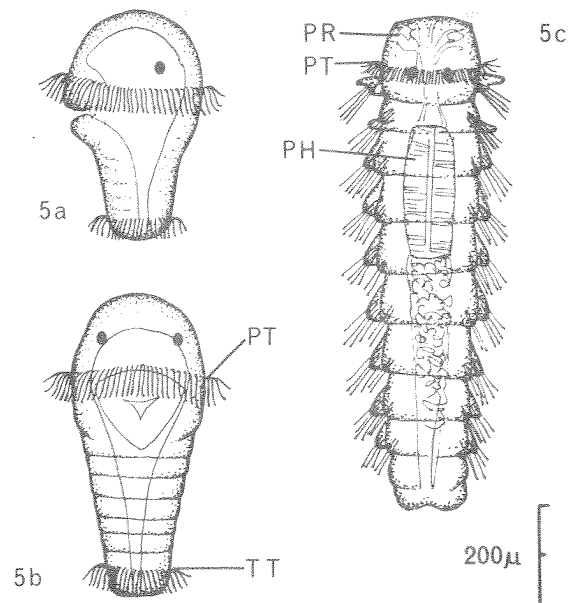


Fig. 5. Nephtyid larvae  
5a-b. metatrochophores  
5c. nectochaete

PHYLLODOCIDAE

Trochophores have a characteristic angular shape with the prototroch girdling the middle. The episphere bears two characteristic structures: (1) a curved and pointed tuft of long, immobile cilia referred to as the ventral sensory organ or frontal organ and (2) a crescent-shaped patch of short, rapidly beating cilia called a meniscotroch. There can be up to two pairs of eyes, and in some species the telotroch is absent.

Nectochaete stages lose the apical cilia and develop the antennae, tentacular cirri, dorsal cirri and compound setae characteristic of the adult. Determination to genus is usually possible using these features.

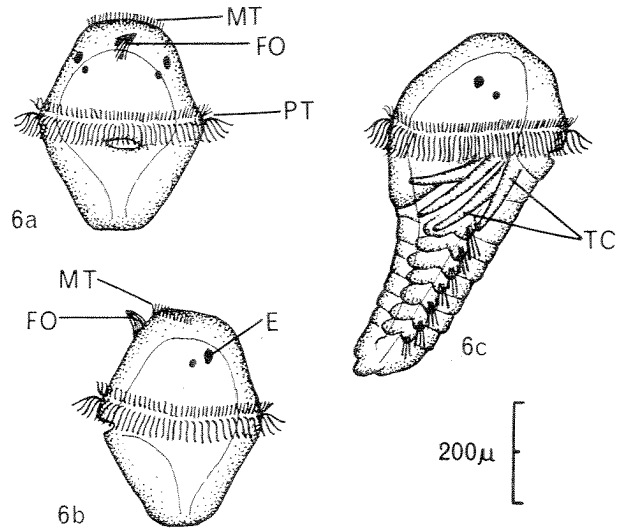


Fig. 6. Phyllodocid larvae  
6a. trochophore, front view  
6b. trochophore, side view  
6c. advanced metatrochophore

NEREIDAE

Nereid larvae usually hatch as nectochaetes or, for species hatching as trochophores, develop rapidly to the nectochaete stage. A minimum of three segments are present, and the larvae usually become benthic before very many additional segments can be added. Parapodial lobes are prominent and bear compound setae. Developing antennae and tentacular cirri may be visible.

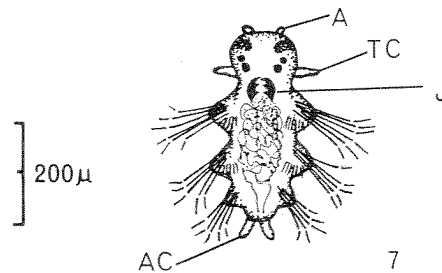


Fig. 7. Nereid nectochaete

# PECTINARIIDAE

Trochophores have a dome-shaped episphere lacking distinct ciliary tufts, and a moderately tapering, cylindrical trunk. Body form is therefore quite similar to nephtyid larvae with which pectinariid trochophores are easily confused. The trochophores can be distinguished, however, on the basis of the large oral lobes on either side of the mouth, the bundle of paleae visible within the first few segments, and the presence of regular rows of small pigment spots on each segment. Unfortunately the oral lobes are not always evident in preserved specimens.

The nectochaete stage is usually collected with its transparent tube, and the paleae are visible projecting dorsally from the body.

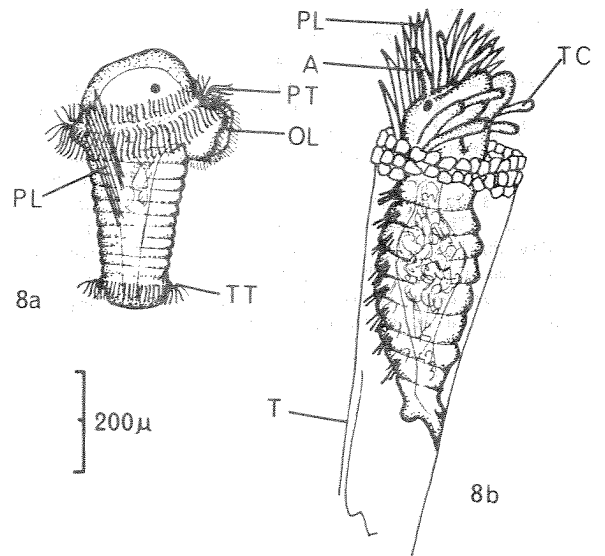


Fig. 8. Pectinariid larvae  
8a. metatrochophore  
8b. nectochaete

# SPIONIDAE

The larvae are segmented and setigerous at hatching and may develop to 20 segments or more before settlement. Long, simple, provisional setae are borne on most segments, and usually the longest are found on the anterior segments. A pair of developing palps is visible in most stages.

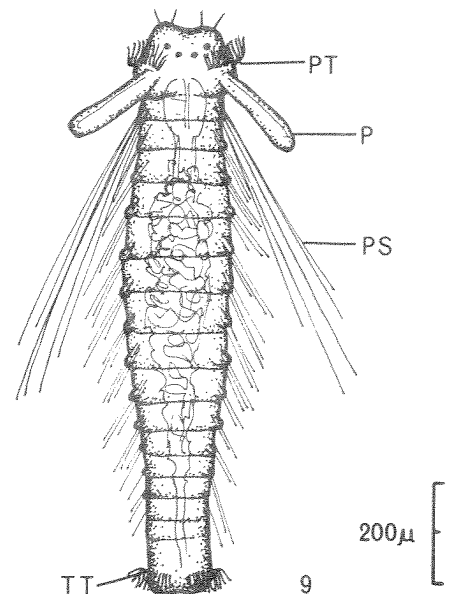


Fig. 9. Spionid larva

CAPITELLIDAE

Larvae of the genus *Capitella* have a cylindrical body, two eyes, and equally prominent prototroch and telotroch. The setigerous stages lack parapodia. The first few segments have capillary setae, but the remainder bear hooked setae that project only slightly from the body. It is difficult to generalize about larvae of the family Capitellidae as a whole because the trochophore stage is quite important in some of the other genera. These genera are probably best dealt with individually (see, for example, the section on *Heteromastus*). The presence of hooked setae in the posterior body segments is, however, an important general characteristic of the family.

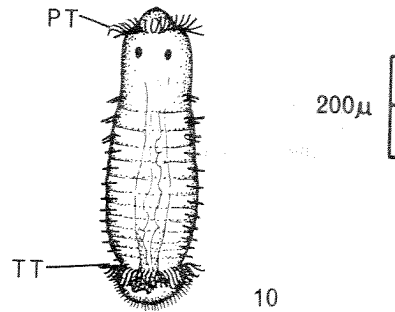


Fig. 10. Setigerous larva of *Capitella*

OWENIIDAE

This family has a characteristic helmet-shaped larva known as a mitraria. Two bundles of long provisional setae project from the body. The setae are usually iridescent. In advanced stages, the everted trunk rudiment and developing setae are visible.

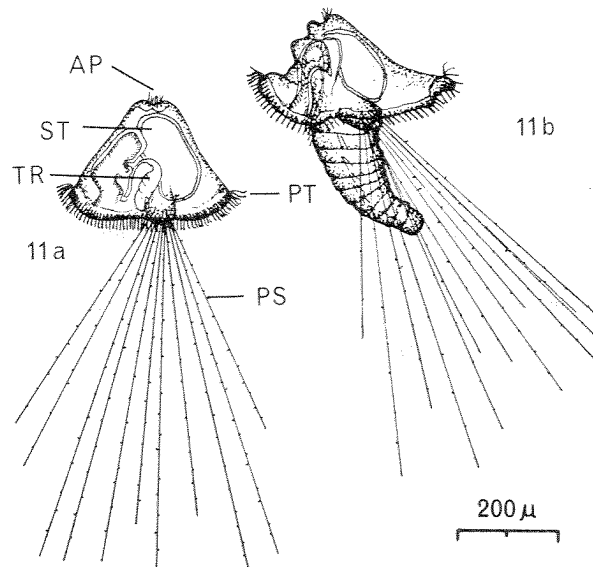


Fig. 11. Oweniid larvae  
11a. mitraria larva  
11b. larva with everted trunk rudiment

LARVAL DESCRIPTIONS BY SPECIES

Family ARABELLIDAE Hartman 1944

*Arabella iricolor* (Montagu 1804)

Few sexually ripe individuals were found, but yolky pink oocytes up to  $180\ \mu$  in diameter were recovered from several specimens. Little is known about the larval development of this species, but there is thought to be some form of larval parasitism on other eunicid polychaetes (Richards 1967; Pettibone 1957). *Arabella iricolor* is common in soft intertidal mud in Passamaquoddy Bay and reaches lengths of 30 cm or more.

Family CAPITELLIDAE Grube 1862

*Capitella capitata* (Fabricius 1780)

Numerous young planktonic stages 150-200  $\mu$  long were recovered in late April and early May, and larvae up to  $470\ \mu$  in length with 16 segments were seen occasionally in the plankton from April to September. All were cylindrical with equally prominent telotroch and prototroch and red eyes. These larvae are all typical for the species as it is classically defined, but recently the existence of a number of sibling species has been demonstrated (Grassle and Grassle 1976). These differ from one another in the form of their larvae and one, at least, has direct development to a benthic juvenile rather than a pelagic larva. The large and small *Capitella* larvae found in Passamaquoddy Bay may therefore be of two sibling species rather than being young and old stages of a single species. In all but the smallest larvae, cells of the lower intestine are pigmented green, greenish-blue or black. Setae develop in the late metatrochophore. They do not project very far from the body surface, but are quite noticeable because they glisten in reflected light. The larvae swim rapidly and can contract lengthwise as shown in the figure. Adults of this species were not collected very often in the Bay, but some juveniles were recovered from settling bottles.

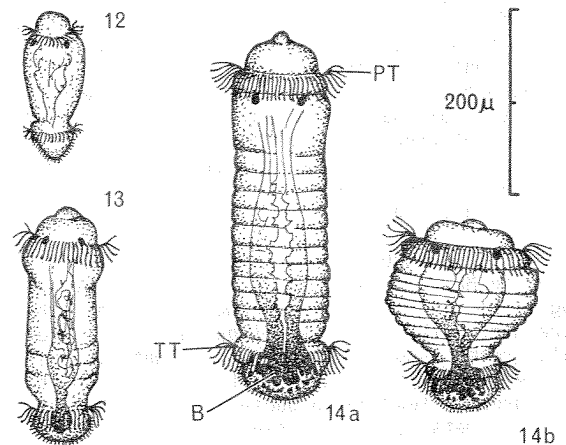


Fig. 12-14. *Capitella capitata*  
12. trochophore  
13. young metatrochophore  
14a. metatrochophore, showing body form while swimming  
14b. same metatrochophore contracting

*Heteromastus filiformis* (Claparède 1864)

Larvae are not common, but can be found in small numbers in the plankton through April, May and the first half of June. Larvae from Passamaquoddy Bay were identical to those described by Rasmussen (1956). The smallest were 130  $\mu$  high. At a height of 300  $\mu$ , the thin layer of trunk mesoderm began to show signs of segmentation. Trochophores of *Heteromastus filiformis* can be readily distinguished from those of other species; the body tissues are transparent and delicate as in some serpulid trochophores (e.g. *Serpula*, *Spirobranchus*) but, unlike the serpulids, the gut is spacious and presses against the body wall so as to effectively obliterate the blastocoel. *Heteromastus* trochophores are usually seen swimming slowly with the episphere held rigid and immobile, but they are capable of greater changes in shape than most other trochophores. The prototroch can be contracted by a band of circular muscle as in phyllodocid larvae. In addition, the episphere can be contracted independently by circular muscle bands above the prototroch. When both are contracted together, the distortion of shape is similar to that produced by a hand puppet when the puppeteer makes a fist. Dark green spots may be found scattered on the body surface in late stages as described by Rasmussen. The eyes are red.

A small number of *Heteromastus* egg masses were found in May. These were similar in appearance to egg masses of *Phyllococe mucosa* except that the eggs were more yolky and pale yellow in color rather than pale green. Eggs were 110  $\mu$  in diameter. The hatched trochophores were kept in finger bowls. They grew by feeding on bacteria in the bowls and began to metamorphose within 2½ wk. Adults of *H. filiformis* have not been recorded for Passamaquoddy Bay and presumably are not very common.

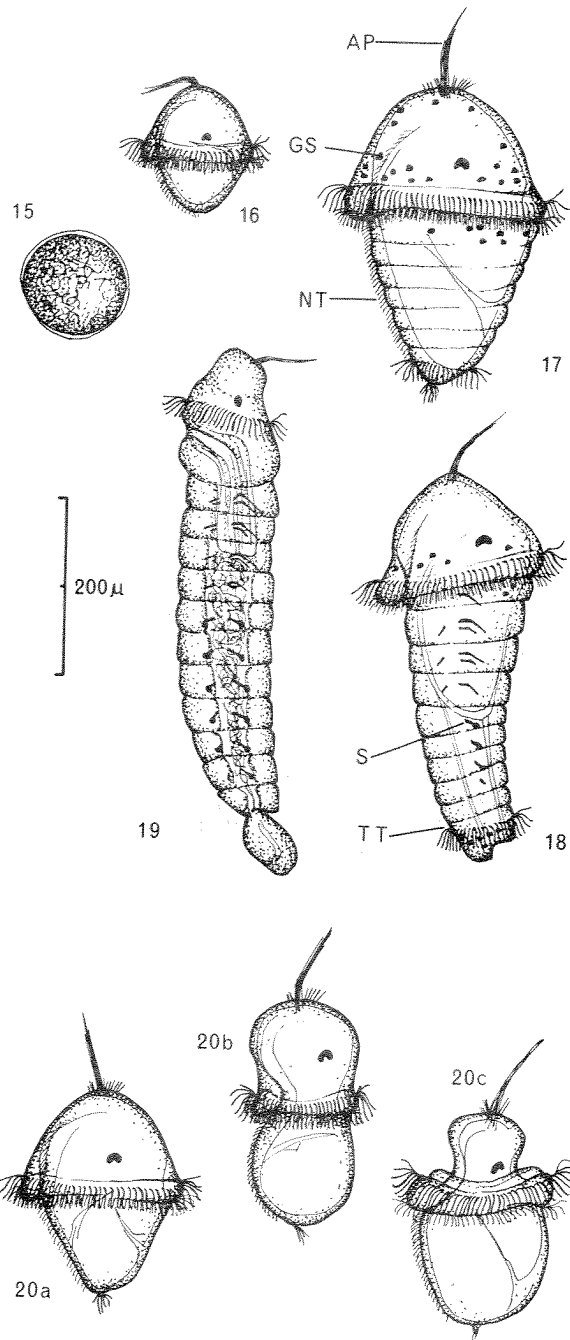


Fig. 15-19. *Heteromastus filiformis*  
 15. cleaving egg  
 16. newly hatched trochophore  
 17-18. metatrochophore stages  
 19. settled larva undergoing metamorphosis  
 Fig. 20. Body shape in *H. filiformis* trochophores  
 20a. normal swimming trochophore  
 20b-c. the same larva showing two types of contraction

Family DORVILLEIDAE Chamberlin 1919

*Dorvillea caecus* (Webster and Benedict 1884)

Eggs and polytrochal larvae similar to those described for *Dorvillea* (Blake 1975, as *Stauronereis* in Richards 1967) and *Ophyrotrocha* (Akeson 1973) appeared in the plankton during the first week of August and the first week of September. This monthly periodicity, with eggs appearing primarily during the time of full moon, suggests a role for lunar phase in the control of spawning. Eggs were translucent, yellowish and 135-145  $\mu$  in diameter. In finger bowls at 16-18°C, development to a stage having six trochal bands required 5 d, to a 2-setiger larva an additional 10 d, and to a 6-setiger stage a total of 1 mo. By then the larvae were 1 mm long with an additional 250  $\mu$  of anal cirrus. Jaws were dark brown and eyes were not observed. All larval stages were translucent with some orange droplets visible in the anterior region and with very fine trochal cilia. *Dorvillea caecus* is recorded for the Bay of Fundy area, but adults were not collected by the author.

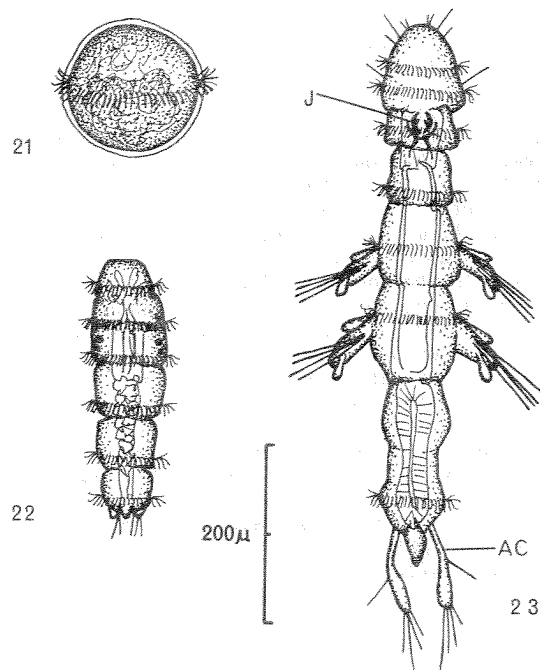


Fig. 21-23. *Dorvillea caecus*  
 21. swimming gastrula  
 22. 2-segment polytrochal larva  
 23. 2-setiger benthic larva

Family GLYCERIDAE Grube 1850

*Glycera dibranchiata* Ehlers 1868

Klawe (1955) reported that spawning in *Glycera dibranchiata* occurs in the last half of May through early June. He reported the eggs as 180-190  $\mu$  in diameter, and trochophores from artificial fertilizations were 140-150  $\mu$  in height. Klawe was unable to find glycerid larvae either in surface or bottom plankton tows, and the present author also failed to find any larvae that could be attributed to a glycerid. General discussions of glycerid larvae are given by Cazaux (1967) and Blake (1975). *G. dibranchiata* is common in intertidal mud flats in Passamaquoddy Bay and is by far the most abundant glycerid. The related forms *Glycera robusta*, *Ophioglycera gigantea* and *Gonadia maculata* are also reported from the Bay.

Family LUMBRINERIDAE Malmgren 1867

*Lumbrineris fragilis* (O. F. Müller 1776)

Numerous specimens of adult *Lumbrineris* were examined. All proved to be *L. fragilis*, so the *Lumbrineris* larvae recovered from the plankton and described here are all attributed to this species. Trochophores and cleaving eggs appeared in the surface plankton during the first weeks of July, August, and September, being most abundant in September. The monthly periodicity, similar to that seen in *Dorvillea*, suggests a role for lunar phase in the control of spawning. Eggs from the plankton were 190-210  $\mu$  in diameter, yolky and very opaque, ranging in color from brown or rose to orange and yellow. Trochophores developed a conspicuous apical tuft and a broad prototroch of fine short cilia by means of which they swam near the water surface when kept in finger bowls. Development led to a settled 1-setiger larva after about 6 d in the laboratory. During this time the tissue of the larva become progressively less opaque, and the body surface developed a pattern of transverse pigment bars which were usually red or brown. Jaws were conspicuous and black in the settled stages, but eyes were not apparent. A general discussion of *Lumbrineris* larval development can be found in Cazaux (1972) and Richards (1967).

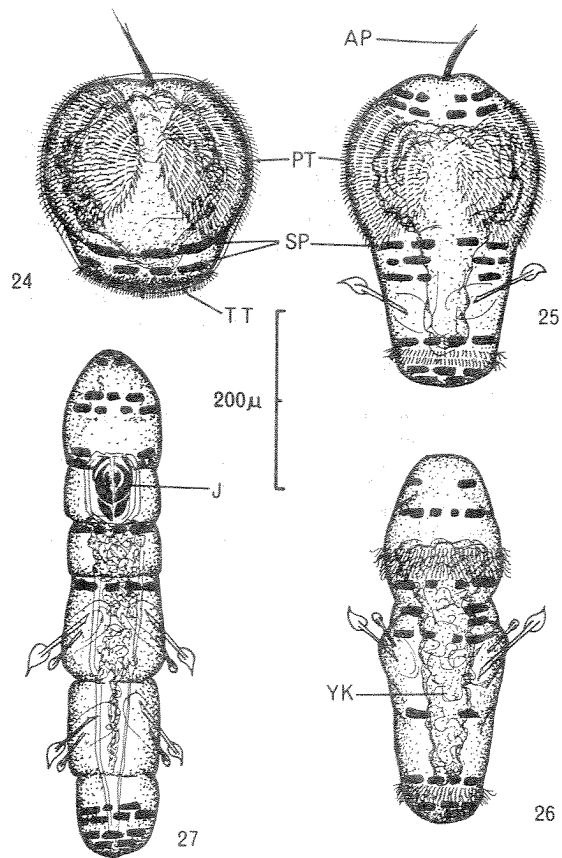


Fig. 25-28. *Lumbrineris fragilis*  
 25. trochophore  
 26. swimming 1-setiger  
 27-28. settled stages

*Ninoe nigripes* Verrill 1873

Through the spring and summer, female worms were conspicuously orange due to the presence of yolky, bright orange eggs. Spawning is presumably in late summer, since the largest eggs, up to 200  $\mu$  in diameter, were found in July and August. The larvae are assumed to be benthic. This species is common in soft intertidal mud along with *Arabella iricolor*.



Family MALDANIDAE Malmgren 1867

*Clymenella torquata* (Leidy 1855)

Ripe eggs are opaque, yolk, yellowish or cream-colored and 200  $\mu$  in diameter. In 1975 the author obtained fertilized eggs and larvae from ripe specimens of *Clymenella* placed in finger bowls and allowed to spawn naturally. The eggs developed as described by Newell (1951), but larvae swam more actively than he described. Thus, by the second day after fertilization, larvae swam actively enough to maintain themselves at the water surface and continued to do so for an additional 2-3 d. They settled and began crawling by the sixth day. The swimming larvae were completely opaque, light yellow, and easily recognizable, but were not seen in the plankton.

*Clymenella torquata* is common on intertidal sand flats in Passamaquoddy Bay. *Praxillella praetermissa*, *Praxillella gracilis* and *Rhodine loveni* have also been collected, and are largely subtidal. *Euclymene collaris* is common elsewhere in the Canadian Atlantic and might be expected in the Bay as well (R. O'Clair, pers. comm.). Nothing is known of larval development in these species with the exception of *Clymenella* and little is known about their spawning. Rowe (1970) and Rowe et al. (1975) found ripe eggs 220  $\mu$  in diameter in *Praxillella praetermissa* and concluded that spawning was in December or January. Both Rowe and the present author have found spawning in *Clymenella torquata* to occur within the space of 2-3 d at the end of June.

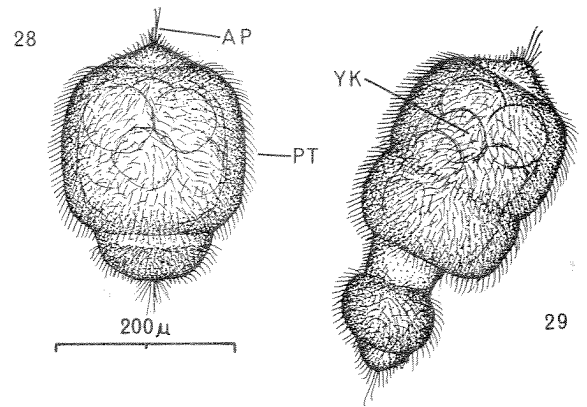


Fig. 28-29. *Clymenella torquata*  
28. lecithotrophic trochophore at hatching  
29. larva 2 d after hatching

*Nephtys incisa* Malmgren 1865

Two main types of nephtyid larvae were identified from the plankton. One was tied directly to *N. incisa* through the collection of metamorphosing and juvenile stages. The other agreed with descriptions of *N. caeca* larvae in Thorsen (1946). A third nephtyid larva was found that possibly belongs to *Aglaophamus neotenus*.

Specimens of *N. incisa* with nearly ripe eggs and ripe sperm were found in March, April and May. Eggs were yolky, opaque and coral pink; the largest found were 100  $\mu$  in diameter. Larvae attributable to *N. incisa* first appeared in the plankton in early April. These were found off and on through May and June, but were never present in large numbers. Large numbers of bottom stages from recently settled stages to juveniles of several millimeters were recovered in late June by use of a bottom sled. The youngest of these shared with advanced planktonic larvae a most distinctive pattern of pigmentation. First, there were irregular bands of brilliant ruby-red pigment on the larval surface which were most noticeable immediately above and below the prototroch and on the pygidium. Similar bands of red pigment appear in other species and may be typical of *Nephtys* larvae in general. In *N. incisa*, however, the gut is also brightly colored. The stomach is olive green, and the intestine is an intense dark blue. The stomach wall contains numerous yellow droplets that give the dorsal region of the stomach a bubbly appearance. The *N. incisa* color pattern was first noticed in trochophores 200

in height. Green and blue colors and yellow droplets were seen in all larger stages and in settling stages which retain a zone of green pigment and yellow droplets behind the developing pharynx followed by a dark blue zone and brilliant red pygidium. The pygidium is frequently a more intense red than the prototrochal region and episphere. Late stage trochophores are characteristic for their general shape as well as bright color, and for the thick tissue developed about the mouth. Since most of the episphere shows the color of the underlying gut, this "lip" region of solid tissue stands out for its lack of color so that larvae appear to have whitish parrot-like beaks. The smallest nephtyid trochophores collected were somewhat nondescript. Those attributed to *N. incisa* showed beginnings of red pigment bands, and the prototrochal cilia were very long. If the author's identifications are correct, the youngest stages of *N. incisa* can be distinguished from those of *N. caeca* by their more conical episphere. Larvae of *N. caeca* have a regular, dome-shaped episphere, and eyes appear sooner than in *N. incisa*. *N. incisa* trochophores are rapid and continuous swimmers at all stages. The body is robust and the tissues fairly thick, but there seems to be only a limited ability to change shape. Larvae may reach 550  $\mu$  in length and nine segments before metamorphosis. After metamorphosis, the 9- to 10-segment juveniles are about 1 mm in length and have simple capillary setae. The eyes in *N. incisa* are red, but usually the red pigment is so dense as to appear brown or black. Larvae of *N. incisa* from Passamaquoddy Bay are very similar to the nephtyid larvae described from Denmark by Thorsen (1946) and attributed to *N. ciliata*, but reassigned to *N. hombergi* by Rasmussen (1973).

*N. incisa* is abundant subtidally throughout the Bay. It can be dredged from all muddy bottoms, particularly from areas of soft mud, and is found commonly with *Lumbrineris fragilis*. *N. caeca* is the only other common nephtyid and is usually collected intertidally. Only occasional specimens of *N. ciliata* have been recorded.

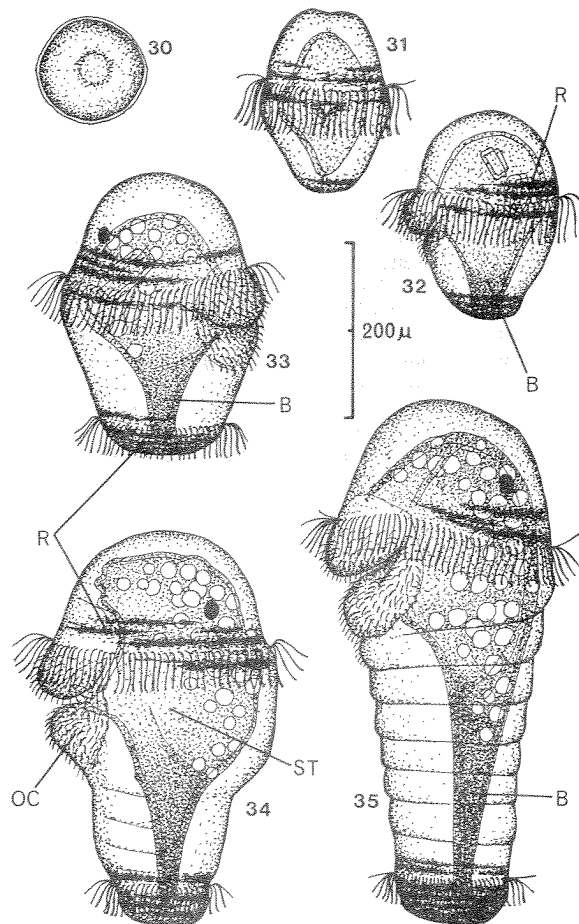


Fig. 30-35. *Nephtys incisa*  
30. unfertilized egg  
31. trochophore stages  
32-35. metatrochophore stages

*Nephtys caeca* (Fabricius 1780)

*Nephtys* larvae of various stages agreeing with the description given for *N. caeca* by Thorsen (1946) appeared in the plankton in May, June and early July. These larvae always have surface pigmentation and, though it may be brilliant red as in *N. incisa*, it is more often a dull red-brown color. In late larvae and in bottom stages, much of the surface of the episphere or developing prostomium may be covered with a dull, opaque, brownish pigment. Pigment on the pygidium also becomes brown and fairly dense in late stages so that two solid bands of brown or reddish-brown mark the pygidium, one directly in front of and one behind the telotroch. The gut in *N. caeca* is olive-colored at all stages though it is often not very dark. The intestine is colorless, and there is no hint of blue pigmentation anywhere in the larva. On this latter characteristic alone most *N. caeca* larvae can be distinguished immediately from those of *N. incisa*. The *N. caeca* trochophores are more regular in shape than those of *N. incisa* and are characterized by a large and dome-shaped episphere. The metamorphosing stage is smaller than in *N. incisa*; 8-setiger bottom stages measure 670  $\mu$  in length. Setae are simple.

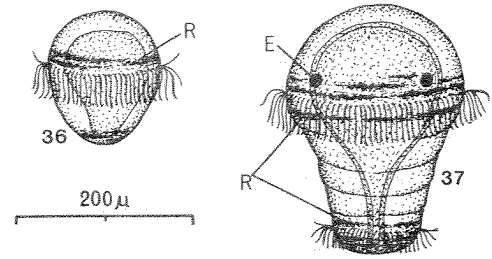


Fig. 36-37. *Nephtys caeca*  
36. trochophore  
37. dorsal view of a young metatrochophore

*Aglaophamus neotenus* Noyes 1980

An 8-setiger nephtyid larva 700  $\mu$  long was found with translucent yellow pigment on head and pygidium, red streaks below the prototroch and an unpigmented gut. This matches descriptions of the larvae of *Aglaophamus neotenus* from estuaries in Maine (Noyes 1970, 1980). *A. neotenus* has not been found in Passamaquoddy Bay, but is recorded for the Saint John River in New Brunswick and Minas Basin, Nova Scotia (M. Dadswell, pers. comm.).

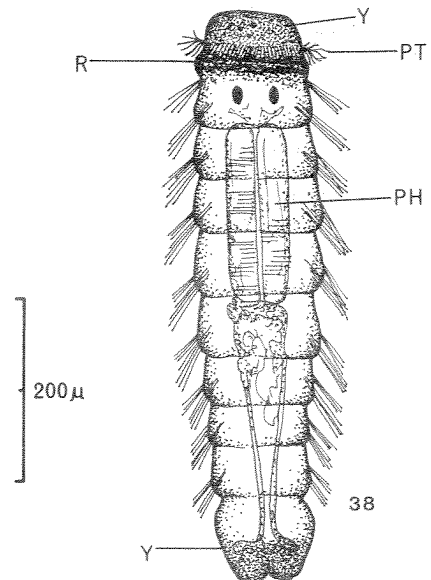


Fig. 38. *Aglaophamus neotenus*, metamorphosing setiger

Family NEREIDAE Johnston 1845

*Nereis virens* Sars 1835

Normal spawning appears to occur over a period of from one to several weeks beginning at the end of April (J. Mardsen, pers. comm.). Eggs and larvae can be collected in small numbers in plankton nets from shallow water. Presumably they are stirred up by wave action as neither eggs nor larvae are pelagic. Eggs are grey-green, yolk and 210  $\mu$  in diameter. A clear, gelatinous capsule 500-600  $\mu$  in diameter develops after fertilization. Hatching larvae have 3-4 setigerous segments, and setae are compound. Larval lengths are: with four setigers, 450  $\mu$ , five setigers, 550  $\mu$ . Eggs fertilized artificially in early April required 4 wk to hatch in the laboratory at 10°C. Ripe adults will often release their gametes if they are placed briefly in cold fresh water (E. Huebner, pers. comm.). Snow (1972) figures eggs and larvae from Passamaquoddy Bay and gives the maximum egg size as 240  $\mu$ . She records sizes for laboratory-reared larvae somewhat smaller than were observed in this study. Sveshnikov (1960) also figures the larvae.

*Nereis virens* is common in intertidal mud flats, but sexually ripe individuals are difficult to find in any numbers. Further information on the reproductive biology of *N. virens* is given by Bass and Brafield (1972).

*Nereis pelagica* Linné 1758

Eggs, trochophores and setigerous larvae of *N. pelagica* appeared in the plankton during the second and third weeks of June. Eggs were 195-200  $\mu$  in diameter with a 400  $\mu$  gelatinous capsule, translucent with conspicuous oil droplets and slightly greenish in color. After 4 d in finger bowls at 14°C, eggs hatched into trochophores with three pairs of differentiating setal sacs on each side and bands of red pigment about the prototroch. The setigerous stages resemble those of *N. virens*, but are smaller. Setae are compound, the eyes are red, and lateral red pigment bands are retained on the head for a time. Lengths are: with three setigers, 230  $\mu$ , four setigers, 270  $\mu$ . Rasmussen (1956) discusses larval development of *N. pelagica* in detail. This species is found on relatively hard bottoms rather than in soft mud. Juveniles are common in dredge samples taken near the Biological Station (Joe's Point).

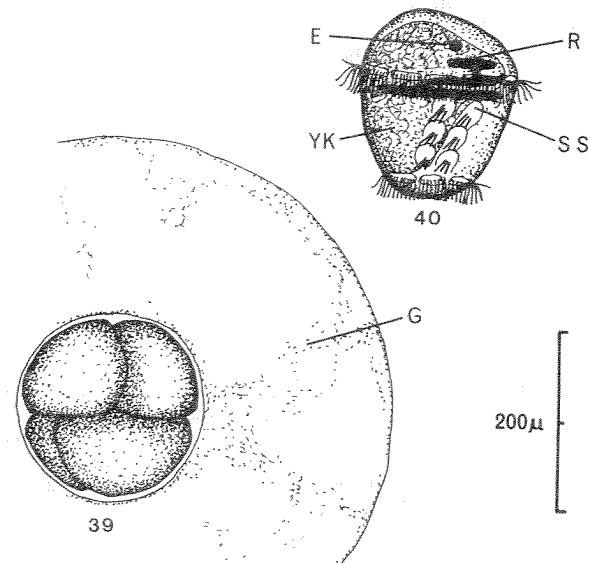


Fig. 39-40. *Nereis pelagica*  
39. cleaving egg  
40. newly hatched trochophore

Family ORBINIIDAE Hartman 1942

*Naineris quadricuspida* (Fabricius 1780)

This species is common in the muddy substratum of mussel beds and in intertidal rock pools where the worms creep about on clumps of algae. Eggs are very yolk, opaque and yellow-orange. They increased progressively in size during the summer of 1974. The largest, found in August, were 210  $\mu$  in diameter. Presumably spawning is in late summer, and the larvae are assumed to be benthic.

*Myriochele heeri* Malmgren 1867

Oweniid larvae of the characteristic mitraria type appeared irregularly and in small numbers in the plankton from the end of May to the end of July. These were of the type attributed to *Myriochele* by Thorsen (1946), lacking the distinct umbrellar lobes characteristic of *Owenia*. There seems little doubt that the larvae belong to *M. heeri*. The umbrella was 200-260  $\mu$  in height. The provisional setae were all capillary, 500-650  $\mu$  in length with tiny lateral projections. They appeared blue or blue-green in reflected light and were iridescent. The body was transparent except for the greenish gut and the ciliary girdle, which may be irregularly marked with yellowish or orange pigment. Distinct red blotches of pigment appeared about the mouth at the beginning of metamorphosis. *M. heeri* was the only oweniid polychaete found in the Bay by the author, though *Owenia fusiformis* might be expected.

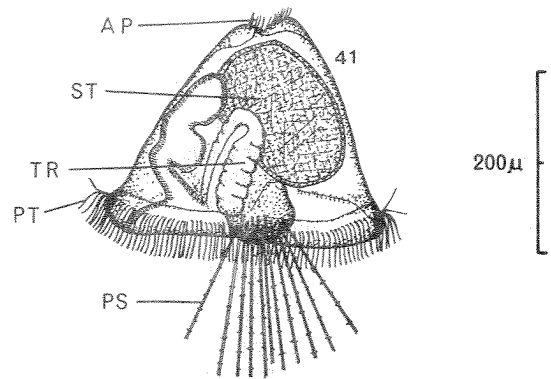


Fig. 41. Mitraria larva of *Myriochele heeri*, with the proximal ends of the provisional setae shown

Family PECTINARIIDAE (AMPHICTENIIDAE) Quatrefages 1865

*Pectinaria granulata* (Linné 1767)

Spawning in 1974 by *P. granulata* was during the first 2 wk of June, and planktonic larvae were recovered in small numbers through June and the first 2 wk of July. Artificial fertilizations made in April and May were successful. In April, gametes had to be cut from the body, but nearer to the natural spawning time the worms would release gametes when disturbed. The eggs in large numbers appear yellow-green. Singly, they are translucent, whitish and 75-80  $\mu$  in diameter. The hatching trochophore is 70  $\mu$  in height and without eyes. At 12°C these survived about 2 wk without feeding. Larvae at all stages, including the hatching stage, are characterized by an elaborate, hood-like oral apparatus. The eyes are red, often a very dark red in older larvae. Also in older stages, the body surface is ornamented with regular rows of round, dark red or brown spots, and the developing paleae can be seen within the body. Metamorphosed larvae with seven pairs of gold paleae were taken from the plankton in their tubes. The transparent part of the tubes were 1200  $\mu$  long and patterned with an irregular pavement of tiny rhomboids. Sand grains mounted around the top averaged 50  $\mu$  in diameter. *P. granulata* appears to be the only species of *Pectinaria* in the Bay. The worms can be collected in some numbers from tide pools, where they are found under rocks and in the substratum of mussel beds.

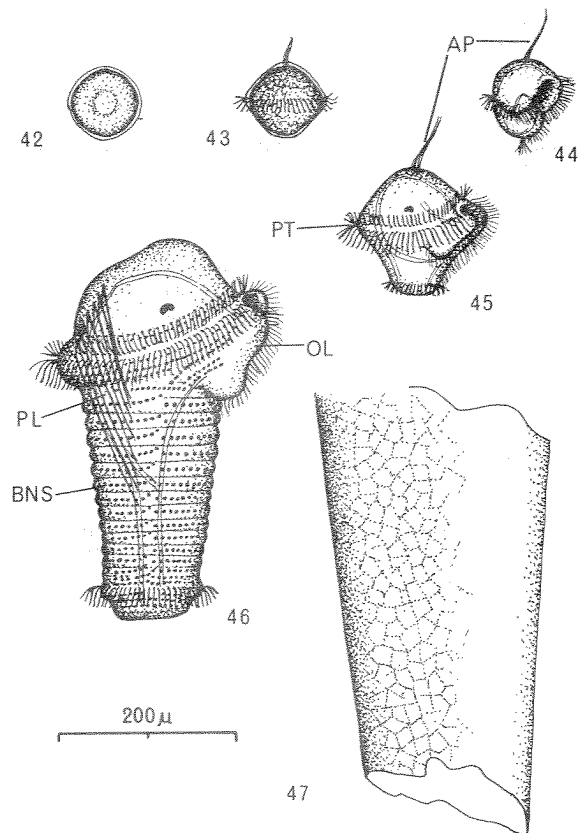


Fig. 42-47. *Pectinaria granulata*  
42. unfertilized egg  
43. trochophore before hatching  
44. newly hatched trochophore  
45. feeding trochophore  
46. metatrochophore  
47. portion of the tube of a nectochaete

*Phyllodoce maculata* (Linné 1767)

The egg masses of *P. maculata* appeared in the intertidal zone during the last 2 wk in May. These were 2-3 cm long and were filled with several thousand dark green eggs 105-110  $\mu$  in diameter. In the laboratory the soft, gelatinous matrix broke down within about 2 d to release swimming trochophores identical to those released from the smaller egg masses attributed (below) to *P. mucosa*. The trochophores were translucent except for the green gut and had red eyes. The apical tuft, conspicuous at hatching, was lost after about 2 d by which time the frontal organ and meniscotroch had developed. By then the larval musculature was sufficiently developed to produce lengthwise stretching and contraction, but *Phyllodoce* trochophores were not as actively contractile as those of *Heteromastus*. The *P. maculata* trochophores were rapid swimmers and survived up to 3 wk without feeding.

*Phyllodoce* larvae from the plankton were attributed with few exceptions to *P. mucosa* because they possessed yellow chromatophores. In mid June a few advanced larvae were found that lacked the pigment cells and differed from *P. mucosa* in their ability to metamorphose. Although they did metamorphose successfully to bottom stages of 13 segments, the change required 4-5 d and the resulting juveniles were fragile and unhealthy looking, not at all robust and active as in *P. mucosa*. These metamorphosed stages were transparent with a green tinge, faint dorsolateral bands of brown and brown markings on the dorsal cirri. Agassiz (1867) attributed larvae colored in this way to *P. maculata* because the adult is similarly colored, so the present author assumes his few larvae were *P. maculata* also. *P. maculata* and *P. mucosa* were the only common species of *Phyllodoce* noted in the Bay. The few adult specimens of *P. maculata* found were much larger than those of *P. mucosa*, about 10 cm in length, so it seems reasonable that the larger of the two types of phyllodocid egg masses found should belong to *P. maculata*. This is further supported by differences in egg color. Ova from ripe *P. maculata* were more darkly pigmented than those of *P. mucosa*, and it was the larger of the two types of egg masses that had the more darkly pigmented eggs. Specimens of *Eulalia viridis* and *Eulalia bilineata* were also collected in the Bay, but no eggs or larvae attributable to this genus were recovered.

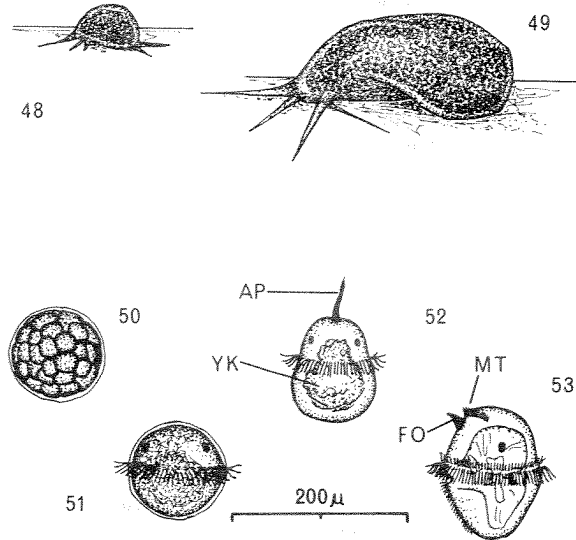


Fig. 48-49. Phyllodocid egg masses, approx. life size  
 48. *Phyllodoce mucosa*  
 49. *Phyllodoce maculata*  
 Fig. 50-53. *Phyllodoce maculata*  
 50. cleaving egg  
 51. swimming trochophore before hatching  
 52. newly hatched trochophore  
 53. trochophore 4 d after hatching

*Phyllodoce mucosa* Oersted 1843

Egg masses that could be attributed to *P. mucosa* were recovered in mid May. These had a soft, gelatinous matrix and contained several hundred pale green eggs 110  $\mu$  in diameter. The egg masses broke apart in 1-2 d to liberate trochophores identical to those from *P. maculata* egg masses. Larger feeding trochophores were taken from the plankton through June and the first half of July. These were never abundant in the surface plankton, but could be collected along with metamorphosed stages in shallow areas. The largest collections of larvae were made with a plankton net attached to a weighted sled and towed along a soft mud bottom.

The larvae agreed closely with the descriptions of Cazaux (1969). Trochophores are unmistakable in the plankton, due to the green color of the gut and to the presence of two pairs of bright yellow chromatophores, a ventral pair flanking the mouth and a corresponding dorsal pair. These are opaque and appear yellow only in reflected light. They are first seen in 200-250  $\mu$  trochophores and are small and round, but at later stages numerous elaborately branched processes develop. They are retained through metamorphosis when similar chromatophores appear dorsally on each segment, thereby producing the characteristic adult color pattern. Larval eyes are red, and faint brown smudges may be present around the mouth. A small number of larvae were discovered with chocolate-brown guts, but otherwise identical to the green larvae. It seems likely that these also belong to *P. mucosa*. The larvae do not develop a telotroch.

Larvae reached a length of 550  $\mu$  and nine segments before metamorphosis occurred. Larvae of this size will metamorphose completely within about a day if the trochophores are isolated into finger bowls. In nature it appears there may be an additional period of trunk elongation before metamorphosis without the addition of new segments since 9-segment larvae up to 800  $\mu$  in length were collected. Segments are added very rapidly after metamorphosis. One specimen increased to 30 segments and a length of 8 mm within 2 wk of metamorphosis, apparently without feeding. Setae are compound. *P. mucosa* is the most abundant phyllodocid in the Bay, present in all intertidal and most subtidal samples of mud. All specimens were small (2-3 cm long) and their ripe ova were pale green.

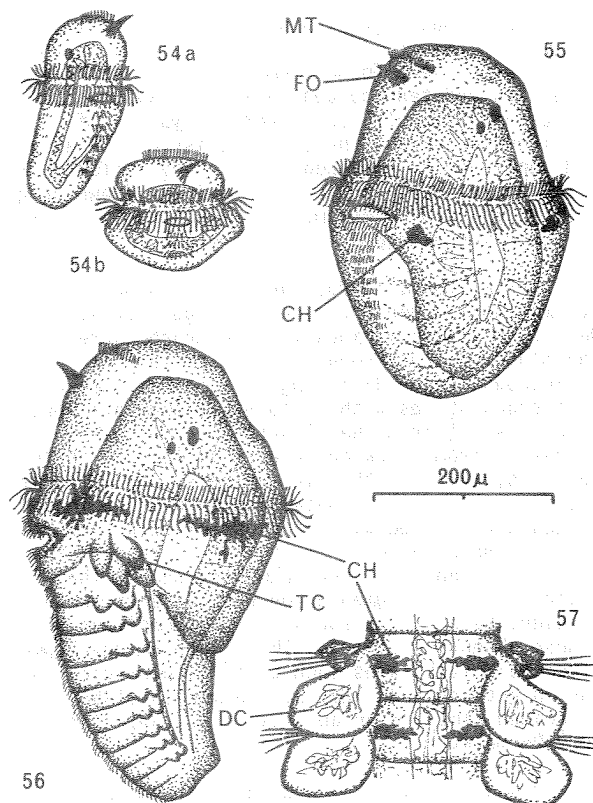


Fig. 54-57. *Phyllodoce mucosa*  
 54a. trochophore, circular muscles contracted  
 54b. trochophore, longitudinal muscles contracted  
 55-56. metatrochophore stages  
 57. dorsal view of segments of a newly metamorphosed juvenile

*Eteone longa* (Fabricius 1780)

The largest eggs found in ripe adults were 110  $\mu$  in diameter, yolk and light brown. Planktonic stages were found from the end of April to mid June with greatest concentration in May. Trochophores had the solid construction typical of phyllodocid larvae, the characteristic frontal organ and meniscotroch, and red eyes. They differed from trochophores of *Phyllodoce* in having a brown or gold colored gut and no chromatophores. Further, *Eteone* larvae never exceeded 300  $\mu$  in height.

All *E. longa* larvae over 200  $\mu$  in height metamorphosed when isolated in finger bowls. Metamorphosis of variously sized trochophores from the plankton thus produced an assortment of setigerous stages differing in number of segments. Setigerous stages with up to eight segments were also obtained from the plankton. Lengths for specimens from plankton were as follows: with four setigers, 350  $\mu$ , with five setigers, 500  $\mu$ , and six setigers, 700-750  $\mu$ . Setae are compound. These stages were marked with a number of dark green spots, concentrated on the dorsal surface of the prostomium and first few segments, and on the pygidium. This pigmentation was quite variable, however, being conspicuous in some specimens and almost absent in others. The degree of development of certain structures such as tentacular cirri also varied between individuals. Rasmussen (1956) described similar variability in *E. longa* larvae from Denmark.

*Eteone longa* was found in small numbers in all mud substrates. *E. longa* is clearly the most common species of the genus in the area, so all *Eteone* larvae found were attributed to this species. These matched descriptions of Rasmussen (1956) for *E. longa* from Denmark. Blake (1975) provides some further discussion of *Eteone* larvae.

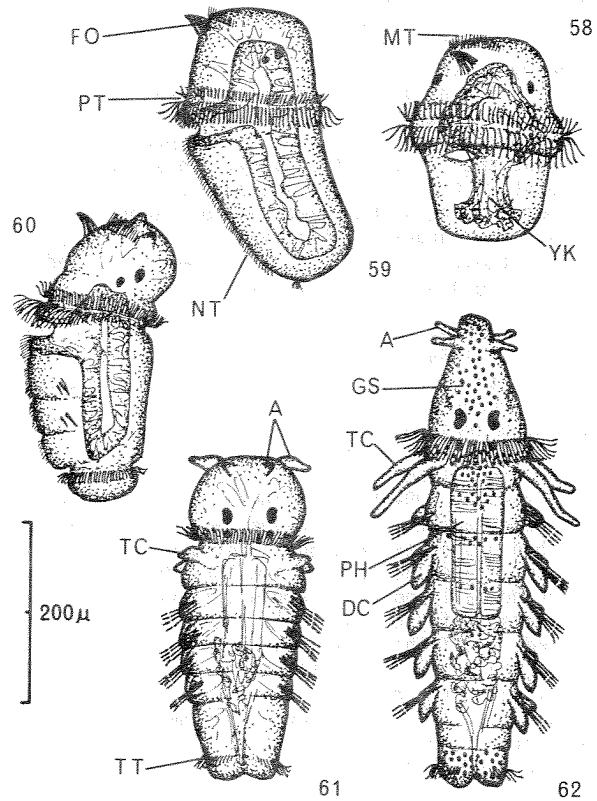


Fig. 58-62. *Eteone longa*  
 58-59. trochophores  
 60. metatrochophore from a laboratory culture  
 61. metatrochophore from the plankton  
 62. nectochaete from the plankton



*Lepidonotus squamatus* (Linné 1758)

Eggs taken from ripe adults were grey-green in masses, but whitish and translucent individually. Eggs were irregular in shape when spawned, but swelled in sea water to a uniform diameter of 100  $\mu$ . Cleavage produced a swimming stage only 85  $\mu$  in diameter so that the typical appearance of the *Lepidonotus* trochophore before hatching was of a whitish rhomboid enclosed within its larger egg membrane. The trochophores developed a prominent mouth, one pair of black eyes and a few black smudges above the prototroch, but grew no larger than 90-95  $\mu$  in diameter without food. Larvae reared in late April at 10°C took 6 d to develop to a feeding stage. Without food, larvae survived about 3 wk. Larvae reared in July at 14°C survived only 1 wk.

Distinctive polynoid larvae were noted in the plankton which could be attributed with certainty to *Lepidonotus squamatus* despite the fact that they could be found only in May, June and July and not through the whole period of time that ripe *Lepidonotus* adults could be collected. In mid April, a large number of eggs and cleavage stages appeared in the plankton identical to those from laboratory fertilizations of *Lepidonotus* eggs. As with the appearance of *Harmothoe* eggs in plankton, this outburst was over in a week and did not recur. *Lepidonotus* trochophores of various early stages were recovered through May. Later stages became more abundant and reached greatest numbers in late June and early July. Larvae were rare by late July and absent in August. *Lepidonotus* trochophores were thus seen over a longer period of time than those of *Harmothoe imbricata*, but were never as numerous as *Harmothoe* larvae were in mid April. Large numbers of recently settled stages of *Lepidonotus* were recovered from the bottom samples in mid July. These were 600-650  $\mu$  in length and agreed in all respects with the description of Rasmussen (1973).

*Lepidonotus squamatus* trochophores from Passamaquoddy Bay are distinctively pigmented. The amount of pigment is variable so that some larvae may appear almost unpigmented, but when pigment is present the pattern is always the same: A prominent band of black pigment grains occurs just anterior to the prototroch with lesser bands about the eyes and mouth. The eyes are black; three pairs develop by the late metatrochophore stage. Tissue around the mouth is yellowish or brown. The trochophore gut did not appear colored; it may contain yellowish debris, but is never green as in *Harmothoe* larvae. It is possible that trochophores of *Lepidonotus* with very little of the black surface pigmentation could be confused with *Harmothoe* larvae since gut color is variable and not a good characteristic on which to separate species. In *Lepidonotus*, the pattern of surface pigment found in the trochophore is maintained through metamorphosis so that the head of the setiger is smudged with black posteriorly while the frontal region is brown or yellow. The remainder of the setiger body may be variously marked with black, but never prominently. Setae are simple. The author's observations on larval pigmentation differ from those of Cazaux (1968).

*Lepidonotus squamatus* is found intertidally and subtidally throughout the Bay on all hard substrates. Sexually mature specimens could be collected throughout the spring and summer. Fertilizations performed in April were of necessity with eggs cut from the female and were not always successful. After June, worms spawned more or less spontaneously during the night after collection. Very few of the worms were found to be spawned out even in late August.

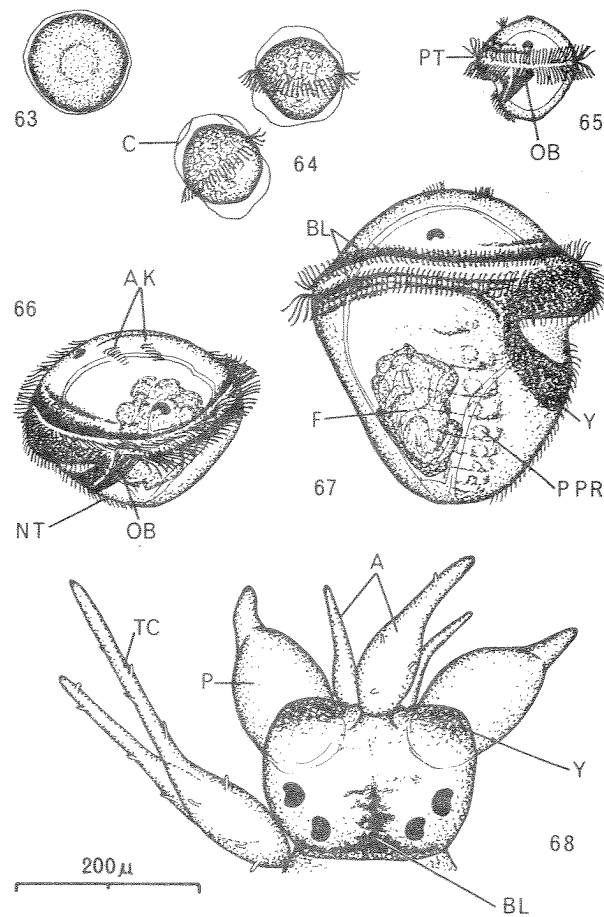


Fig. 63-68. *Lepidonotus squamatus*  
 63. unfertilized egg  
 64. trochophores before hatching  
 65. newly hatched trochophore  
 66. feeding trochophore  
 67. metatrochophore  
 68. dorsal view of prostomium of a nectochaete

*Harmothoe imbricata* (Linné 1767)

Eggs taken from ripe adults were white, somewhat yolky and 145-150  $\mu$  in diameter. Spawning occurs readily in the laboratory, and artificial fertilizations can be done without difficulty.

A single series of *Harmothoe* larvae was collected in the plankton from late March through April. These were the only trochophore-like larvae in the plankton during this period. On settling, late-stage larvae proved to be *H. imbricata*. It seems reasonable to assume that most if not all of the larvae of this series belong to *H. imbricata*.

The first sign of spawning was the appearance in the plankton during the third week of March of large numbers of eggs and cleavage stages. Throughout April the number of feeding trochophores in the plankton increased steadily, reaching greatest numbers in the third week of April, but eggs and cleavage stages were not found in the plankton after March. The eggs and cleavage stages were white and opaque, and developed brownish smudges during cleavage so that the resulting swimming stage was at first opaque with a brownish tinge. During early April the feeding stages were transparent, and their guts were usually empty. Later in April larvae were greenish or yellowish due to the presence of colored oil droplets in the walls of the stomach. The development of color in the gut paralleled the increase in diatom numbers and so is possibly a consequence of increased feeding.

Various late stages of *H. imbricata* were found during May, but were never abundant after April. There was slight overlap of spawning in *H. imbricata* and *Lepidonotus squamatus* so that trochophores of both species could be found together, but this happened only in early May. Juveniles of *H. imbricata* collected in mid July by dredge were all 2-3 mm in length. Bottom stages of *Lepidonotus squamatus* taken in the same collection were all recently metamorphosed.

Throughout its development the *H. imbricata* larva is without distinct surface pigmentation. Faint brownish markings may appear around the mouth, and three pairs of black eyes are developed by the late metatrochophore stage. The larval body is of typical polynoid shape and is dominated by the large and spacious stomach. Both gut and ectoderm are constructed of relatively delicate epithelia. In this respect *Harmothoe* larvae are structurally rather different from the very solid larvae of phyllodocids. The larvae swim rapidly when small and more slowly as they enlarge. The body is not very muscular. This is especially noticeable in the late metatrochophore when parapodia, though developed, remain immobile, the setae projecting rigidly from blocks of developing trunk mesoderm. Metamorphosing stages are 670-700  $\mu$  long with eight segments and simple setae. Rasmussen (1956) provides quite complete descriptions of *H. imbricata* larvae. The present author's observations support his descriptions very closely, but differ somewhat from those of Thorsen (1946) and Cazaux (1968), especially with regard to pigmentation and egg size. Egg size appears to be quite variable in *H. imbricata* however (Rasmussen 1956; Blake 1975).

*Harmothoe imbricata* is found subtidally throughout the Bay in large numbers and on all types of bottoms. *H. extenuata* and *H. oerstedii* are also reported, but the author encountered adults of these species only rarely. Adult *H. imbricata* taken by dredge were found with ripe gametes through mid April after which sexually ripe specimens became rare.

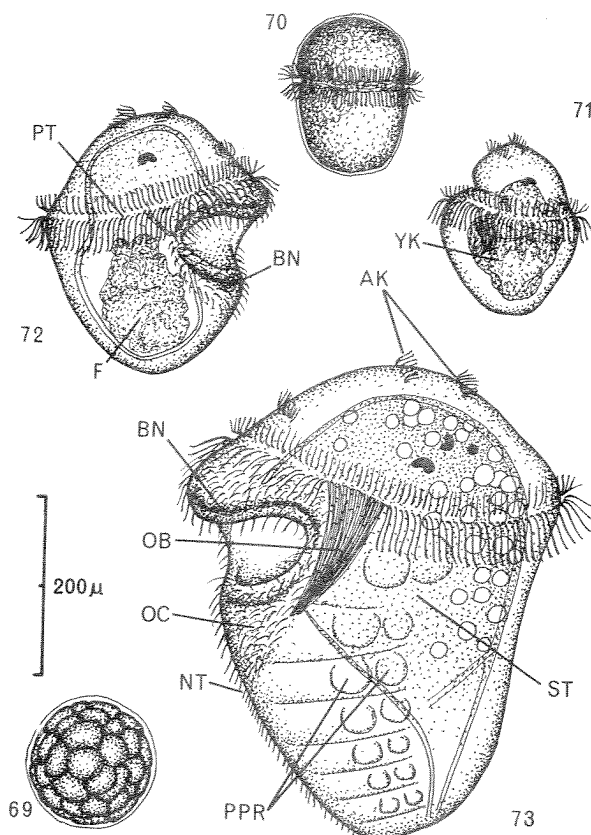


Fig. 69-73. *Harmothoe imbricata*  
 69. cleaving egg  
 70. trochophore before hatching  
 71. newly hatched trochophore  
 72. feeding trochophore  
 73. metatrochophore

Family SERPULIDAE Johnston 1865

*Spirorbis spirillum* (Linné 1758)

Eggs of *S. spirillum* are yolky, pink and about 180  $\mu$  in diameter. Eggs are brooded in the parent tube and hatch as typical *Spirorbis* larvae to swim about and settle within about a day. Individuals of *S. spirillum* breed throughout the spring and summer in Passamaquoddy Bay beginning about mid April, but do not appear to breed in the winter as reported by Rothlisberg (1974). Larvae are sometimes found in plankton hauls and are distinguished by the pink yolk still present in the gut region. In *S. borealis* eggs and larval yolk are dark brown, and the larvae are more robust. *S. borealis* was not as common in the Bay as elsewhere along the coast and larvae were not seen in the plankton. Hoglund (1951) describes and figures larvae of both species from Sweden and gives references to additional larval descriptions. *S. spirillum* is found attached to hydroids in deeper parts of the Bay near the passages where tidal currents keep the bottom relatively free of mud.

Family SIGALIONIDAE Malmgren 1867

*Pholoe minuta* (Fabricius 1780)

The eggs are translucent individually and 85  $\mu$  in diameter when ripe. Planktonic stages, mostly of four and five segments, were found in small numbers for about a month beginning the second week of June. Larvae are similar to those of polynoids differing from *Harmothoe* and *Lepidonotus* chiefly in size, in having compound rather than simple setae, and in the precocious development of setae relative to elytra. Trochophores are transparent with one pair of black eyes. Parapodial lobes with setae develop when the trochophores are about 250  $\mu$  in height. Average lengths for setigerous larvae are: with three setigers, 280  $\mu$ , four setigers, 320  $\mu$ , and five setigers, 360  $\mu$ . Judging from the egg size, *P. minuta* trochophores clearly must be planktotrophic. The well filled guts of recently metamorphosed larvae may, however, distend the body dorsally to give a hump-back appearance. This has caused them to be confused with lecithotropic nereid larvae in the past. Larger eggs are recorded from *P. minuta* populations in more northerly latitudes, suggesting the larvae may rely less on planktotrophy in those regions (Curtis 1977; Sveshnikov 1960). Various larval stages are figured by Blake (1975) and Sveshnikov (1960, 1967), and a general discussion of *Pholoe* larvae is given by Cazaux (1968).

Adult *P. minuta* are inconspicuous because of their small size, but are found in some numbers subtidally in soft mud along banks at the mouth of St. Croix River (Navy Island). Ripe females are pink or pink-orange ventrally due to the presence of eggs in the body.

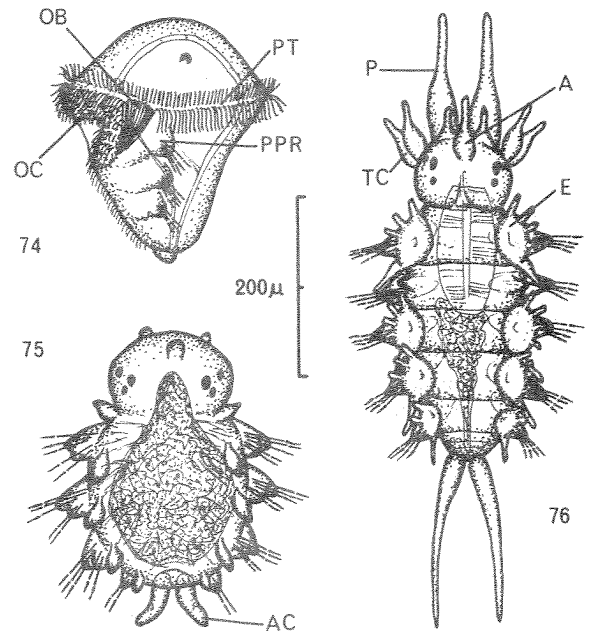


Fig. 74-76. *Pholoe minuta*  
74-75. metatrochophore stages  
76. nectochaete

Spionid larvae, though a conspicuous part of the larval plankton, were not examined in detail for this study, and the adults have not been well collected in Passamaquoddy Bay. Late stage larvae collected from the plankton will survive and metamorphose if isolated in finger bowls and kept free of bacteria, so it is relatively easy to trace development through to juvenile benthic stages. There is an extensive literature on spionid larvae covering most of the species that are known for the Passamaquoddy Bay area. Hannerz (1956) provides the most complete survey of larval structure, and Simon (1967, 1968) has sorted out the synonymies among the species that would be encountered.

The family Spionidae is subdivided into two major groups. Species in the first of these have eggs with a thick-walled chorion and larvae with entirely pelagic development. In the second group, the eggs have a thin-walled chorion and the larvae may be brooded. Spionid larvae of advanced stages appeared in large numbers in the plankton throughout the spring. These, with the exception of larvae of *Prionospio steenstrupi*, belonged exclusively to the second group, being species of *Polydora* and *Spio*. Larvae of *Polydora quadrilobata* appeared first and in greatest numbers. They could be collected from late March to late May. An additional type of *Polydora* larva was abundant from late April to June. These were of the *P. ciliata* type with two dorsal rows of stellate black chromatophores on the more posterior segments, and presumably were larvae of *P. ligni* or *P. websteri*. Larvae of two other *Polydora* species were found in smaller numbers in May and June. Blake (1969) provides descriptions and a key for determining the larvae with remarks on the times of their appearance off the coast of Maine. Some *Spio* larvae were found in April and May, and settled stages of *Spio filicornis* were recovered from settling bottles.

Three types of thick-membraned eggs were found in the plankton. Eggs, cleavage stages and 3-setiger larvae of the first type appeared during the last 2 wk of March and into April with the last eggs being found in mid April. Eggs were very yolky, opaque and cream-colored. They ranged from 180-200  $\mu$  in diameter and had a delicate chorion 250-300  $\mu$  in diameter with a reticulate pattern on its surface, but without obvious vesicles. Eggs could be raised in finger bowls to trochophores 210  $\mu$  in height and so opaque, brownish hatching stages with three segments and 230  $\mu$  long. The chorion was closely molded around the trochophore stage, but had fragmented and sloughed off by the setiger stage. A single pair of black eyes, long provisional setae and the telotroch developed at about the same time in the late trochophore. Both trochophores and setigers were sluggish swimmers. Larvae more advanced than the 3-segment stage were not found in the plankton and, during the next few months, no larger larvae turned up that could have belonged to a genus with thick-membraned eggs except those of *Prionospio*. Adults of *Scolecopsis squamata* (Müller 1806) have been collected near Eastport (M. Pettibone, pers. comm.) and *Laonice cirrata* (Sars 1861) is known from Passamaquoddy Bay. Both have thick-membraned eggs, but the eggs and larvae just described most closely resemble published descriptions for *Scolecopsis squamata*. A more complete discussion of the larval development of *S. squamata* (as *Nerine foliosa*) is given by Hannerz (1956).

A second type of thick-membraned egg was recovered from the plankton at various times from mid September to November. Eggs were very opaque, yolky, brown and 250  $\mu$  in diameter. The chorion was much thicker than that of the egg attributed to *Scolecopsis* (above) with both a reticulate surface pattern and prominent vesicles. The eggs probably belong to *Laonice cirrata*, a few specimens of which were collected around the Biological Station. Ripe adults collected in early summer were filled with very yolky, brown eggs 230  $\mu$  in diameter with a thick chorion. Hannerz (1956) describes the larvae of this species, but larvae matching his descriptions were not recovered from Passamaquoddy Bay.

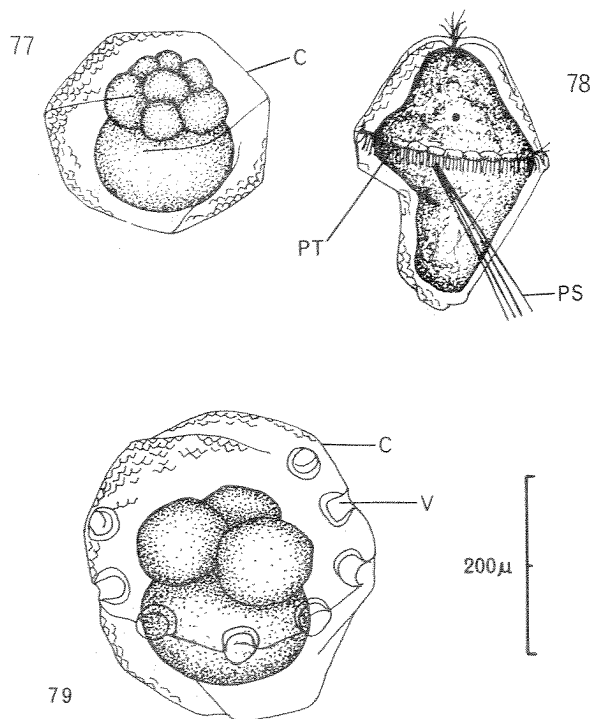


Fig. 77-78. *Scolecopsis squamata*  
 77. cleaving egg  
 78. 1-setiger larva enclosed in the egg membrane  
 Fig. 79. *Laonice cirrata*, cleaving egg

*Prionospio steenstrupi* Malmgren 1867

The third type of thick-membraned egg appeared in the plankton during the second week in May. These were translucent, whitish and 100  $\mu$  in diameter with a delicate and very faintly textured chorion. The planktonic eggs could be attributed to *Prionospio steenstrupi* by comparing them with unspawned eggs from the adult worms. These are found in large numbers in shallow mud along the lower St. Croix channel (Navy Island). Eggs and hatching stages were recovered from the plankton throughout May and early June. The hatching stage was 200-250  $\mu$  long with a transparent body and small red eyes, so dark as to appear black in some cases. The two anal cirri are characteristic. Advanced stages were common from late June through July, and could be recovered as late as mid August. The larvae were extremely abundant in early July, sometimes comparable in numbers to the April outburst of *Harmothoe* larvae. Advanced *Prionospio* larvae can be easily distinguished from all the other spionid larvae mentioned here by their extreme length and slenderness, by the presence of four anal cirri, and by the shortness of the palps in all but the most advanced stages. *P. steenstrupi* larvae are unpigmented, though the head and pygidium may develop an orange tinge in older larvae. The larvae swim very rapidly and coil into a tight ball with their setae directed outward when disturbed.

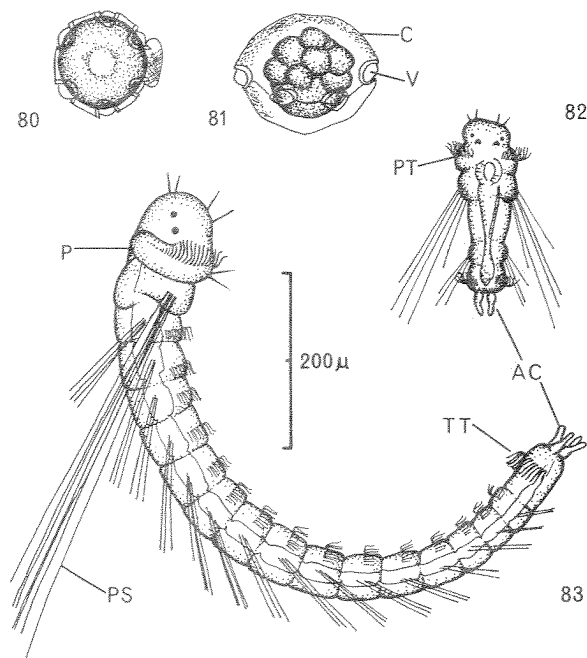


Fig. 80-83. *Prionospio steenstrupi*  
80. unfertilized egg  
81. cleaving egg  
82. newly hatched setigerous larva  
83. advanced pelagic stage

Family SYLLIDAE Grube 1850

*Autolytus* sp.

Four species of *Autolytus* were found in the Bay: *A. cornutus*, *A. fasciatus*, *A. prismaticus* and *A. alexandri*. The benthic stem form of *A. cornutus* was abundant subtidally on rocks and hydroids while other *Autolytus* species were found mainly as swimming stolons. Figures 84-89 illustrate gastrulae and larvae of various species. According to Pettibone (1963) the reproductive stolons are produced during the whole year in all four species, but are produced more rapidly and so are more abundant in the summer months. The only other syllids recovered in any numbers from benthic habitats were species of minute mud-dwelling forms such as *Exogone hebes*, *Exogone verugera*, *Parapionosyllis longicirrata* and *Sphaerosyllis erinaceus*.

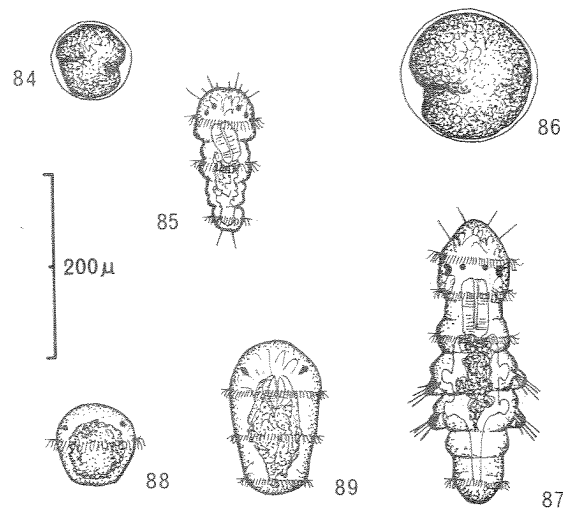


Fig. 84-89. *Autolytus* sp., gastrulae and larvae taken from the brood sacs of swimming stolons  
84-85. *A. cornutus*  
86-87. *A. alexandri*  
88. *A. fasciatus*  
89. *A. prismaticus*

# ACKNOWLEDGMENTS

This work was carried out during a 1-yr stay, from September 1973 to September 1974, at the Huntsman Marine Laboratory and during shorter visits in the springs of 1973, 1975 and 1977. The original research was supported by the National Research Council of Canada. The National Museums of Canada assisted in preparing the manuscript, and funds for publication were provided by Fisheries and Environmental Sciences, Biological Station. St. Andrews. The author thanks the Director and staff of the Biological Station and of the Huntsman Marine Laboratory for assistance with the research, and Drs. Joan Marsden, John Calaprice, Dan Faber and David Wildish for encouragement and assistance with the compilation of the information. The figures were prepared with the help of Mr. David Y. W. Wong.

## REFERENCES

- Akesson, B. 1973. Reproduction and larval morphology of five *Ophryotrocha* species (Polychaeta: Dorvilleidae). Zool. Scr. 2: 145-155.
- Agassiz, A. 1867. On the young stages of a few annelids. Ann. Lyc. Nat. Hist. New York 8: 303-342.
- Bass, N. R., and A. R. Brafield. 1972. The life cycle of the polychaete *Nereis virens*. J. Mar. Biol. Assoc. 52: 701-726.
- Blake, J. A. 1969. Reproduction and larval development of *Polydora* from northern New England (Polychaeta: Spionidae). Ophelia 7: 1-63.
1975. The larval development of Polychaeta from the northern California coast III. Eighteen species of Errantia. Ophelia 14: 23-84.
- Cazaux, C. 1967. Développement larvaire de *Glycera convoluta* Keferstein. Vie Milieu, Ser. A., 18: 559-572.
1968. Etude morphologique du développement larvaire d'annélides polychètes (Bassin d'arcachon). I. Aphroditidae, Chrysopetalidae. Arch. Zool. exp. gén. 109: 477-543.
1969. Etude morphologique de développement larvaire d'annélides polychètes (Bassin d'arcachon). II. Phyllodocidae, Syllidae, Nereidae. Arch. Zool. exp. gén. 110: 145-202.
1972. Développement larvaire d'annélides polychètes (Bassin d'arcachon). Arch. Zool. exp. gén. 113: 71-108.
- Curtis, M. A. 1977. Life cycles and population dynamics of marine benthic polychaetes from the Disko Bay area of West Greenland. Ophelia 16: 9-58.
- Grassle, J. P., and J. F. Grassle. 1976. Sibling species in the marine pollution indicator *Capitella* (Polychaeta). Science 192: 567-569.
- Hannerz, L. 1956. Larval development of the polychaete families Spionidae (Sars), Disomidae (Mesnil) and Poecilochaetidae (N. fam.) in the Gullmar Fjord (Sweden). Zool. Bidrag. Uppsala 31: 1-204.
- Hoglund, L. B. 1951. Notes on the morphology and biology of some *Spirorbis* larvae. Zool. Bidrag. Uppsala 29: 216-276.
- Ketchum, B. H., and D. J. Keen. 1953. The exchanges of fresh and salt waters in the Bay of Fundy and in Passamaquoddy Bay. J. Fish. Res. Board Can. 10: 97-123.
- Klawe, W. L. 1955. The biology of the bloodworm *Glycera dibranchiata* Ehlers, and its relation to the bloodworm fishery of the Maritime provinces. MA Thesis, Univ. Toronto.
- Newell, G. E. 1951. The life history of *Clymenella torquata* (Leidy) Polychaeta. Proc. Zool. Soc. Lond. 121: 561-586.
- Noyes, G. S. 1970. The biology of *Aglaophamus neotenus* (n. sp.) (Polychaeta: Nephtyidae) from Maine. M.Sc. Thesis, Univ. Maine at Orono.
1980. The biology of *Aglaophamus neotenus* (Polychaeta: Nephtyidae). A new species from Maine and Canada. Biol. Bull. 158: 103-117.
- Pettibone, M. H. 1957. Endoparasitic polychaetous annelids of the family Arbellidae with descriptions of new species. Biol. Bull. 113: 170-187.
1963. Marine polychaete worms of the New England region. I. Aphroditidae through Trochochaetidae. Bull. U.S. Nat. Mus. 227: 1-356.
- Rasmussen, E. 1956. Faunistic and biological notes on marine invertebrates. III. The reproduction and larval development of some polychaetes from the Isefjord, with some faunistic notes. Biol. Meddr. 23: 1-84.
1973. Systematics and ecology of the Isefjord marine fauna (Denmark). Ophelia 11: 1-495.
- Richards, T. L. 1967. Reproduction and larval development of the polychaete *Stauronereis rudolphi* including a summary of development in the superfamily Eunicidae. Mar. Biol. 1: 124-133.
- Rothlisberg, P. C. 1974. Reproduction in *Spirorbis* (*Spirobella*) *marioni*. J. exp. mar. Biol. Ecol. 15: 285-297.
- Rowe, V. L. 1970. The reproductive biology and ecology of maldanid polychaetes from Passamaquoddy Bay, New Brunswick. M.Sc. Thesis, Univ. Waterloo.
- Rowe, V. L., H. B. N. Hynes, and A. V. Tyler. 1975. Reproductive timing in the polychaetes *Clymenella torquata* and *Praxillella praetermissa*. Can. J. Zool. 53: 293-296.
- Simon, J. L. 1967. Reproduction and larval development of *Spio setosa* (Spionidae: Polychaeta). Bull. Mar. Sci. 17: 398-431.

1968. Occurrence of pelagic larvae in *Spio setosa* Verrill (Polychaeta: Spionidae). Biol. Bull. 134: 503-515.

Snow, D. R. 1972. Some aspects of the life history of the nereid worm *Nereis virens* Sars on an intertidal mud flat at Brandy Cove, St. Andrews, New Brunswick. M.Sc. Thesis, McGill Univ.

Sveshnikov, V. A. 1960. Pelagic larvae of some Polychaeta in the White Sea. Zool. Zh. 39: 343-355.

1967. Larvae of archiannelids and polychaetes of the Possjet Bay (Sea of Japan). Explor. Fauna Sea 5: 125-129.

Thorsen, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound (Øresund). Meddr. Komm. Danm. Fish. -og. Havunders. Ser. Plankton 4: 1-523.

82-4  
3-2