AN ABSTRACT OF THE THESIS OF

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Title: THE SWIMMING RESPONSE OF THE SACCONEREIS STAGE
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        OF AUTOLYTUS VARIUS TO CHANGES IN HYDROSTATIC
        _____

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The syllid polychaete Autolytus varius reproduces in the spring

and early summer in Yaquina Bay, Oregon. The fertilized female

epitokes, or Sacconereis, carry the developing eggs and larvae in a

ventral sac until the larvae are ready to be released; incubation

lasts 14 to 18 days in the laboratory. The effects of a small increase

in hydrostatic pressure on the activity of Sacconereis were tested.

When placed in a pressure vessel, these epitokes responded to in-

creases of 0.39 Bar by orienting dorsally and swimming upward,

and by increasing their swimming rate. Peak activity occurred in

the first minute after a pressure stimulus. Following this, there

was a period of accommodation until the epitokes returned close to

their normal level of activity; the period of accomodation lasted

around 11 minutes. When the pressure was released, the worms

either slowed their swimming rate, or they coiled and sank rapidly

to the bottom of the vessel. Decerebrate Sacconereis of A. varius did not respond to pressure stimuli. The Sacconereis of A. magnus and A. prismaticus, and the Polybostrichus of A. prismaticus demonstrated swimming responses similar to A. varius Sacconereis. Three other species of polychaetes did not respond to pressure changes. The hydrostatic pressure response is possibly an adaptation of a planktonic stage of a normally benthic animal.

The Swimming Response of the Sacconereis Stage
of Autolytus varius to Changes in Hydrostatic Pressure

by

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INTRODUCTION

Early Studies

The effects of pressure on living marine animals has been a

popular study since deep water forms were first brought up from

the ocean floor. The ship Talisman in 1882 and 1883 brought up

organisms from 6,000 meters (Johnson, Eyring and Polissar, 1954).

As a result of this expedition, P. Regnard began studying the effects

of pressure on some fresh water organisms in the laboratory, under

experimental conditions (Johnson, Eyring and Polissar, 1954). His

early studies tested the effects of pressure up to 1000 Bars, which is

the pressure of the deepest ocean trenches. The results of these

experiments by Regnard indicated that at 100 Bars the animals be-

came agitated, and at greater pressures they were tetanized.

Later Ebbecke (1935) used pressure of 100 to 600 Bars to test

the responses of several shallow water marine animals. In the 100

to 200 Bar range the animals generally increased their activity

while under pressure, and decreased their activity below normal

once the pressure was released. Above 100 Bars the animals went

into a coma or a contracted state.

Since these primary studies, pressure techniques and apparatus have improved. However, most of the experimental work has been directed toward the effects of pressures higher than that found in nature. Today, pressures of 10,000 to 100,000 Atmospheres can be used. Since I will be dealing with moderate pressure, I will not discuss further high pressure studies. The book by Johnson, Eyring and Polissar (1954) summarizes much of the high pressure technology up to that time. The effects of small and moderate pressures were neglected until more recently.

Recent interest stems from the suggestion by Hardy and Patton (1947) that Calanus finmarchicus, and possibly other animals that undergo vertical migrations, have a sense of depth. This sense of depth was subsequently found experimentally in decapod larvae by Hardy and Bainbridge (1951). They found that the zoea and megalopa larvae of Portunus and Carcinus responded to a pressure increase by swimming to the upper half of the pressure vessel. Responses were obtained at pressure increases of 0.5, 1.0, 1.5, and 2.0 Bars. About half of the larvae responded in each experiment. The authors also noted that no pressure receptor was evident.

Harris (1953) stated that animals without gas filled bladders could not perceive hydrostatic pressure variations. Teleost fish and some aquatic insects had previously been shown to respond to pressure changes. They had either gas bladders, hydrofuge

micropiles with sensory hairs, or modifications of the tracheal system (Harden-Jones and Marshal, 1953; Thorpe and Crisp, 1947). Harris reasoned that animals without gas had only nearly incompressible body fluids which probably could not be used as a sensing medium. He discredited the findings of Hardy and Bainbridge (1951) by stating that the response was only found in larvae, which were probably specialized.

In 1955, the responses of several marine planktonic animals to changes in hydrostatic pressure were reported (Knight-Jones and Qasim, 1955). Several animals showed a positive response, although no gas bubble receptor was seen. The following animals responded: The larva of Blennius pholis (Teleostei), the megalopa larva of Carcinides moenas and the corresponding stage of Galathea sp. (both Decapoda), Eurydice pulchra (Isopoda) and Caligus repax (Copepoda), Pleurobrachia pileus (Ctenophora), and several hydro-medusae: Phialidium hemisphericum, Gossea coryneta, and Eutima gracilis (Hydrozoa). Two species of polychaetes also responded. They were the larvae of Poecilochaetus serpens and the pelagic adults of Autolytus auranticus (Polychaeta). In this study, four animals showed no response: Calanus (Copepoda), Tomopteris (Polychaeta), Sagitta (Chaetognatha), and the larvae of Alloteuthis (Cephalopoda). The typical response shown by these animals when a pressure of 0.01 to 0.8 Bar was applied, was an increase in

activity with swimming directed dorsally. When the pressure was decreased or released, the animals became less active, or they became completely inactive and sank.

Qasim and Knight-Jones (1957) reported that Temora longicornis (Copepoda) and barnacle nauplii larvae (Cirripedia) were similarly pressure sensitive. However, these animals tended to move towards light at increased pressure, and away from light at decreased pressure. Pressure increase caused movement to the light source, whether it involved upward, downward, or horizontal swimming. Evidently, the pressure response of these animals also involved an orientation to light.

Baylor and Smith (1957) defined the range of experimental pressure changes as small changes of 10 psi or less (0.69 Bar); medium pressure of 30 to 500 psi (2.1 to 35 Bars); or high pressure of 750 to 6000 psi or above (52 to 420 Bars or above). They found that responses of plankton crustaceans to pressure changes occurred in the small and moderate ranges. However, in the high range, paralysis and death occurred in minutes after the onset of pressure. The conversion factors for pressure units are found in Table 1.

In the low pressure range, Baylor and Smith (1957) found that most plankton animals were sensitive to pressure increases of 2 to 10 psi (0.14 to 0.69 Bar). The most sensitive animals they found were some unidentified pteropods that responded to pressure

increases as small as 0.1 psi (0.007 Bar or 7 millibars). They also

noted that the pressure sensing mechanism is delicate, and is easily

destroyed. When the pressure was maintained at 15 to 30 psi (1.5

to 2.1 Bars), the barosensitive mechanism was sometimes destroyed.

Since Harris (1953) had stated that a gas receptor would be neces-

sary, the animals were subjected to a vacuum, so that the water in

which they were placed boiled at room temperature. Theoretically,

any baroreceptor containing gas would expand and become visible,

or would change the buoyancy of the animals by its expansion. How-

ever, the animals showed no change in buoyancy, nor did any

bubbles form within the animals. Baylor and Smith (1957) felt that

this was a satisfactory proof that a gas receptor was not present.

The papers that I have just discussed were some of the first

ones that dealt experimentally with the responses of marine inverte-

brates to changes in hydrostatic pressure. Subsequently, several

authors began work in this area. To summarize the more recent

works, I will survey the problem by topic rather than by individual

papers.

Animals Observed

The list of animals responding to small pressure changes is

now extensive. The papers by Rice (1964), and by Knight-Jones and

Morgan (1966) have summarized the animals tested. Without

mentioning the many species involved, the groups that contain responding animals are the following: Hydrozoa (hydromedusae), Siphonophora, Scyphozoa, Ctenophora, Polychaeta, Copepoda, Cirripedia, Cumacea, Isopoda, Amphipoda, Mysidacea, Decapoda, Pycnogonida, Mollusca, Pisces, and Insecta. Both adults and larval forms are well represented in the above list. It includes not only planktonic adults and larvae, but also a few benthic and littoral species.

A few polychaetes have been observed. Baylor and Smith (1957), reported that several small pelagic annelids responded to pressure increases of 2 psi (0.14 Bar). Unfortunately, the worms were not identified. Knight-Jones and Qasim (1955) reported that the larvae of Poecilochaetus serpens responded to pressures of 0.8 Bar. Two species of Nephtys responded to a pressure decrease by stopping swimming activity (Knight-Jones and Morgan, 1966). Pressure changes appear to alter the release of larvae from Spirorbis borealis adults (Knight-Jones and Morgan, 1966). The pelagic polychaete Tomopteris helgolandica has been subjected to pressure by several authors, but has been unresponsive (Knight-Jones and Qasim, 1955; Rice, 1964; Knight-Jones and Morgan, 1966).

The polychaete Autolytus auranticus has been subjected to pressure increases. Only the pelagic adults were tested. Initially Knight-Jones and Qasim (1955) reported that the pelagic adults

responded to a pressure increase of 0.8 Bar. Knight-Jones and

Morgan (1966) subjected the pelagic adults to pressure increases of

1.0 Bar for a short duration of time; they responded by swimming

upward.

Threshold and Experimental Pressure

The threshold is the minimum pressure increase or decrease

necessary to bring about a response. Knight-Jones and Morgan

(1966) stated that the minimum pressure changes needed to elicit

overt responses were usually considerably larger than the threshold.

For this reason, the experimental pressures have been larger than

the reported threshold, and have varied in magnitude. Hardy and

Bainbridge (1951) originally subjected various decapod crustaceans

to 0.5 to 2.0 Bars. Baylor and Smith (1957) found a threshold of

0.007 Bar for an unidentified pteropod, and Knight-Jones and Qasim

(1955) used 0.8 Bar usually, but thresholds of 0.005, 0.01 and 0.05

Bar were also found for a few crustaceans, coelenterates, and poly-

chaetes. Enright (1961, 1962) found that sudden increases of 10

millibars (0.01 Bar) were sufficient to elicit a response in the amphi-

pod Synchelidium, and used pressures of 10 to 100 millibars (0.01 to

0.1 Bar) in his experiments. Bayne (1963) used pressures from 0.5

to 1.6 Bars to study Mytilus edulis larvae. Digby (1961a) used

pressures of 2.8 to 6.9 Bars on the prawn Paleomonetes. Rice (1962,

1964) used pressures of 0.5 to 1.0 Bar, and mentioned that he often
had only a 50% response with <u>Calanus</u> <u>finmarchicus.</u> In the experi-
ments with <u>Autolytus</u> <u>auranticus</u> adults, Knight-Jones and Qasim
(1955) used 0.8 Bar, and Knight-Jones and Morgan (1966) reported
pressure of 1.0 Bar. There has been no uniformity or consistency
in the experimental pressures used.

Pattern of the Pressure Response

The basic pattern of the response to a pressure increase,
which is similar in most cases, consists of increased activity fol-
lowing increased pressure. Peak activity occurs immediately after
the pressure increase and may remain at a high level while pressure
is maintained (Hardy and Bainbridge, 1951; Rice, 1961; Digby,
1967), or may decrease regularly while pressure is applied (Enright,
1961, 1962). The amphipod studied by Enright (1962) accommodated
rapidly to a pressure increase, and after a brief activity period,
returned to its normal state. Knight-Jones and Morgan (1966) stated
that rapid accommodation is probably not well developed in truly
planktonic animals, although most seem to show some accommodation.

Although accommodation may not be present in the responses of
some animals, it may not have been noticed in the studies where the
time period that pressure was applied was short, or where the study
dealt only with the initial vertical response (Baylor and Smith, 1953;

Knight-Jones and Qasim, 1955; Bayne, 1963). Some investigators have also correlated activity and accommodation under experimental pressure with tidal cycles (Rice, 1961; Enright, 1962; Morgan, Nelson-Smith and Knight-Jones, 1964; Morgan, 1965). However, most experiments have dealt only with the initial response of the animals when a sudden increase in pressure was applied for a short period of time, and was then released.

Once pressure was released, the animals either became inactive and sank, slowed their activity to the pre-pressure rate or below, or swam actively downward (Rice, 1964; Knight-Jones and Morgan, 1966). The activity after pressure release may be close to the pre-pressure activity (Hardy and Bainbridge, 1951; Rice, 1961; Enright, 1962), or the new steady state may be below the previous pattern (Knight-Jones and Morgan, 1966).

Apparently the pattern of variation of activity with pressure increases is similar in many animals (Knight-Jones and Morgan, 1966). The portion of the basic response pattern that has been most studied has been the initial response of increased activity following an experimental pressure stimulus.

Mechanisms of Pressure Sensitivity

Receptors for pressure sensitivity have not been positively

identified, and the several theories conflict with one another. Since

a gas receptor of any size has not been seen by investigators who

have looked for it, this does not seem likely to exist (Knight-Jones

and Qasim, 1955; Baylor and Smith, 1957; Enright, 1962; Morgan,

1965). Also, when the animals were placed under a vacuum, no

bubble became visible, and there was no change in buoyancy in the

animals (Baylor and Smith, 1957; Enright, 1962). The animals were

as sensitive to small changes in pressure when they were at high

pressures as when they were at low pressures (Enright, 1963). Any

gas receptor, theoretically, would be compressed at high pressure,

and the response lowered (Enright, 1963; Knight-Jones and Morgan,

1966). Digby (1961a, 1961b, 1965, 1967) has published several

papers proposing that the pressure response is due to a very thin

layer of adsorbed gas on the surface of crustacean cuticle. Enright

(1963), however, believed that crustaceans are less compressible

than sea water, and that proprioceptors in the flexible membranes

between exoskeletal junctions sense any tension. Enright (1963) also

believed that Digby's hypothesis did not adequately account for sensi-

tivity to very small pressure changes.

The pressure sensing mechanism is also sensitive to mechanical

disturbances, and may be destroyed by them. Baylor and Smith
(1957) noted that the barosensitivity of plankton was destroyed when
increases of 15 to 30 psi (1.0 to 2.1 Bars) were maintained for a few
minutes. Recovery of sensitivity did not occur within a week. Rice
(1964) also stated that pressure sensitivity may have been destroyed
by handling. These observations agree very much with the theories
of Digby, who believed that the pressure sensitive mechanism is a
surface or integumentary phenomenon using adsorbed gas (Digby,
1961a, 1961b, 1965, 1967). This evidence indicates the importance
of care in the handling of experimental animals.

Reproductive Stages

In the experiments that have been performed, only pelagic
larvae, pelagic or benthic developmental stages, and adults, with no
reference to the sexual condition of the adults, have been tested. For
only Spirorbis borealis has a reproductive individual been involved
(Knight-Jones and Morgan, 1966). Here, an experimental pressure
of tidal amplitude delayed the release of these polychaete larvae that
were being retained and incubated by the adult. Other reproductive
stages, such as the pelagic epitokes of other polychaetes, have not
been tested.

Many polychaetes undergo epitoky, which is the formation of a
sexual individual. Gidholm (1967a) has redefined the different terms

involved, particularly in the Autolytinae. He defines epitoky as a term referring to the secondary sexual characteristics in general. Epigamy occurs when the whole worm transforms to the mature sexual form; nereids commonly produce epigamous epitokes. Schizogamy is then defined as reproduction by stolons, which is the epitokous transformation and the budding off of part of the adult to form a free swimming, sexual individual. Schizogamy may be scissiparous, where a single stolon is formed at the posterior of the adult, or gemmiparous, where several reproductive individuals are formed at one time (Gidholm, 1967b). All of the free swimming forms are commonly referred to as epitokes, although special terms may be used.

Special names have arisen many times when the reproductive individual was originally placed in a separate genus. Just as metamorphosed Nereis epitokes were originally described as the genus Heteronereis, the sexual stolons of Autolytus were first described as the genera Sacconereis and Polybostrichus, according to Dales (1963). The epitokes of Autolytus are dioecious and sexually dimorphic. The Sacconereis stage of Autolytus is the female epitoke, and the Polybostrichus is the male epitoke. The females, or Sacconereis, of Autolytus carry fertilized eggs and developing larvae in a ventral brood sac secreted by the female after mating (Gidholm, 1965). Most of the Autolytinae form reproductive individuals by schizogamy,

either by scissiparity or gemmiparity, although some are produced

epigamously (Gidholm, 1963, 1967a).

Purpose and Scope of the Thesis

In this thesis, I hope to establish the basic type of response of

Autolytus varius to experimental changes in hydrostatic pressure,

and to relate this as an adaptive feature in the life history of this

worm. Most of the experiments deal with the basic responses of

the Sacconereis stage of A. varius to increases in hydrostatic pres-

sure, although I have completed some shorter tests with the

Sacconereis of A. magnus, and both epitokes of A. prismaticus.

Three additional genera of polychaetes were also tested qualitatively

to evaluate the hypotheses involved. I will attempt to correlate

quantitative and qualitative material with the ecology of reproduction

of Autolytus varius and other polychaetes in a tidal estuary.

MATERIALS

The Experimental Animals

Autolytus is a polychaetous annelid of the Family Syllidae Grube, the Subfamily Autolytinae Rioja, and the Genus Autolytus Grube (Imajima and Hartman, 1964). The Syllidae characteristically bud asexually to produce sexually dimorphic reproductive stages.

Autolytus varius

The Sacconereis of this species was first described by Tread-well (1914), from San Francisco Bay. It has also been reported from Puget Sound (John, 1960), and from Canada, near Nanaimo, B. C. (Berkeley and Berkeley, 1938). Neither the Polybostrichus nor the adult have been described. The Sacconereis was the principle ex-perimental subject in this study.

Autolytus magnus

The Sacconereis of this species was first described by E. Berkeley (1923), from the Nanaimo, B. C. region. A. magnus closely resembles A. varius, and I was fortunate to have both for comparison. A. magnus is widely distributed along this coast, from Alaska (Hartman, 1948), and Canada (Berkeley and Berkeley, 1938, 1945, 1948), to Puget Sound (John, 1960). Neither A. magnus

nor A. varius had been previously reported from Yaquina Bay,

Oregon, although Hartman and Reish (1950) reported finding speci-

mens of Autolytus sp.

Autolytus prismaticus

This species was first described from the Greenland coast by

Fabricius, 1780, as Nereis prismatica. It is found from Oregon

northward, and is also circumpolar in distribution (Berkeley and

Berkeley, 1948). Hartman and Reish (1950) reported that it was found

in Yaquina Bay in 1936. It has been reported from Puget Sound (John,

1960).

Exogone gemmifera

This small syllid polychaete was found in Yaquina Bay by

Hartman and Reish (1950). The females have the interesting repro-

ductive phenomenon of externally attached ova and zygotes. The ex-

ternal ova are a striking pink color. The eggs are retained on the

ventral side of the adults, which are free swimming for a time

(Viguier, 1883). The adults are normally benthic in mud (Hartman

and Reish, 1950). This species is widely distributed, and has been

recorded from Canada, the United States, Mexico, Europe, and the

Mediterranean.

Nereis pelagica neonigripes

This subspecies of the cosmopolitan Nereis pelagica has been reported from Yaquina Bay, and the Northeastern Pacific (Hartman and Reish, 1950). The adults are littoral, and the heteronereids swarm in shallow water, according to Berkeley and Berkeley (1948).

Armandia bioculata

This polychaete of the Family Opheliidae is common in Oregon (Hartman and Reish, 1950). It is distributed from Alaska to California. The adult is benthic in mud.

Collection and Maintenance

Collection

All the free swimming worms used were from the Port Dock five and seven facilities of Yaquina Bay, Oregon. I collected during the day and night, and at high and low tides. The most productive collections occurred at the evening high tides. The worms were removed from the surface of the water with a hand dip net, and were placed in an insulated container of water taken at the site of collection. At night, a sealed mast light was dipped into the water to illuminate the worms swimming on the surface, and to attract any worms in the area. The night-light illuminated many small worms

which were not seen during the day, such as <u>Autolytus</u> <u>prismaticus,</u>

<u>Exogone</u> <u>gemmifera,</u> and <u>Armandia</u> <u>bioculata.</u> The adults and stolons

of <u>A.</u> <u>prismaticus</u> were collected from <u>Obelia</u> sp. from the same Port

Docks. All worms were then taken to the Marine Science Center.

Laboratory Facilities

The Marine Science Center on Yaquina Bay, Oregon is well

equipped with laboratories, tanks, and a sea water system that

pipes water from the bay at 9 to 15°C. At the Center, I used two

rooms for the experiments, a wet laboratory with running salt water

and large tanks holding eighty gallons of water, and a cold laboratory

without running salt water. The larger Sacconereis (<u>A.</u> <u>varius,</u> <u>A.</u>

<u>magnus</u>) were maintained in the tanks in the wet laboratory. The

ambient temperature of the wet laboratory was 18 to 19°C, and that

of the cold laboratory was 11°C. Both were illuminated by overhead

fluorescent light. Readings of light reflected off white paper were

recorded on a Weston Master IV light meter with an arbitrary scale

of 0 to 1000. Sunlight varied between 500 to 800, sunset light was

10 to 25, and the two laboratories were 9 to 11. A small microscope

lamp produced a light intensity of 0.4. These readings gave only a

comparative idea of light conditions, but confirmed that the inten-

sities of the two fluorescent lighting systems were at a moderately

low level, and were close to sunset values.

Maintenance in the Laboratory

The large Sacconereis of A. varius and A. magnus were kept

in large fiberglass tanks equipped with running salt water. This gave

the animals adequate room to swim. The smaller worms were kept

individually in small glass dishes or fingerbowls in the cold labora-

tory, with enough water so that they could swim. The dishes were

covered with a lid or another dish to prevent evaporation. All the

animals remained active and survived well using the above methods.

Pressure Apparatus

After several models were made, I developed one which was

used in the experiments. Three different types were considered.

The first type was a glass tube, one meter long, with an I. D. of

3. 0 cm, stoppered at each end and set vertically. The tip of a

30 cc. syringe was inserted into the upper stopper. The second

type was a 70 cm. piece of half inch Tygon tubing arranged in a

circle, and connected to the syringe with a glass T-tube and a

piece of pressure tubing. The third type was constructed from

a 2000 ml. Erlenmeyer aspirator flask. The top of the flask was

sealed off with a solid rubber stopper during the experiments. A

piece of pressure tubing connected the aspirator flask to the syringe.

In all three types, the pressure was obtained by placing weights on the syringe, which connected to the experimental chamber. All bubbles were removed from the system. The weights used in the experiments were usually three-pound lead divers' weights, although some smaller weights were used to obtain the minimum threshold value for a response of Autolytus varius Sacconereis. The syringe, when supported by burette clamps, could support the weight of 21 pounds.

The final apparatus is illustrated in Figures 1 and 2. It consists of a 2000 ml. Erlenmeyer aspirator flask. The worms were introduced into the mouth of the flask, which was then sealed with a solid rubber stopper during the experiments. On top of the stopper was placed a small rectangle of three-quarter inch plywood. This piece of wood had two holes toward the edge. Brass bolts fit through the two holes in the wood and through two small pieces of half-inch plastic pipe, which are secured to the neck of the vessel by a stainless steel hose clamp. Once tightened, the bolts held the stopper securely against the internal pressure. Another small hose clamp secured the pressure tubing to the side arm of the flask. A third hose clamp secured the other end of the pressure tubing to the syringe. This end also had a piece of Tygon tubing between the pressure tubing and the tip of the syringe, to produce a tight connection. When air bubbles were removed, and about 20 cc. of water

Figure 1. Diagram of pressure vessel closure.

     a. Bolt.

     b. Board.

     c. Rubber stopper.

     d. Lip of 2000 ml. Erlenmeyer aspirator flask.

     e. Plastic pipe used to space bolt.

     f. Stainless steel hose clamp.

     g. Washer.

     h. Nut.

     i. Side arm of aspirator flask.

Figure 2. Diagram of hose attachment to side arm
           of flask.

     d. Lip of 2000 ml Erlenmeyer aspirator flask.

     f. Stainless steel hose clamp.

     i. Side arm of aspirator flask.

     j. Rubber pressure hose.

Figure 1. Diagram of pressure vessel closure.
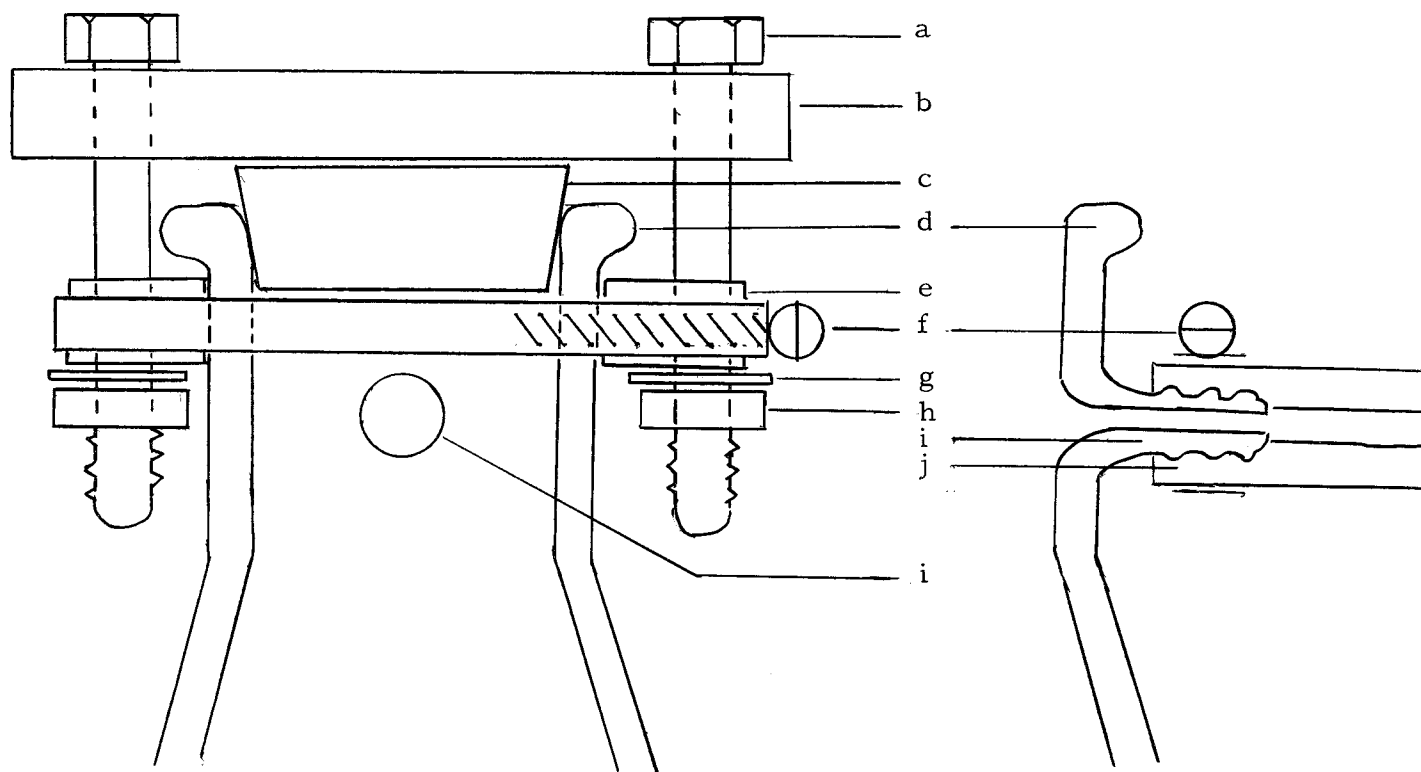
Figure 2. Diagram of hose attachment to side arm of flask.

was in the syringe, the system worked well without leaks or loss of pressure. This apparatus was similar to that of Enright (1961, 1962), who used 250 ml. Erlenmeyer flasks and 50 cc. syringes with weights, to obtain his pressures. The whole apparatus was supported by a ring stand and large burette clamps, and was portable.

EXPERIMENTAL PROCEDURES

Calibration of the Pressure Apparatus

Once assembled, the apparatus was calibrated by means of a volume compression depth gauge, which is simply a tube, open at one end, and initially filled with air. As the pressure increases, the air is compressed, and the tube fills partially with water. For example, at 33 feet depth the pressure is increased approximately one atmosphere, and any volume of air is compressed to one half the original volume. Using an S.O.S. Brand (Italy) depth gauge, which is made of plastic tubing, and a table provided in the U.S. Navy Diving Manual (U.S. Navy, 1963), I was able to construct a depth gauge from a glass tube, with a scale calibrated in feet depth. I was able to compare readings on the S.O.S. meter and my own meter. The readings of depth in feet were then converted to pressure in Bars and Atmospheres (Table 1).

Transfer of Animals

The pressure sensing mechanism of the animals is possibly sensitive to mechanical disturbances (Baylor and Smith, 1957; Rice, 1962, 1964). Care was taken in the handling of the animals. Although the animals were collected with hand dip nets, I did this as gently as possible. In the laboratory, when I was transferring

Table 1. Table of Pressure Conversion Factors. Based on Chemical
Rubber Co. (1958) Tables.

To Convert From	to	Multiply by
Bars	Atmospheres	0.9869
	Bayres	1×10^6
	Cm. of Hg. (0°C.)	75.01
	Dynes/sq. cm.	1×10^6
	Ft. of Water (60°F.)	33.48
	In. of Hg. (32°F.)	29.53
	Kg./sq. cm.	1.0197
	Millibars	1000
	Pounds/sq. in.	14.50
Atmospheres	Bars	1.013
Bayres		1×10^{-6}
Cm of Hg. (0°C.)		0.013
Dynes/sq. cm.		1×10^{-6}
Ft. of Water (60°F.)		0.02988
In. of Hg. (32°F.)		0.03386
Kg./sq. cm.		0.9807
Millibars		0.0001
Pounds/sq. in.		0.06895

animals to the pressure vessel, utmost care was taken. I found that

I could transfer animals easiest by using a long piece of glass tubing

with a diameter of one centimeter. Holding a finger over one end of

the tube, I placed the other end in the water near a swimming ani-

mal. I then released the finger, and a column of water with the worm

rose into the glass tube for a few centimeters to the water level in

the tank. By placing my finger over the end again, I could withdraw

the worm and some water. I placed this tube and worm in the water

in the neck of the pressure vessel so that the level of the water in the

glass tube and the level of water in the vessel were the same. By

releasing my finger, I could withdraw the glass tube leaving the

worm and his column of water inside the pressure vessel relatively

undisturbed. This seemed to be satisfactory.

Timing Procedure

During most of the experiments with _Autolytus varius_ it was

necessary to time the swimming rate of the worms. I found that the

easiest way to do this was to watch the posterior of the Sacconereis.

The posterior, which is coiled ventrally while swimming, rocks

from side to side as undulatory body swimming movements are made.

The movements are easy to time in the posterior while anterior or

parapodial undulatory movements are more confusing due to adjacent

parapodial movements. To determine swimming rate, I timed ten

complete undulations of the posterior end with a stopwatch. Thus my units were seconds per ten body undulations or sec./10. I confirmed that the posterior movements were approximately the same as the other undulatory movements by timing and comparing the swimming rate of the various regions of the worm. Similar results were obtained.

The Dorsal Response of Autolytus varius

This experiment was designed to test whether the Sacconereis swims in an upward direction when the pressure is increased. Six to ten epitokes were tested at any one time. They were placed in the vessel, and the vessel was sealed. For several minutes, one reading every minute was taken of the number of epitokes swimming in the upper half of the vessel (e.g. six in the upper half of the vessel out of ten epitokes). When the worms were all swimming at steady rates, one weight was placed on the syringe. The positions of the worms were noted every minute, for four minutes. The pressure was then released (i.e. the weight was removed), and additional counts were taken. When the worms had again established a steady rate, the weight was again added and the test repeated. The number of trials with each group of worms varied, but usually there were three trials with each group.

The experiments on the dorsal response of Autolytus varius

were done in the cold laboratory in the dark. A small microscope lamp was temporarily lighted to count the number of animals in the upper half of the vessel. A total of 42 worms were tested. Including repetitions, 128 observations of responses to pressure increases were made.

A few observations were made while holding the dim microscope lamp in various positions in relation to the pressure vessel to ascertain any orientation change of the worms to the light. I also completed several tests with the overhead lights on, in the cold laboratory.

The Threshold of Autolytus varius

This short test was done to indicate the magnitude of the threshold necessary to effect a dorsal response of Autolytus varius. Six epitokes were tested. A 100 gram weight, a 1000 gram weight, and a three-pound lead divers' weight (1,362 gms.) were used, and had depth equivalents of 3, 9, and 13 feet. The pressure equivalents were 0.09, 0.27, and 0.39 Bar. The threshold is the minimum pressure required to elicit a response.

The Swimming Response of Autolytus varius

This experiment was designed to demonstrate whether A. varius increased its swimming rate when pressure was increased. In the

experiments, individuals were tested in the apparatus. The swim-ming rate was measured by counting the seconds elapsed for ten body undulations. An average swimming rate was taken from epi-tokes swimming in the maintenance tank in the laboratory, and from the pressure vessel before pressure increases. The animals were tested for their response to pressure increases of 0.39 Bar above atmospheric pressure. A total of 26 Sacconereis were tested, and 56 repetitions were completed at 0.39 Bar. Seventeen trials in-volving higher pressures were also completed.

The above trials were run for fifteen readings under pressure. It became evident that some of the worms were not accommodating within this time range. Extended readings were made on 12 worms for 35 repetitions. During these extended trials, pressure was main-tained until the epitoke returned to within two-tenths of his swimming rate before pressure had been applied. Thus, an epitoke swimming at 4.6 sec./10 before pressure was applied, would have accommodated under pressure when its swimming rate returned to a level of 4.4 sec./10. I also arbitrarily decided that the level had to be main-tained for two consecutive readings to be considered accommodation.

All the timings took place in the cold laboratory or in the wet laboratory. Timings were made with the room lights on. It was necessary to have the lights on in order to time the body movements. Subdued light was not adequate to accurately time the body movements,

as bright reflections from the setae made it difficult to concentrate on the body undulations of one body region.

The Response of Decerebrate Autolytus varius

Since A. varius epitokes have a well developed head, this experiment was performed to determine whether or not the head was necessary for the response. The heads of the epitokes were removed by placing the worms on moist filter paper, and cutting the head off with a razor blade, just behind the second pair of eyes. The animals were then placed individually in Stender dishes with filtered salt water. These worms were maintained in the cold laboratory. Two epitokes were amputated on May 22, 1968. They swam normally after the operation, and were tested that day. On June 12, thirteen epitokes were decephalized. These all swam normally after the operation. Two of these epitokes were tested on June 17, and the remainder were tested on June 22, and 23, 1968. Pressures of 0.39, 0.72, 1.05, and 1.36 Bars, were used. These experiments took place in the wet laboratory in the light. The experimental animals were visually checked for anterior regenerative growth, but none was evident.

The Response of <u>Autolytus varius</u> after a Vacuum

This experiment involved subjecting the epitokes to a vacuum before testing their responses to a pressure increase. Baylor and Smith (1957) and Enright (1962) subjected a few animals to a vacuum to test for a gas organ sensitive to pressure. I also tested a few animals to check this possibility. Eleven epitokes were placed under an aspirator vacuum for four minutes. Although the water was not boiling, dissolved gases were evolving from the water, and any gas bubbles in the worm would have expanded. The animals were observed for changes in activity and buoyancy, and for the appearance of internal bubbles. Following this, the animals were placed in the pressure vessel and tested for their swimming response to an increase in pressure of 0.39 Bar. No measurement of the degree of vacuum was made due to the lack of an adequate gauge. A total of eleven epitokes were tested in the wet laboratory with the lights on.

The Swimming Responses of Older <u>Autolytus varius</u> Sacconereis

As the epitokes were maintained in the laboratory, they aged, and the larvae in the ventral sac developed. After 12 to 14 days in the laboratory, the epitokes swam near the bottom of the tank in circles. After 14 to 22 days they attached themselves to the bottom of the tank. Since it was evident that they had lost some of their

swimming activity, I tested their response to a pressure increase

to compare it with the normal responses. I also observed any

changes in their orientation. A pressure of 0.39 Bar was used. A

total of 11 older Sacconereis were tested in the wet laboratory with

the lights on.

The Response of Autolytus varius to Pressure Release

Following the above experiments on normal responses of the

Sacconereis, the worms either coiled or slowed their swimming

rate, and sank when the weight was removed and pressure released.

I added data from the other experiments to compare the responses

of all the epitokes to this sudden decrease in pressure. Data taken

from the first and second experiments are found in Tables 4 and 5,

and in Figure 4.

The Responses of Autolytus magnus

Although only one specimen of this species was found, I was

able to test it. The swimming response to a pressure increase of

0.39 Bar was tested. I also observed the orientation of the animal.

Three repetitions were completed. These were done in the wet

laboratory with the lights on.

The Responses of <u>Autolytus prismaticus</u> Epitokes

Both the Sacconereis and Polybostrichus stages of this species were available. Two experiments were run to establish the responses of these epitokes to increases in pressure. Since the worms were small, the swimming movements were difficult to count or time. Their orientation and swimming rate were observed. The responses to a pressure of 0.39 Bar were tested in the wet laboratory with the lights on. Their response to the release of pressure was also noted. Nineteen female epitokes were tested in one experiment, and 20 male epitokes were tested in the other.

The Responses of <u>Autolytus prismaticus</u> Adults

These were the only adults, i.e. non-sexual stages, of the genus <u>Autolytus</u> I was able to locate. They were taken from <u>Obelia</u> sp. from the Yaquina Bay Port Docks. Berkeley (1923) also found the adults on <u>Obelia</u> sp. Most of the adults had incomplete posterior ends since epitokes had been formed and released recently. I also tested some stolons, or adults with the epitoke still attached. These stononiferous adults had a single posterior epitoke.

I tested the adults as I have tested other worms. When first placed in the apparatus, the adults wandered, but soon formed membranous tubes. They are found naturally in these tubes. Since

the worms were not swimming, I observed orientation and crawling.
The worms were tested in the cold laboratory in light and in dark.
A range of pressures from one to seven three-pound weights, or
0.39 to 2.40 Bars were used. Twenty adults were tested; six
stoloniferous adults were tested.

The Response of Exogone gemmifera

Exogone is a syllid polychaete that forms the reproductive epi-
toke epigamously. I tested the response of the swimming stage, be-
cause little sexual modification, other than the development of
swimming setae occurs. The pressure response was tested as in
the other experiments. From one to five weights, or pressures of
0.39 to 1.71 Bars were used. The tests were carried out in the wet
laboratory in the dark. Thirteen epitokes, four females and nine
males, were tested.

The Response of Nereis pelagica neonigripes

The heteronereis of the polychaete is likewise a reproductive
stage formed by epigamy from the adult. The five specimens were
tested individually in the pressure vessel. One to five weights, or
pressures of 0.39 to 1.71 Bars, were used. These experiments
were done in the wet laboratory in the light, and in the cold labora-
tory in the dark.

The Response of <u>Armandia bioculata</u>

As in <u>Nereis</u>, <u>Armandia</u> forms the reproductive stage by epigamy from the adult. These epitokes, however, are little modified from the adult. The only secondary sexual modifications are swimming setae. Two specimens were tested on June 11 and 23 specimens on June 16. One to three weights, or pressure of 0.39 to 1.05 Bars were used, both in the wet laboratory in the light, and in the cold laboratory in the dark.

DATA

Calibration of the Pressure Apparatus

Using the air compression depth gauge, I calibrated the pressure apparatus by adding three-pound weights one at a time. When seven weights were on, I then removed the weights one at a time. The procedure was repeated a second time. The S.O.S. brand (Italy) diver's gauge was also tested once for comparison. The data are summarized in Table 2. The data from the gauge are in the equivalent depth in feet. I converted feet to Bars and Atmospheres. Each three-pound weight had a depth equivalent of 11 feet, and a pressure of 0.33 Bar. Including the 0.06 Bar which registered due to the weight of the water and the syringe plunger, the experiments that used one weight were at a pressure of 0.39 Bar above atmospheric pressure, or an equivalent depth of 13 feet. A range to 80 feet or 2.40 Bars was possible with the apparatus.

Reproductive Cycles of Autolytus varius

On the basis of collections, there appear to be at least three seasonal reproductive cycles of Autolytus varius in Yaquina Bay. The largest collections were made on the evenings of April 23, 34 Sacconereis; May 16, 32 Sacconereis; and June 10, 1968, 30 Sacconereis. A total of 18 Sacconereis were collected in about 50

Table 2. Calibration of the pressure vessel.**

No. of weights	Pounds applied (lbs.)	Equivalent depth (feet)	Pressure (Bars)	Atmospheres pressure (Atm.)
0	*	2*	0.06	0.06
I	3	13	0.39	0.38
II	6	24	0.72	0.71
III	9	35	1.05	1.03
IV	12	46	1.38	1.36
V	15	57	1.71	1.69
VI	18	69	2.17	2.14
VII	21	80	2.40	2.36
0	*	2*	0.06	0.06

*Although no weight was applied, the weight of the water above the gauge in the vessel, and the weight of the syringe plunger accounted for this initial depth equivalent of two feet or 0.06 Bar.

**The readings shown here were taken from the depth gauge constructed from a glass tube. Nearly identical readings were taken from the S.O.S. Brand (Italy) divers' depth gauge.

other attempts extending through July, 1968. This totals 96 speci-

mens on the three evenings, and 114 specimens during the season.

Thus, 84% of the worms were collected on three occasions. Of the

18 remaining worms, 11 were collected at an evening high tide, and

seven were collected at daytime high tides.

In the laboratory, the Sacconereis lived 14 to 22 days before

they attached to the bottom of the tank, deposited the egg sac with

larvae, and died. The Sacconereis appeared to adhere to the bottom

using an adhesive from the egg sac.

The Dorsal Response of Autolytus varius

This experiment indicated the degree that the worms swam

dorsally when pressure was applied in the dark. The data are com-

piled in Table 3 and in Figure 3. The latter is a plot of time vs the

percent of the epitokes swimming in the upper half of the vessel.

Point M on the graph represents the mean number of animals swim-

ming in the upper half of the apparatus while not under pressure.

Times (minutes) 1 and 2 represent the two readings prior to the on-

set of pressure. Time 3, or point P_o is the first reading made as

soon as possible (about 30 seconds) after pressure was applied.

Time 4 is one minute later, and so on. The last three points repre-

sent the readings made after pressure was released. Point P_o indi-

cates that 90 percent of the epitokes were in the upper half of the

Table 3. Dorsal response of Autolytus varius.

Time (min.)	Pressure (Bar)	Epitokes in upper half of vessel		Worms coiling	
		No.	%	No.	%
M*	0.06	267/480	56	0	0
1	0.06	69/128	54	0	0
2	0.06	64/128	50	0	0
3 (P_o)**	0.39	115/128	90	0	0
4	0.39	107/128	84	0	0
5	0.39	100/128	78	0	0
6	0.39	95/128	74	0	0
7	0.06	58/99	59	29	23
8	0.06	42/78	54	50	39
9	0.06	25/52	48	76	59

*Point M represents a mean value established by readings from 42 epitokes measured 10 to 12 times each, in groups of six to ten. They were in the pressure vessel without pressure applied.

**Point P_o is the initial reading after the pressure stimulus was first applied.
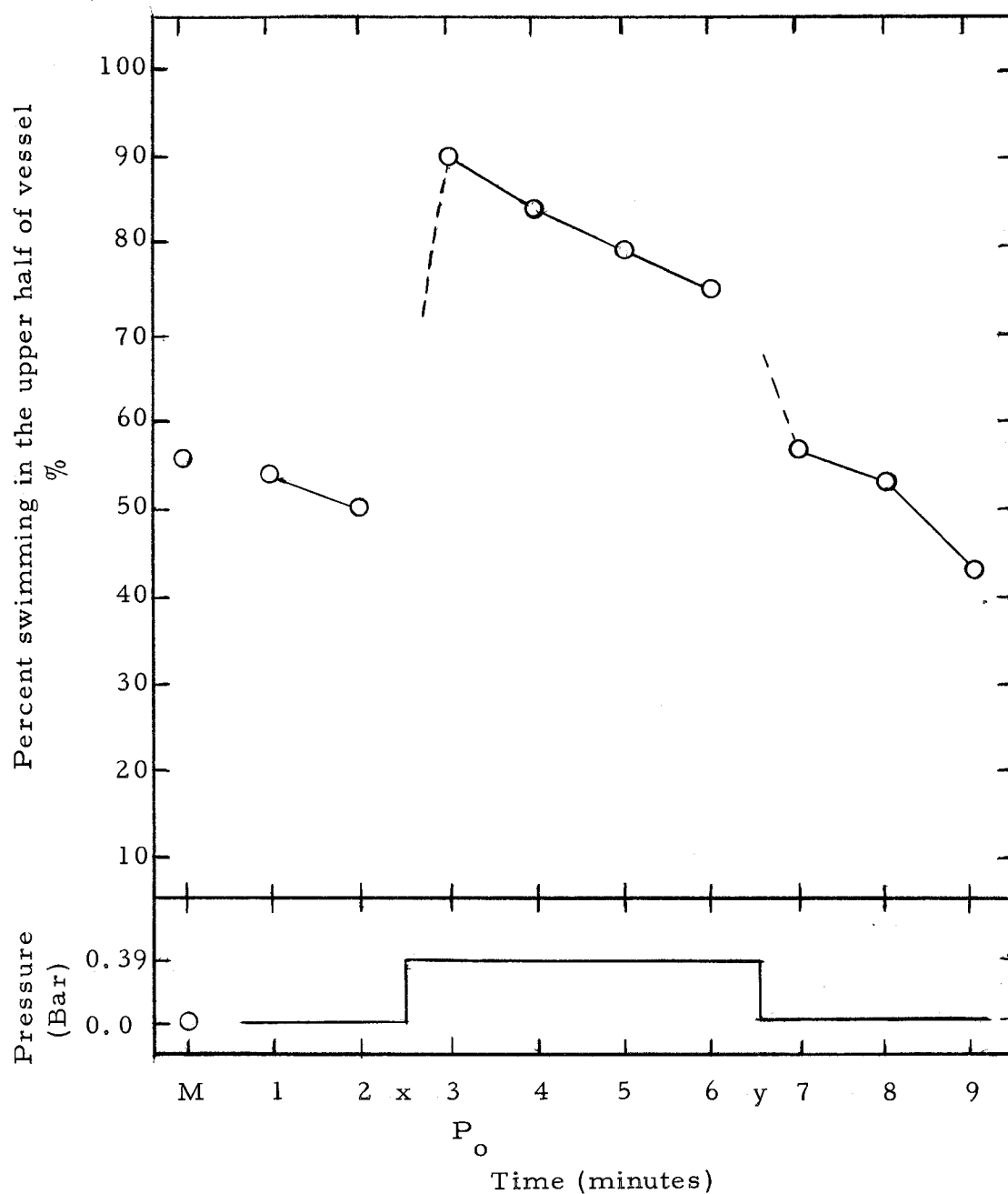
Figure 3. The dorsal response of <u>Autolytus</u> <u>varius</u> to a pressure in-
crease. Time vs. percent swimming in upper half of
vessel. Sacconereis swim upward when a pressure in-
crease is applied for four minutes. Point P_o is the first
reading taken after the pressure increase. Pressure
was applied at time x, and removed at time y.

vessel after the pressure stimulus. This compares with an average figure of 50 to 56 percent before the pressure addition. Times 4, 5, and 6, follow point P_o with a decreasing number of epitokes in the upper half of the apparatus. Following pressure release, a number of epitokes coiled and sank; this is recorded in Table 3. Of the epitokes still swimming, only 58 to 49 percent were still in the upper half of the vessel.

Observations on identical experiments in the light indicated that the response was the same. If the lights were turned on during an experiment, the epitokes would coil and sink for a few moments, and then return to their normal swimming. A dim microscope lamp, held at one side of the pressure vessel in the dark, modified the dorsal response in some of the worms, indicating a partial orientation to light.

The Threshold of Autolytus varius

As the different weights were applied, the number of epitokes making a dorsal response were recorded. With the 100 gram weight, or 0.09 Bar, two of the six epitokes responded. With the kilogram weight, or 0.27 Bar, all the epitokes responded, as they did with the three-pound weight. This is summarized again in Table 4.

Table 4. Threshold values.

No. of weights	Weight applied (gms.)	Equivalent depth (feet)	Pressure (Bars)	Worms responding (No.)
1	100	3	0.09	2/6
1	1000	9	0.27	6/6
1	1365	13	0.39	6/6

The Swimming Response of Autolytus varius

This experiment was designed to test the increase in swimming rate of Autolytus varius Sacconereis in response to a pressure increase. The data are compiled in Table 5 and plotted in Figure 4. The graph is a plot of the swimming rate of the epitokes vs. time in minutes; swimming rate is plotted on an inverted scale. On Table 5, M is the mean of 200 readings of twenty epitokes swimming in the maintenance tank. Times (minutes) 1 through 4 are the mean values for the four readings preceeding the onset of the pressure stimulus. Time 5 (P_o) is the mean of the first reading following the onset of pressure. The readings continued for 15 minutes. Following time 20 are eight points representing the swimming rate of the epitokes following pressure release. The proportion of epitokes that coiled and sank after pressure release is also indicated in Figure 4. The squares represent a plot of percent coiling vs. time.

Table 5. Swimming response of Autolytus varius.

Time (min.)	Pressure (Bar)	Mean swimming rate (sec./10)		Worms coiling	
		Rate	± s*	No.	%
M	0.00	4.4	0.5	0	0
1	0.06	4.7	0.6	0	0
2	0.06	4.6	0.5	0	0
3	0.06	4.6	0.6	0	0
4	0.06	4.6	0.6	0	0
5 (P_o)**	0.39	2.9	0.3	0	0
6	0.39	3.2	0.5	0	0
7	0.39	3.4	0.6	0	0
8	0.39	3.6	0.6	1	2
9	0.39	3.7	0.7	0	0
10	0.39	3.8	0.7	0	0
11	0.39	3.9	0.9	1	2
12	0.39	4.0	0.8	0	0
13	0.39	4.0	0.9	2	4
14	0.39	4.1	0.8	0	0
15	0.39	4.0	0.6	0	0
16	0.39	4.1	0.7	0	0
17	0.39	4.1	0.7	0	0
18	0.39	4.1	0.8	0	0
19	0.39	4.2	0.7	0	0
20	0.39	4.2	0.7	0	0
21	0.06	4.4	0.7	5	9
22	0.06	4.4	0.4	26	48
23	0.06	4.5	0.4	26	48
24	0.06	4.6	0.4	30	55
25	0.06	4.4	0.6	32	58
26	0.06	4.6	0.7	32	58
27	0.06	4.5	0.6	32	58
28	0.06	4.5	0.6	32	58

*The figures of the column headed by ± s are the standard deviations computed for each time interval. The formula $s = \sqrt{x^2/n-1}$ was used, where x is the deviation from the mean. When the square root of a number less than one was needed, the formula $1/1000 \ n = 1/100 \ \sqrt{10n}$ was used.

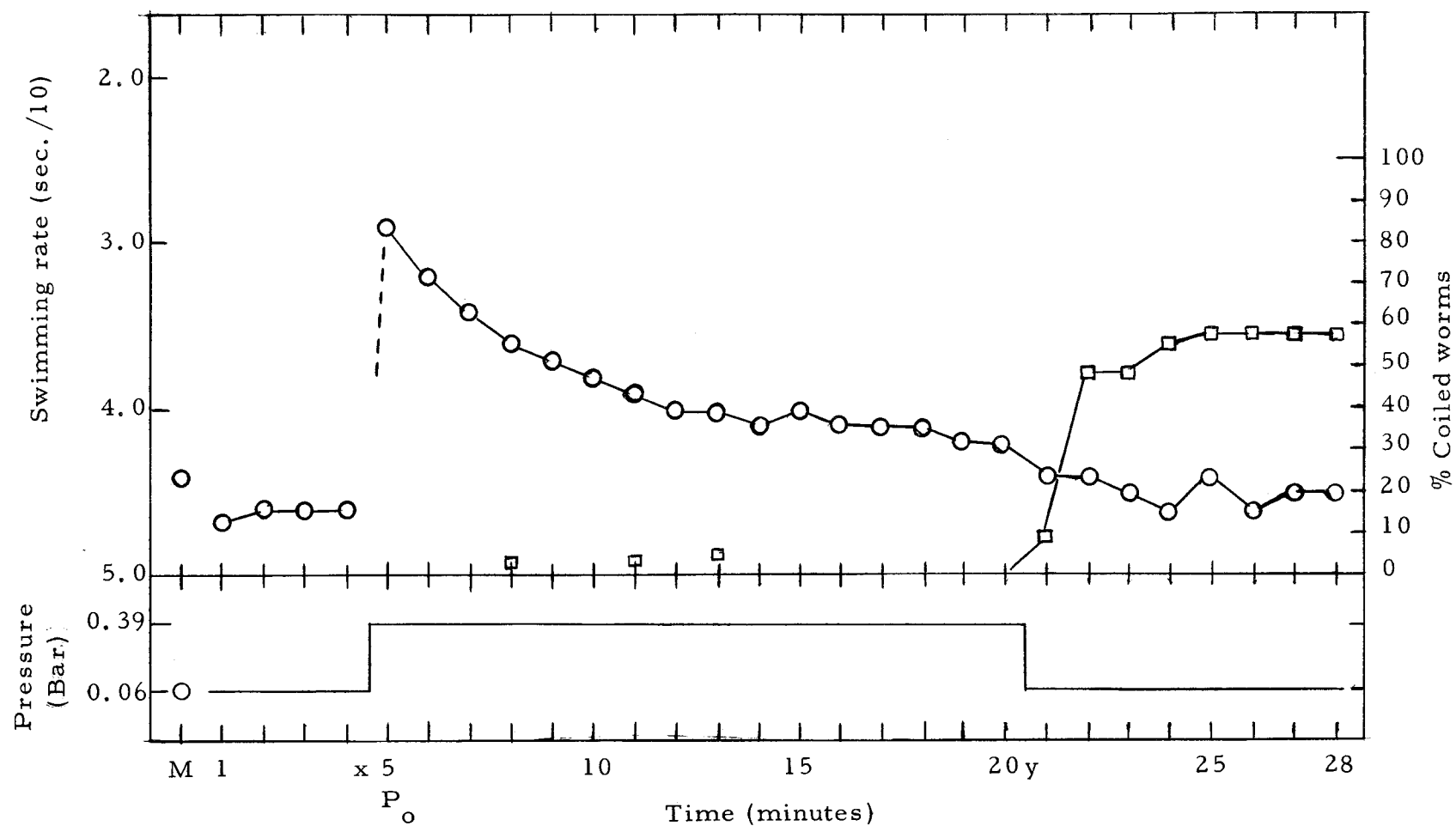**Point P_o is the initial reading after the pressure stimulus was first applied.

Figure 4. Swimming response of _Autolytus varius_. Time (minutes) vs. swimming rate (sec./10 undulations) vs. percent coiling (%). Pressure was applied at time x, and removed at time y. Squares represent coiled worms (%) vs. time.

The average swimming rate in the maintenance tank was 4.4 sec./10 undulations ± 0.5 (Point M, Table 5, and Figure 4). Point M is based on 200 readings of 20 epitokes; the other figures from Table 5 are based on timings of 56 repetitions of 26 worms. Time 4, immediately preceeding the beginning of the pressure stimulus, has a mean of 4.6 sec./10 ± 0.6. Time 5 (P_o) has a mean of 2.9 sec./10 ± 0.3; the standard deviation is low compared to other values of Table 5. The range of values from point P_o was from 2.0 to 4.0 sec./10. Even the slowest individual responded to a pressure stimulus to give the low value of 4.0 sec./10; at time P_o (5); at time 4 its rate was 6.0 sec./10. Times 6 through 20 indicate an accommodative decrease in swimming rate from 3.2 sec./10 ± 0.5 to 4.2 sec./10 ± 0.7. Times 21 through 28 also indicate a continued decline from 4.4 sec./10 ± 0.6 to 4.5 sec./10 ± 0.6, not including the 58% of the epitokes which had coiled. Since the decline in swimming rate between times 20 and 21 is small (4.2 to 4.4 sec./10), I cannot tell if this is a significant drop, which would be expected at the release of pressure. The extended-time experiments indicated that accommodation occurred in 11 minutes ± 8, while pressure was maintained.

Figure 5 is a frequency distribution of the components of point P_o compared with the frequency distribution of the normal swimming rate of the 200 readings of 10 epitokes in the maintenance tank.
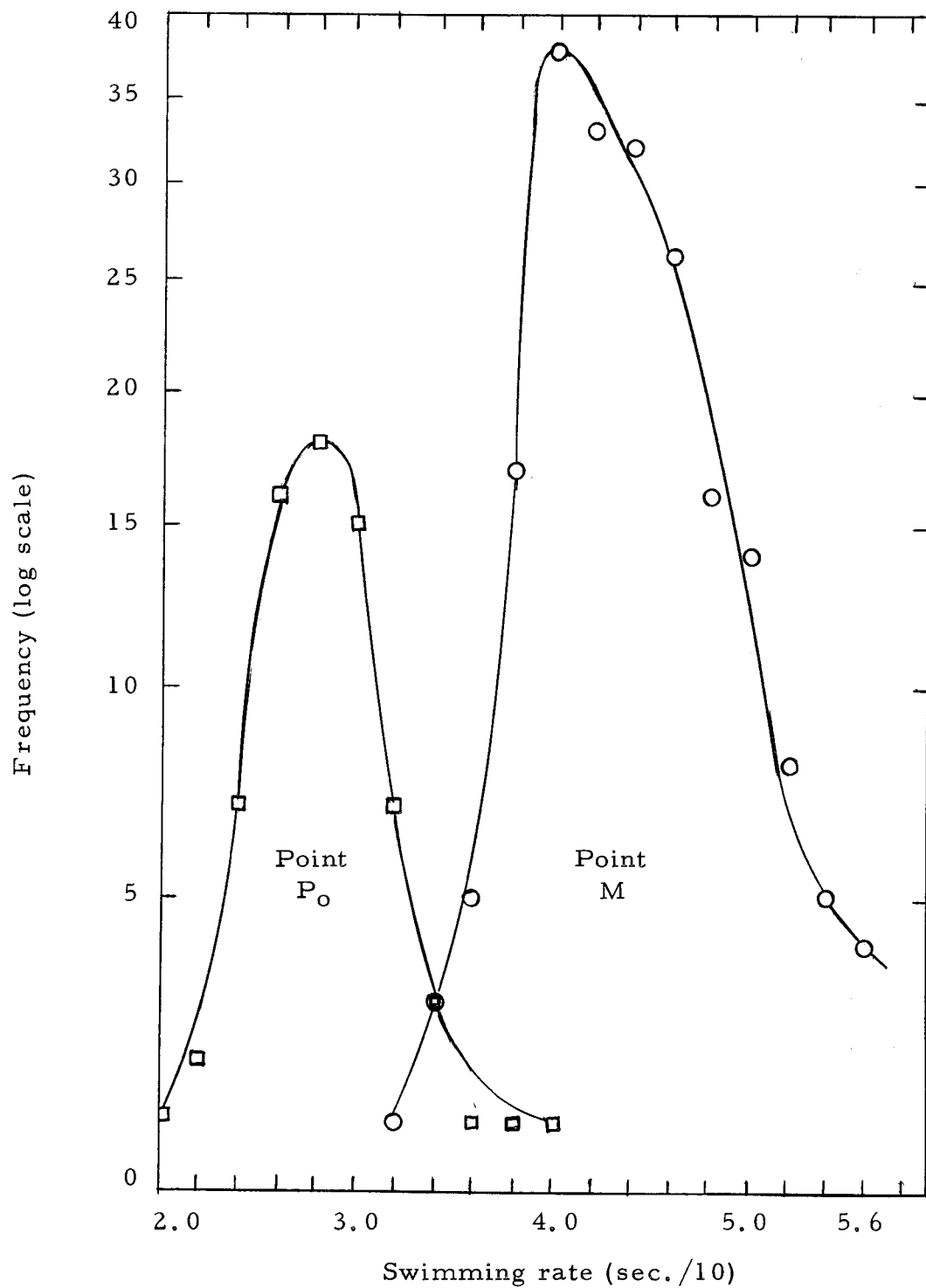
Figure 5. Swimming response of <u>Autolytus varius</u>. Frequency distribution of point P_0 and point M. Point M is the normal distribution of swimming rates. Swimming rate (sec./10 undulations) vs. frequency (log scale).

These are the components of point M of Table 5. Two separate

curves are plotted. A log scale was used on the frequency axis to

smooth the curves, and to reduce the size differences of the two

curves due to the different numbers of worms used. Fifty-six

readings were used in the first curve, and 200 were used in the

normal distribution. The mode of the P_o distribution is 2.8

sec./10; the mean is 2.9 sec./10. The mode for the normal distri-

bution is 4.2 sec./10; the mean is 4.4 sec./10. Only four percent

of the readings overlap at the base of the curves, and the standard

deviations do not overlap.

The Response of Decerebrate Autolytus varius

This experiment was similar to the previous experiment ex-

cept for the condition of the animals; Table 6 and Figures 6 and 7

follow the same plan as the previous ones. In Table 6, time M

represents 180 readings from 12 decephalized epitokes swimming in

individual dishes; fifteen readings were taken from each worm. The

remainder of Table 6 is based upon 32 readings from 15 epitokes.

Times 1 through 3 were taken without pressure; times 4 through 15

were under pressure; times 16 through 18 follow the release of

pressure. The means of the swimming rates of all these time inter-

vals range from 4.6 sec./10 undulations to 4.9 sec./10. The

standard deviations vary from $\pm$ 0.5 to $\pm$ 0.9. There is no large

Table 6. Response of decerebrate <u>Autolytus</u> <u>varius</u>.

Time (min.)	Pressure (Bar)	Mean swimming rate (sec./10)		Worms coiling	
		Rate	± s*	No.	%
M	0.00	4.7	0.6	21/180	12
1	0.06	4.8	0.6	3/32	9
2	0.06	4.8	0.6	2	6
3	0.06	4.6	0.6	6	18
4 (P_o)**	0.39	4.7	0.5	6	18
5	0.39	4.9	0.7	7	22
6	0.39	4.7	0.6	6	18
7	0.39	4.7	0.6	5	16
8	0.39	4.8	0.6	5	16
9	0.39	4.7	0.8	7	22
10	0.39	4.8	0.6	3	9
11	0.39	4.7	0.7	6	18
12	0.39	4.7	0.6	5	16
13	0.39	4.6	0.5	4	13
14	0.39	4.6	0.8	2	6
15	0.39	4.7	0.7	3	9
16	0.06	4.8	0.7	7	22
17	0.06	4.8	0.9	4	13
18	0.06	4.7	0.8	6	18

*The figures of the column headed by the figure "s" are the standard deviations computed for each time interval.

**Point P_o is the initial reading after the pressure stimulus was first applied.
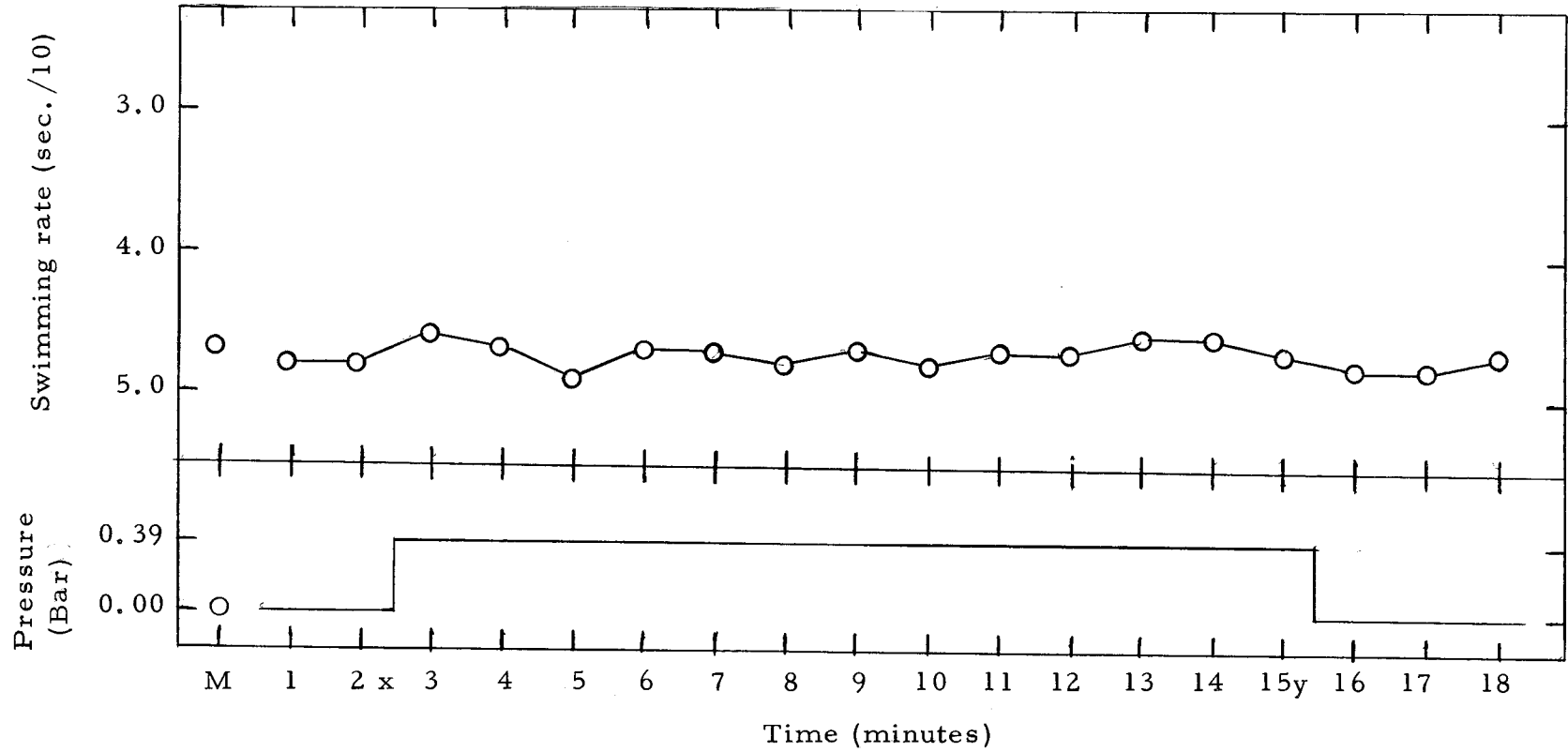
Figure 6. Response of decerebrate <u>Autolytus</u> <u>varius</u>. Time (minutes) vs. swimming rate (sec./10 undulations). Pressure was applied at time x, removed at time y.
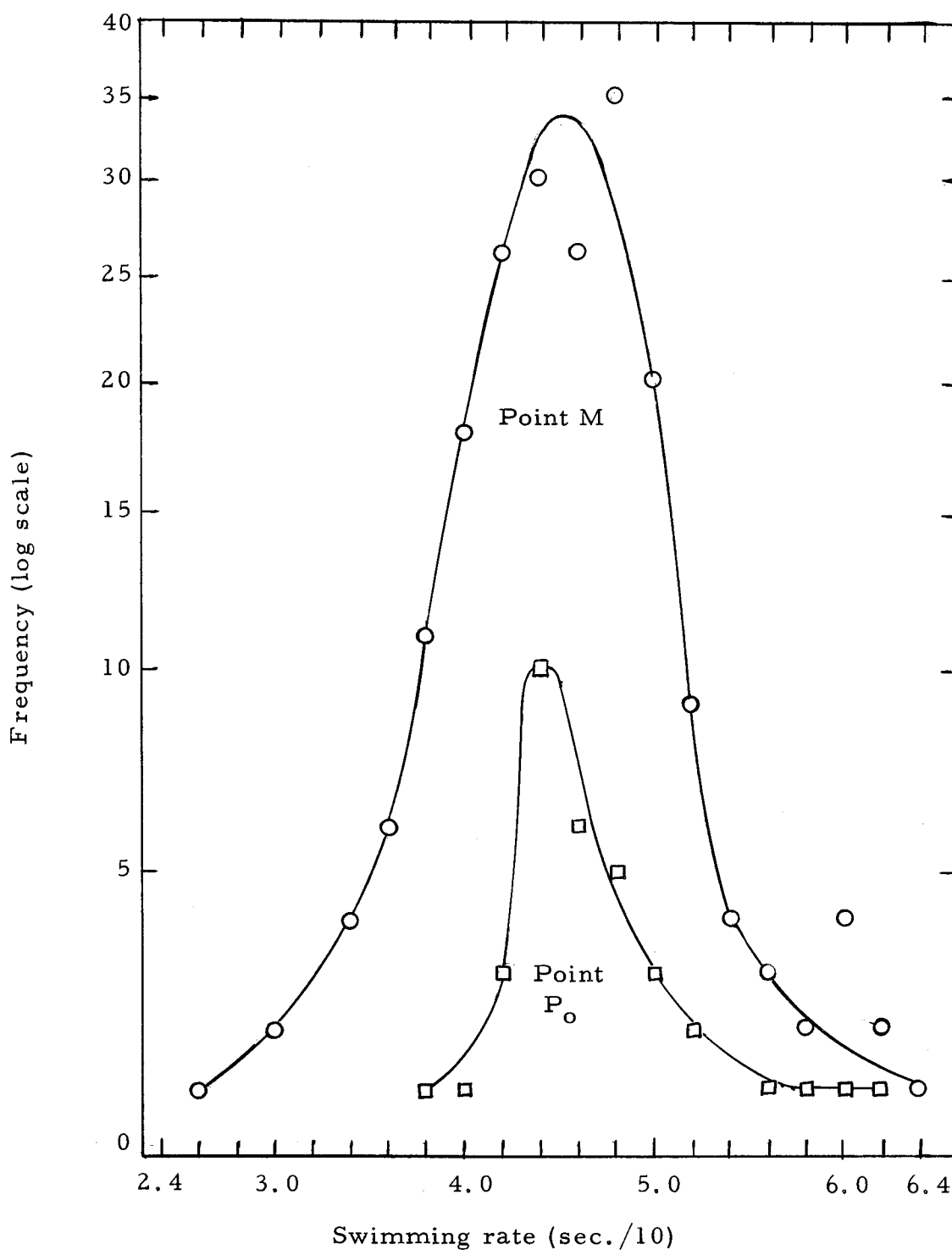
Figure 7. Response of decerebrate <u>Autolytus</u> <u>varius</u>. Frequency
distribution of point P_o and of Point M. Point M is the nor-
mal distribution of swimming rates of decerebrate
Sacconereis. Swimming rate vs. frequency (log scale).

fluctuation of swimming activity in these data comparable to that of normal epitokes given a pressure stimulus. Figure 6 is a plot of time vs. swimming rate for the decerebrate worms. Again, the swimming rate is uniform with time, considering the standard deviation. Figure 7 is a frequency distribution of time M and time 4 (P_o) from Table 6. Time M represents the normal swimming rate of decerebrate epitokes. The mean for time M is 4.7 sec./10 $\pm$ 0.6; the mode is 4.8 sec./10 undulations. The mean for time 4 (P_o) is 4.7 $\pm$ 0.5 sec./10; the mode is 4.4 sec./10. The distribution for point P_o is within the normal distribution of activity of decerebrate Sacconereis.

The number of epitokes coiling is also tabulated in Table 6. Coiling was much more frequent among the decerebrate epitokes. Coiling usually did not last longer than two or three minutes, however. The anterior end of the decerebrate worms appeared to be much more sensitive to disturbances, so that if a collision occurred with the vessel, the worm coiled and sank. Thus a low level of coiling was usually present. A high level of coiling after pressure release also did not occur, although a few epitokes seemed to be slightly agitated at the release of pressure.

The Response of Older Autolytus varius

The older A. varius Sacconereis normally swam in slow

circles near the bottom of the maintenance tank. Subsequently,

they attached themselves to the bottom of the tank by the adhesive

ventral brood sac, and deposited it. The sac then contained fully

developed larvae. The epitokes maintained slow swimming move-

ments for about 24 hours, while attached, and then died. In the

pressure apparatus, the older epitokes swam in circles near the

bottom, as they had done in the tank. When pressure was increased,

no dorsal response was evident. The swimming rate increased, but

they continued swimming in circles near the bottom of the vessel in-

stead of swimming dorsally. The mean swimming rate before pres-

sure increase was 4.8 sec./10, and was 3.6 sec./10 immediately

after. Accommodation was also evident while pressure was main-

tained. The swimming rate pattern was similar to that of normal

epitokes, but no dorsal orientation was observed.

The Response of Autolytus varius After a Vacuum

When the worms were first subjected to a moderate vacuum,

they were agitated, but no internal bubbles or changes in buoyancy

were evident. There was an increase in swimming rates, but no

definite orientation change in the epitokes. Subsequently, when they

were placed in the pressure vessel, their responses to an increase

in pressure were similar to those described above in swimming rate

and dorsal response.

The Swimming Response of Autolytus magnus

The experiments were with only one individual Sacconereis.

This species, which has a slightly larger Sacconereis, responded

similarly to increases and decreases in pressure. A dorsal response,

and an increase in swimming rate occurred, followed by an accommo-

dative decrease in the response while pressure was maintained. A

slowing of the swimming rate also occurred to a small degree when

pressure was released.

The Responses of Autolytus prismaticus Epitokes

I was able to make observations and to confirm that these epi-

tokes responded similarly to those of A. varius. However, in addi-

tion to 19 Sacconereis, I observed 20 Polybostrichus as well. These

were the only male epitokes that I found and observed. The dorsal

response and the increase in swimming rate occurred when pressure

was increased. When pressure was released, most individuals coiled

and sank. The body undulations of these epitokes were too rapid for

me to count.

The Response of Autolytus prismaticus Adults

After the adults had settled down in the pressure apparatus, and

had constructed membranous tubes, they did not normally leave these

tubes. Pressure increases or decreases did not cause them to leave their tubes, or to make any overt response or movement. Thus their activity showed no response to pressure changes. However, some of the stoloniferous adults occasionally responded. The atoke, or anterior adult portion of the stolon, did not respond. The posterior, which consisted of the developed Sacconereis or Polybostrichus, made occasional swimming movements that lifted the anterior end off the substrate, or at least moved the entire stolon forward. The posterior end was more robust and muscular than the anterior atoke. Under pressure the same movements occurred, but not definitely in response to pressure. The stolons broke apart easily at this tage of development, particularly during transfer to the pressure vessel. Once the atoke and epitoke were separated, the epitokes responded to pressure increases.

The Response of Exogone gemmifera

These specimens were swimming at night when collected; they swam only occasionally in the laboratory or in the pressure apparatus. No responses to pressure changes occurred. The stationary worms made no movements in response to pressure changes, and the swimming worms made no overt changes in their activity or orientation.

The Response of <u>Nereis pelagic neonigripes</u>

The five heteronereids that I observed swam normally in the pressure vessel, but did not respond to pressure changes. Neither a dorsal nor a swimming rate response occurred. When they were motionless in the bottom of the vessel, a pressure increase neither disturbed them, nor caused them to begin swimming.

The Response of <u>Armandia bioculata</u>

As in the heteronereids, these stages showed no response in the pressure vessel. The few swimming worms made no changes in swimming rate or orientation, and the ones on the bottom made no movement or other response to pressure.

DISCUSSION

The most important problem in this thesis has been the deter-

mination of responses of the Sacconereis stage of Autolytus varius to

experimental changes in hydrostatic pressure. I have also carried

out several lesser experiments on other species to compare with A.

varius, and experiments using A. varius to determine effects of

vacuum and likewise of pressure on older epitokes.

The selection of a satisfactory pressure apparatus was neces-

sarily the first problem to be attacked. Of the three main types that

I considered, both the long glass tube and the flexible Tygon tubing

leaked around the connections at the higher pressures. The Tygon

tubing also restricted the dorsal movements of the worms, which

was reflected in occasional interrupted swimming movements. The

2000 ml. Erlenmeyer aspirator flask provided several convenient

solutions: It sealed easily, and did not leak at higher pressures; it

limited the swimming movements of the worms only slightly; it pro-

vided easy addition and removal of worms without disconnecting the

syringe, or lowering the water level; it was easy to handle, empty

and refill.

The pressure apparatus itself is modified from one used by

Enright (1961, 1962). His vessel was smaller (250 ml.), and his

syringe was attached directly to the mouth of the flask through the

stopper, and not by a tube as mine was. However, mine is essentially the same form of apparatus he used.

To obtain the necessary hydrostatic pressure, most of the other workers have used either a column of mercury in a flexible tube, which could be raised or lowered, or a pump to raise the air pressure over water within a vessel. Because of the potential poisonous hazard of using mercury in a marine laboratory, and because of the simplicity of using weights as Enright had done, I chose this type of apparatus for my experiments.

The calibration of the apparatus was an easy matter since I had a simple, commercial divers' meter to work with. The simple design of the meter allowed me to modify its design, and to construct one for easier use with the narrow necked flask. The modified form, which was a straight glass tube, could be easily inserted and removed. The first reading in the sealed pressure vessel without any weight added to the syringe was two feet. This was apparently due to two factors: the weight of the water above the meter, and the weight of the syringe plunger. In the vessel there were nine inches of water above the mouth of the meter. The syringe was placed so that it was level with the tip of the flask. In this way, the flask could be filled with water, some of which would siphon into the syringe. The water levels at the top of the flask and the tip of the syringe were the same. The syringe plunger could then be inserted without air bubbles, and

adjusted to the proper level. Similarly, the flask could be loaded

and sealed without air bubbles. Calibration with the weights was

straightforward, and the data are summarized in Table 2. The

pressure equivalent for each three-pound weight was 0.33 Bar or 11

feet depth. Including the initial two feet, the pressure of the first

weight was 0.39 Bar above atmospheric pressure or 13 feet depth.

A range of 2.40 Bars or 80 feet depth was possible.

In the experiments with the adults of Autolytus auranticus, the

amount of pressure used was 0.8 Bar (Knight-Jones and Qasim,

1955) and 1.0 Bar (Knight-Jones and Morgan, 1966). The threshold

of crustaceans ranged from 10 millibars (0.01 Bar) to 0.5 Bar, and

the experimental pressures ranged from 0.01 Bar to 6.9 Bars.

Since my own preliminary tests indicated a threshold of 0.09 Bar

with an overt response occurring at 0.27 Bar, the three-pound

weights made possible a reasonable range of experimental pressure.

The pressure reached by the first weight was also within the low

pressure range as defined by Baylor and Smith (1957) as 0.69 Bar

(10 psi) or less. My upper pressures were also within the lower

part of the moderate range of pressures defined by Baylor and Smith

as 2.1 to 35 Bars.

I was able to make collections of worms from three periods of

spawning of Autolytus varius. The three most productive collection

dates, when 84% of the Sacconereis was collected, were April 22,

May 16, and June 10, 1968. The epitokes lived for 14 to 18 days in the laboratory before depositing their larvae. Successive spawning periods were 24 to 25 days apart. I was not able to collect any Sacconereis at the end of March; I did not find any in July. Potts (1913) reported that Odontosyllis phosphorea swarmed at sunset of the last quarter of the moon, August, 1911, and the first quarter of the moon, August, 1912. He also reported that O. enopla swarmed every 26 days from early July through late August at sunset. Gidholm (1965) mentioned that Autolytus edwarsi reproduced monthly all year around, and that A. prolifer reproduced from April to September in Scandinavian waters. The spawning period of A. varius is consistent with these reports.

Gidholm (1965) did not mention any correlation with the moon or tidal cycles in the spawning of A. edwarsi or A. prolifer, any my collections did not show any direct correlation with the moon, although most of the worms were collected at evening high tides. The April 22, collection was on a waning moon five nights before the new moon. The May 16 collection was on a waning moon four nights after a full moon and 11 nights before the new moon. The June 10 collection was on the night of the full moon, although it was overcast and raining. Likewise, the tidal cycles do not correlate with the spawning; the April and June collections were the highest tides of the cycle, but the May collection was at the low high tide of the cycle.

The only consistent fact is that they were collected at evening high

tides shortly after sunset.

The first experiment was on the dorsal response of <u>Autolytus</u>

<u>varius</u> Sacconereis. It was instructive in several ways. It indicated

that the epitoke did respond to an increase in hydrostatic pressure;

it indicated that a dorsal response was present; and it was compar-

able to previous experiments on other animals. It also pointed out

an inadequacy in the measurement of the dorsal response. The data

indicated a 90 percent response at point P_o, although I knew I was

getting a hundred percent response by observation. The discrepancy

involved the behavior of the worms in the apparatus. If the worm

responded to a pressure stimulus in an effort to reach a higher level

in the water column, as <u>Calanus</u> <u>finmarchicus</u> responds (Rice, 1962),

then that column would extend well above the vessel. The worm

would then try to swim farther than the top of the vessel. In hitting

the top of the vessel its dorsal response would be interrupted. In

fact, most of the worms swam at the top, but some would occasionally

coil or swim downward for a moment, and then swim up again.

Enough of these occurred to lower the initial response value. This

encouraged me to try swimming rate measurements in the second

group of experiments, since these were not so often interrupted by

the top of the vessel. Even if a worm did swim downward, his initial

rate was still high. Thus the measurement of swimming rate was

more consistently related to the pressure changes.

The dorsal response of Autolytus varius, as graphed in Figure 3 corresponds with the basic response of other pelagic forms. The pelagic adult of A. auranticus, when measured against a vertical scale, responded to a pressure of 1.0 Bar by swimming to the top of a tube (Knight-Jones and Morgan, 1966). The peak activity occurred in the first minute after the onset of pressure. Following this the response decreased somewhat. Upon the release of pressure, the worms dropped to a position near the bottom of the tube, at a level below their initial distribution. The accommodation, or decrease in response while under pressure, is possibly more rapid in A. varius epitokes than for A. auranticus adults. However, the duration of the pressure application was short enough, and the methods differed enough, so that direct comparison of the differences in accommodation are difficult. The basic pattern is similar for most animals tested with a pressure application of short duration. On the other hand, some forms, such as the several genera and species of mysids tested by Rice (1961), did not decrease their response while under pressure, but maintained their activity at a high level as long as pressure was maintained. Knight-Jones and Morgan (1966) summarized the response in this way "... the swimming output of Autolytus (auranticus adults) and probably of many other animals, shows a very similar pattern of variation with pressure." Enright (1962) thought that

truly planktonic organisms accomodate very little.

Rice (1964) attempted to classify the responses to changes in hydrostatic pressure on the basis of the responses to gravity and light as well as pressure. His categories were as follows: Orientation to gravity alone; orientation to gravity, with a subsidiary light influence; orientation to light; failure to respond. In the second category, the animals responded by swimming toward a light placed horizontally to the pressure chamber. Otherwise, the animals responded to gravity, and swam up in darkness and in light from above and below. Although the epitokes did not swim directly to the light held horizontally, neither did they follow their normal pattern. They swam in circles near the middle of the vessel. For this reason, I would place the responses of A. varius in category two, of orientation to gravity, with a subsidiary light influence.

Threshold is defined as the minimum pressure required to elicit an overt response, even though the proportion of individuals responding to the minimum may be small (Knight-Jones and Morgan, 1966). The response of two of six epitokes to a pressure of 0.09 Bar appears to fit this category. The next pressure of 0.27 Bar brought about a total response. Both of these values are within the range reported by other workers. Pressures used in the studies by Morgan, Nelson-Smith and Knight-Jones (1964) and Morgan (1965) ranged to 8 decibars (0.8 Bar). Baylor and Smith (1957) recorded 3

to 6 decibar thresholds (0.3 to 0.6 Bar) for several coelenterates.

However, most of the crustaceans seem to have a threshold of less

than 50 millibars (0.05 Bars). The amphipod Synchelidium has a

threshold of 5 to 10 millibars (0.005 to 0.01 Bar) (Enright, 1961,

1962). Rice (1961) found a threshold of less than 50 millibars (0.05

Bar) for the mysid Schistomysis. The thresholds of polychaetes have

not been recorded accurately, but seem to be in the range of 50 milli-

bars (0.05 Bars) to a few decibars (Knight-Jones and Morgan, 1966).

My results are within these reported thresholds.

Most of the previous studies on hydrostatic pressure responses

have dealt with a dorsal response, measured on a vertical scale.

The swimming response of A. varius, measured by timing body un-

dulations, followed a similar pattern when it was plotted (Figure 4).

An increase in the swimming rate occurred in the first minute after

a pressure stimulus. Following this there was a regular decrease

in the intensity of the response, or a period of accommodation, and the

swimming rate slowed to nearly the pre-stimulus level in 15 minutes

of continued pressure (Figure 4). When pressure was released after

15 minutes, little difference in the swimming rate was noted, since

many worms had already slowed to nearly the average rate. How-

ever, swimming rate does not measure the number of animals coil-

ing and sinking to the bottom, and always some do respond in this

way. Figure 4 includes time vs. percent coiling taken from Table 5.

Coiling was also common in the dorsal response experiment when pressure was released (Table 3). Both experiments had nearly 60 percent coiling of A. varius Sacconereis upon pressure release. I observed similar responses to pressure release in the A. magnus Sacconereis, and in A. prismaticus Sacconereis and Polybostrichus. The epitokes of A. prismaticus almost all coiled and sank following pressure release. The basic pattern, then, is similar in the three species of Autolytus tested.

The only three works with which I can compare the swimming rate response of A. varius are those of Hardy and Bainbridge, 1951; Rice, 1961; and Enright, 1962. Hardy and Bainbridge (1951) subjected Portunus and Carcinus larvae to pressures of 0.15 and 0.60 Bar for periods of three hours. Dorsal swimming was slow; the larval crabs took nearly an hour to swim to the upper half of the tube. While pressure was maintained, no accommodation was evident. The larvae then swam downwards to a normal level when pressure was released. The mysids tested by Rice (1961) also showed no accommodation; they swam at a consistently high level when tested at 0.3 to 1.3 Bar. The pressure was usually maintained for 10 to 40 minutes. The animals then slowed and sank when pressure was released. These patterns differ from the pattern of Autolytus.

The two papers by Enright (1961, 1962) on Synchelidium, a beach amphipod, reported patterns of response similar to those of

Autolytus. His animals were more sensitive, responding to pres-

sures in the 10 millibar (0.01 Bar) range. The swimming activity

was of a normally benthic amphipod. Its response consisted of a

short-duration swimming activity lasting several seconds. The in-

creased activity had a sharp onset with a gradual return to a normal

level, including intermittent spontaneous activity of occasional

swimming from the bottom. Accommodation was rapid; activity lasted

only 8 to 13 seconds before returning to the initial background level.

The experimental pressures used were 37, 53, 72, and 110 milli-

bars (0.037, 0.053, 0.072, 0.11 Bar). A. varius does not accommo-

date so rapidly, but does follow a similar accommodative decrease in

response over a period of around 11 minutes $\pm$ 8, although some did

not accommodate for 30 minutes.

Enright (1962) mentioned that most of the other observations

had been made on planktonic organisms; these evidently accommodate

only after a few hours, if at all. However, Autolytus epitokes are

temporary plankton organisms in that they are a reproductive stage

derived from a benthic adult. Autolytus may be responding more like

an animal with a tidal activity response, such as the amphipods

Synchelidium and Corophium. In his work on Corophium, Morgan

(1965) ran most tests at an equivalent pressure of eight meters (0.8

Bar), for one minute. A few tests for four and seven minutes at this

pressure indicated that accommodation was possibly occurring. During

this time, the response decreased in intensity, but the tests were not

of sufficient duration for the response to approach the initial level

of activity. This accommodation was in the same range as Autolytus;

both were in the magnitude of tens of minutes. Contrarily, the

pycnogonid Nymphon gracile, which also had a tidal response similar

to Corophium, did not seem to demonstrate any accommodation

(Morgan, Nelson-Smith, and Knight-Jones, 1964). More experi-

mental work is needed to clarify the role of accommodation in the

pelagic planktonic animals, and in the neritic planktonic and littoral

benthic animals with tidal rhythms and wave transport responses.

The decerebrate Sacconereis of Autolytus varius possibly indi-

cated the importance of the new head formation in epitokes formed

non-epigamously. Although they swam normally, the experimentally

decerebrate epitokes did not show an overt response to a pressure

increase. A few were agitated when the pressure was released. The

head formation appears to be necessary for the normal response to

occur. This could indicate that whether a gas or some other type

receptor is present it must be mediated by the anterior ganglion, or

be located in the head. An anterior ganglion is developed in the epi-

tokes of the genus Autolytus (Gidholm, 1967). Actual pressure sense

could also occur in the anterior region, but not necessarily. This

experiment, however, indicated that the normal response is neither

just a body tissue response, nor a segmental ganglion reflex. Some

Sacconereis with a few anterior cirri missing responded normally,
as did one worm with a portion of the posterior missing.

The normal responses demonstrated by the epitokes of A.
varius and of other animals (Baylor and Smith, 1957; Enright, 1962)
that had been exposed to a vacuum, have indicated that a bubble pres-
sure receptor was not involved. Under the vacuum, any gas bubble
present should expand and float the organism to the surface, or at
least become visible, according to Baylor and Smith (1957) and
Enright (1962). Enright (1962) also used microscopic examination of
live animals, under reduced pressure. In all of these cases, includ-
ing my own pressure studies, no gas bubble receptor was made
visible or otherwise demonstrated by changes in buoyancy during
reduced pressure.

The estimation of swimming rate also has the advantage that a
measurement can be made, even if the epitoke has lost or changed
its orientation. The swimming rate response also included a dorsal
orientation, and dorsal swimming, but this was not indicated in the
graph (Figure 4). In the older epitokes of A. varius, changes in
orientation were observed, while the basic increases in swimming
rate indicated that a response was occurring. The slower response
evident in the older epitokes may also have value. At this stage of
the life cycle of the worm, the brooded larvae were well developed,
and deposition of the larvae was imminent. The worms responded

by swimming faster, but not dorsally; they swam in circles. This would tend to keep them on the bottom. Although long range dispersion would probably not occur, this decrease in response might aid in selecting a proper deposition site.

The other species of Autolytus confirmed in general the results obtained from A. varius. Although only one specimen of A. magnus was observed, it responded similarly to pressure changes, both in orientation and in swimming activity. The small A. prismaticus provided male epitokes or Polybostrichus for comparison with the Sacconereis of the three species of Autolytus. In addition, I was able to observe the activities of the adults, and the stolons. The two sexes of A. prismaticus both responded similarly to A. varius. Their swimming rate was much more rapid, and they seemed to reach the top of the vessel sooner, but this was not quantified. I did not time the swimming movements of the epitokes of A. prismaticus, because they moved too rapidly for me to do so, and they were so small that it was difficult to observe a portion of their body long enough to count the movements. The adults did not respond. They did not vacate their mucous tubes when pressure stimuli were given, either in the light, or in the dark. They made no crawling movements in response to stimuli, once they had formed their tubes. Thus the benthic adult does not respond, while the temporary planktonic epitoke does respond. The adults of A. varius and A. magnus

were not found.

The epitokes of A. prismaticus stolons are more muscular than the atokes, and appear capable of nearly independent motion by pushing the stolon forward along the substrate. This could bear more intensive study to determine at what stage of development the epitoke is able to respond to pressure change independently of the atoke.

In some of the other polychaetes that I tested, several swimming forms were not responsive to pressure changes. These were Exogone, Nereis and Armandia. Although all of these were collected swimming at the surface of the water, Nereis was the only strong swimmer in the laboratory. The others were only occasional swimmers, and never in response to a pressure stimulus. One difference between these polychaetes and the members of the genus Autolytus is that the former are temporary stages of adult animals that do not break apart. All of the three genera: Exogone, Nereis and Armandia form free swimming reproductive stages epigamously, that is by direct epitokal modification of the adult without stolonization or budding, or the formation of a second head. If the normally benthic adult is not responsive to pressure changes, the epigamously produced epitoke with no new head formation would probably also not respond to pressure change. A future study comparing the hydrostatic pressure response in reproductive stages and adults in relation to the mode of epitoky probably would yield additional new information.

Initially, Hardy and Bainbridge (1951) thought that a sense of depth would be important to animals that undergo vertical migrations. Knight-Jones and Qasim (1955) felt that most of the animals that responded to pressure changes were planktonic animals with a high specific gravity. The animals would tend to sink if they stopped swimming, and a depth stimulus would initiate a return to a higher level. This is true in Autolytus epitokes, as they do sink when they stop swimming, and a sinking Sacconereis in the pressure vessel may begin swimming again as it sinks. Thus a sense of pressure would keep them from sinking too far, and would act as a means of keeping them at a level in the water column.

I believe that it is important in the life cycle of these epitokes of Autolytus that this temporary stage is able to respond to changes in hydrostatic pressure. This stage is relatively short-lived, but it still must be adequately adapted to maintain a planktonic existence in the bay for over half a month. During this time the Sacconereis must mate, swim, avoid predation, and promote dispersion. The hydrostatic pressure response may play a role in all of these activities. The epitokes, swimming in high tides and especially in evening ones may avoid predation, since the worm would be more difficult to see during the night and in the increased volumes of water. The high tide itself would promote dispersion as well as increase the pressure at the bottom.

On the other hand, the benthic adult, at least Autolytus prismaticus, and possibly other species of Autolytus adults, need no response, and do not show one. It would be an advantage for the adult to remain concealed, and depend on the epitoke for dispersion. The epitokes that did not respond to hydrostatic pressure changes do not incubate the young, and depend on the tides themselves for dispersion of eggs, sperm and planktonic larvae. Both groups of epitokes are adapted for life in an estuary, but in different ways.

SUMMARY AND CONCLUSIONS

1. Many marine organisms respond to small changes in hydro-
   static pressure.

2. The Sacconereis stage of _Autolytus varius_, a syllid polychaete,
   was subjected to pressure increases of 0.39 Bar above atmos-
   pheric pressure.

3. The pressure apparatus consisted of a 2000 ml. Erlenmeyer
   aspirator flask, a 30 cc. syringe, and several three-pound
   weights. The apparatus could be sealed to prevent leaks and
   loss of pressure.

4. Pressures to 2.40 Bars were obtained when the weights were
   placed on the syringe plunger.

5. _Autolytus varius_ Sacconereis responded to pressure increases
   as small as 0.09 Bar.

6. All _A. varius_ Sacconereis responded to increases in hydro-
   static pressure of 0.39 Bar by orienting dorsally, and by in-
   creasing swimming rate.

7. Basic orientation of _A. varius_ Sacconereis was an orientation
   to gravity with a subsidiary light influence.

8. After a peak activity during the first minute of pressure, there
   was a decrease in the intensity of activity to a level near the
   initial rate. This was termed accommodation.

9. When pressure was released, the epitokes either slowed their activity, or coiled and sank to the bottom of the vessel.

10. Similar responses to these hydrostatic pressure increases occurred with A. magnus and A. prismaticus epitokes.

11. The benthic adults of A. prismaticus did not respond to pressure changes.

12. Decerebrate Sacconereis of A. varius did not respond to pressure changes.

13. Older Sacconereis of A. varius did not orient dorsally in response to a pressure increase, possibly in preparation for the deposition of the brood sac on the bottom.

14. Several non-responsive species of polychaetes were found (Exogone gemmifera, Nereis pelagica neonigripes, Armandia bioculata), all of which form epitokes by epigamy, and do not incubate their developing larvae.

15. The free-swimming epitokes of Autolytus may have unique adaptations for sensing pressure not present in benthic adults.

16. A hydrostatic pressure response regulates swimming depth, aids in dispersion, promotes mating, and decreases predation.

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