THE EARLY LIFE HISTORIES OF SOME AMERICAN PENAEIDAE, CHIEFLY THE COMMERCIAL SHRIMP, PENAEUS SETIFERUS (LINN.)[1]

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INTRODUCTION

The common southern shrimp, *Penaeus setiferus* (Linn.), supports the most important fishery on the South Atlantic and Gulf coasts of the United States, ranking third in value among all the fisheries of the eastern seaboard. The future existence and development of this fishery depend not only on the ability of the adult shrimp to perpetuate itself but also on the ability of the young to complete its unique and complex larval development, to be successfully distributed into favorable environments and attain commercial size. As remarked by Gurney (1924): "The adult stage is only one phase in the individual cycle, and it is hardly logical to concede to one phase the importance which is denied to another." The present study, therefore, is concerned primarily with the neglected field of the early development of this species of shrimp.

A comprehensive program of research on the life histories of the commercial American shrimps or prawns of the family *Penaeidae* was initiated in 1931 along the South Atlantic and Gulf coasts of the United States. The following report is based on the data obtained from an examination of plankton collections and on specimens obtained by rearing planktonic eggs and young. It is a presentation of the available data on the early life histories of the principal commercial shrimps of the family *Penaeidae* occurring on the coast of the United States; *Penaeus setiferus* (Linn.) and *Penaeus brasiliensis* Latreille, together with information on the larvae of three noncommercial species, *Trachypenaeus constrictus* Stimpson, *Parapenaeus longirostris* (Lucas), and *Eusicyonia stimpsoni* (Bouvier).

The plankton was taken largely by power boat in those areas now included within the estuarine and inner littoral limits of the southern shrimp fishery off the Louisiana and South Atlantic coasts—the estuarine waters in and adjacent to Barataria Bay, La., and the inner littoral waters from Cape Romain, S. C., to Cape Canaveral, Fla. Collections made outside of these boundaries comprised a relatively deep-water zone off the Delta of the Mississippi River, an offshore zone from 12 to 30 miles south of Barataria Pass, La., and a subtropical estuarine area at Ft. Pierce Inlet, Fla.

The plankton collections were secured principally by means of a standard Bureau of Fisheries conical meter net, the upper half consisting of No. 0XX (38 meshes to the linear inch) and the lower half of No. 2XX (52 meshes to the linear inch) Swiss bolting cloth. At certain times of the year, and at some localities, a conical foot net of No. 6 silk cloth (72 meshes to the linear inch) was substituted for the meter net. In order to obtain samples from or near the bottom off the Delta of the Mississippi River where irregular "mud lumps" and deep alluvial deposits occur, a standard nonclosing meter net was tied to a heavy rectangular iron frame equipped with wide steel runners. This gear caused the net, when towed, to travel within a foot of the bottom in depths ranging down to about 40 fathoms. At St. Augustine and Ft. Pierce Inlets a meter net was suspended in the inlet channel from a bridge where the tidal current brought oceanic plankton into the net on flood tide. This method of stationary inshore collection of plankton proved extremely economical and valuable, and provided larval material that could not be secured in the open sea.

Collections in areas having a depth of less than 5 fathoms were generally limited to the surface zone largely because of the simultaneous operation of a commercial shrimp trawl along the bottom. However, in the deeper oceanic waters off the Delta of the Mississippi River and off Barataria Pass both surface and bottom collections were usually made. The collections at St. Augustine and Ft. Pierce Inlets obtained a

mixture of both surface and bottom plankton because of the velocity of the tidal current in the shallow channels.

No attempt was made to sample the plankton quantitatively. The towing period was generally 20 minutes for inshore surface hauls and 60 minutes for offshore and bottom hauls. All plankton taken at sea and at Ft. Pierce Inlet was immediately preserved in formalin. The plankton taken at St. Augustine Inlet was frequently transported alive to a laboratory, 4 miles distant, for examination.

Approximately 900 plankton collections were available for examination. These were gathered over a 6-year period from May 1931 to June 1936. Spring and summer collections were far more numerous than winter collections, partly because of better weather conditions and because of the apparent greater value of material obtained during the spawning period of *P. setiferus*. Collections at St. Augustine and Ft. Pierce Inlets were made at regular intervals, either daily or triweekly, for more than a year.

The hatching of peneid shrimp eggs and the rearing of the larval and postlarval young was conducted at St. Augustine, Fla., during 1936. Specimens were removed from fresh samples of plankton and kept isolated in small glass aquaria for observation. The lack of running sea water in the temporary laboratory handicapped efforts to rear the young shrimp and prevented the full realization of the attempt to rear three species of *Penaeidae* from the egg to pre-adult size. However, sufficient data were obtained through these experiments to provide confirmation of the identification of various series of peneid eggs and larvae, previously secured in the plankton, to enable unidentified material to be assembled systematically, and to permit establishment and verification of such diagnostic characters among peneid eggs, larvae, and postlarvae as are described and illustrated in this report.

The general status of knowledge of the eggs and larvae of the *Penaeidae* previous to 1924 was summed up by Gurney (1924):

> The fact that the majority of the *Penaeidae* are deep-sea forms, and that the eggs are always set free before hatching, makes the difficulty of connecting the larvae with the adults very great. Thanks to the splendid work of Müller (1863) and Claus (1876) we know with sufficient detail the general course of development from the nauplius to the mysis stage, but we do not know with what genera they were dealing, or whether the larval series which they succeeded in tracing is typical for the whole family. Later authors have added remarkably little to our knowledge. Brooks (1882 was able to trace a series of larvae up to a stage recognizable as belonging to *Penaeus*, but his description is not illustrated and is too brief to be of much help to others. Kishinouye (1900) and Lo Bianco and Monticelli (1900, 1901) alone have actually observed the hatching of the nauplius, while the latter authors have had the singular good fortune to follow the complete metamorphosis in two species—*Sicyonia sculpta* and *Solenocera siphonocera*—and in part that of *Parapenaeus longirostris* and a species of *Gennadas*. It is most unfortunate that, with the exception of *Solenocera* and *Aristaeomorpha*, they have published no figures of any of the stages observed, and their written description is often exceedingly difficult to understand or to make use of.

Noteworthy contributions by Gurney (1927), Hudinaga (1935), and Menon (1937) followed. Gurney described the egg and larval stages of a peneid, probably *Penoeopsis stebbingi*, and Menon discussed various larval stages of *Penaeus indicus*. The research of Hudinaga on the larval development of the commercial Japanese prawn, *Penaeus japonicus*, is an outstanding contribution to the literature, for the exact parentage of the eggs and resultant larvae was known to the investigator who held the spawning adults in aquaria.

It is realized that at least 10 species of Penaeidae occur within the areas under investigation. There is the possibility that a species with at least 10 distinct larval stages may be indistinguishable in certain larval stages from other closely related

forms. The desirability of obtaining peneid eggs and larvae from spawning adults held in aquaria is obvious, but this approach to the problem did not appear feasible to the author. It has been particularly difficult to draw conclusions on the distributions of peneid eggs and larvae found to occur along such an extended coast line as the region from Cape Romain, S. C., to Ft. Pierce, Fla. Those conclusions which have been thought justified are based solely on the material derived from the most extensive collections of plankton yet made along this coast line and the coast line adjacent to the Delta of the Mississippi River. Until additional material becomes available it seems desirable, however, to set forth the seasonal and geographic distributions of eggs and larvae as they were found to occur.

To Milton J. Lindner and William W. Anderson of the Bureau of Fisheries, to Gordon Gunter of the Texas Oyster Development Corporation, and to Nelson Gowanloch and William Burgess of the Louisiana Conservation Commission credit is due for collecting certain material off the coasts of Louisiana and the South Atlantic States.

The diagnostic drawings, made with the aid of camera lucida and pantograph, form an indispensable part of the report and clarify what might otherwise be obscure. It should be stated here that the cilia on the setae of the larval *Penaeidae* have deliberately been eliminated in the drawings because of their great number and minute size, together with the fact that their presentation might obscure certain diagnostic characters of the larvae.

PENAEUS SETIFERUS (LINN.), THE COMMON SHRIMP

DESCRIPTION

EGG

Eggs of the southern commercial shrimp, *Penaeus setiferus*, taken in plankton at St. Augustine Inlet, Fla., were isolated in small glass dishes kept at room temperature, and were hatched into the first nauplius stage. The latter was reared to the first protozoea stage. The first protozoea was linked to an extensive series of first, second, and third protozoea, first and second mysis, and early postlarval stages obtained from preserved plankton. Specific identity was determined by rearing planktonic second mysis to the first postlarval stage and by rearing planktonic first and second postlarval stages to preadult size (35 mm.).
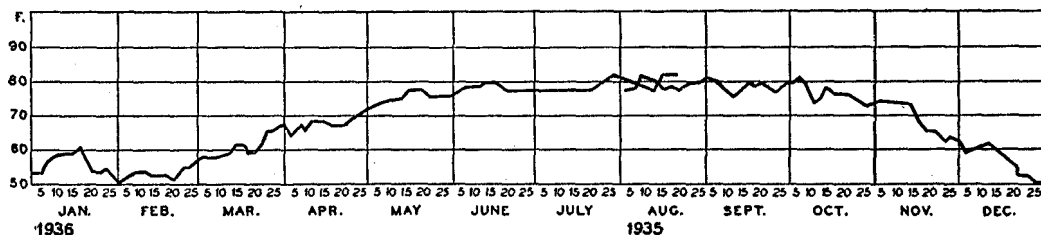

FIGURE 1.—Water temperatures at St. Augustine Inlet, Fla., from January 1 to August 20, 1936, and from August 2 to December 31, 1935. Planktonic postlarval shrimp, *P. setiferus*, taken from April 5 to August 25, 1936.

The egg of *P. setiferus* is demersal and sinks promptly in still sea water. The demersal nature of the eggs of the *Penaeidae*, noted by Hudinaga (1935) for *P. japonicus*, probably accounts for the rarity of these eggs in most oceanic plankton collections. Although the eggs may be scattered on the sea bottom, those of *P. setiferus*, as in the case of *P. japonicus*, may be moved quite freely throughout the water area in aquaria by current agitation.

The egg is nonadhesive and spherical. The diameter of 25 live eggs uniformly measured 0.28 mm. The egg after preservation in formalin may lose about 0.01 mm. in diameter. Hudinaga (1935) recorded a difference of 0.021 mm. in diameter range among a series of 10 eggs of *P. japonicus*. Although the writer did not find it practical to measure eggs in less than 0.02 mm. units, a somewhat comparable size range may exist for the eggs of *P. setiferus*.

The egg possesses a thin, transparent membrane, or chorion, that in living and preserved eggs shows a characteristic purplish-blue color in reflected light under the microscope. This bluish hue contrasts sharply with a pinkish-red coloration shown by the egg of another peneid shrimp, *Eusicyonia*.

Nearly all eggs of *P. setiferus* were obtained in late developmental stages in which the embryo was generally well-differentiated. In these eggs the embryo almost completely fills the egg, leaving only a very narrow perivitelline space. The length of the embryo in most eggs measured approximately 0.26 mm. The embryo is invested with an embryonic membrane which is thin, transparent, and colorless. Details of

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structure of the dark-brown embryo, closely invested by both embryonic and egg membranes, are not discernible under the microscope either in living or preserved eggs. Three pairs of appendages, corresponding to the first and second antennae, and mandibles, are observed closely folded to the body. (See fig. 2.)

A total of 5 eggs hatched out of the 15 that were available for rearing experiments. These eggs hatched within 12 hours after capture. The low percentage of the hatch may possibly have been caused by the death or weakening of the embryo prior to removal of the egg from the plankton. The eggs of several other species of *Penaeidae*, taken at the same time, did not, however, show as large a death rate. Generally it appeared that the egg-nauplius failed in its efforts to break through the egg membrane and to free itself.

Several hours prior to hatching, the embryo commences to make convulsive movements and tends to rotate within the egg sphere. The embryonic membrane is readily
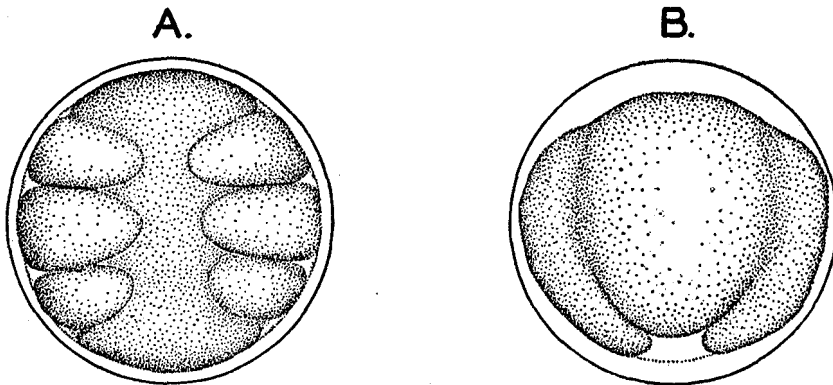

FIGURE 2.—Egg of *Penaeus setiferus*. Diameter 0.28 mm. (A) Ventral aspect; (B) anterior aspect.

stretched and broken by the antennae and normally the egg membrane is soon after ruptured, thus permitting the emergency of the first nauplius larva. Actual emergence from the egg occupies only a few seconds.

Inasmuch as the nature of the material did not permit a study of the complete embryological development of the egg of *P. setiferus*, it seems highly desirable to present here a summation of the development of the egg of *Penaeus japonicus*, as recently determined by Hudinaga (1935), particularly as this most useful account is in Japanese and not so readily available to American workers.[2] It is assumed that the method and rate of development of the egg of this Japanese shrimp is fairly comparable to that of *P. setiferus* for the following reasons: First, the eggs of both species are nearly identical in size (0.28 mm.), are both spherical and demersal; second, both eggs were hatched in glass dishes and reared in sea water approximating from 80° to 85° F. in temperature; third, larval development, subsequent to the hatching of the egg, appears quite similar in both species.

The egg of *P. japonicus*, immediately after spawning and prior to the first cell division, shows the spherical egg mass lying to one side within the egg. All cell divisions are equal and complete, the first division occurring about 15 minutes following spawning. The portion of the egg mass which lies adjacent to the egg membrane becomes slightly flattened and the egg mass loses its spherical shape, becoming irregularly ovoid. This ovoid egg mass then starts to divide on the shorter diameter

[2] The writer is indebted to Taro Inazaki, of the Imperial Japanese Embassy, Washington, D. C., for a complete translation of the paper by M. Hudinaga.

surface. At the end of the cell division the egg mass becomes situated in the center of the egg and lies in a concentric plane within the egg membrane. The time required for the first cell division is from 2 to 3 minutes, after which the egg enters into a rest period.

The second cell division starts 30 minutes after spawning. The two cells become oval-shaped and division starts along the shorter axis of each cell. As the process of division proceeds, the cells of the first division migrate gradually in opposite directions to each other so that the angle of the two lines connecting the two foci of the cells increases gradually. The cells lose their oval shape. When the second cell division is complete and four cells are created, the angle of the two lines connecting the two foci of the cells just divided maintains a degree varying from 45° to 60°. The time of the second cell division is about 3 minutes, after which the egg enters into another rest period.

The third cell division begins about 12 minutes after the end of the second division and is completed in about 3 minutes. No evident movement of the cells occurs in this or subsequent cleavage stages. In all future cell divisions cleavage always occurs at right angles to the surface of the previous cell division. Generally, 2 to 3 minutes are required for each cell division and a rest period of about 13 minutes occurs between each division.

About the time when the number of cells has increased from 64 to 128, the vegetative pole of the embryo becomes somewhat flat and starts to invaginate. Within 2½ hours after spawning a thin embryonic membrane appears surrounding the embryo. Three hours after spawning the lateral surfaces of the embryo become depressed, although within 30 minutes the embryo becomes oval in shape.

Four hours after spawning the middle section of the embryo commences to swell. This swelling gradually projects and surrounds the embryo in a ring. This structure however, is not regular in width. The wider side is dorsal and the narrower side is ventral. This structure is the root of the second appendage or second antenna of the nauplius.

Five hours after spawning, just below the root of the second antenna, there appears the root of the third appendage or mandible. This structure is much smalle than that of the second antenna.

Six hours after spawning, above the root of the second antenna, the root of the first appendage or first antenna becomes differentiated.

About 8 hours after spawning small setae appear at the tips of the three pairs of appendages. There appears also a slight cleft about midway along the lateral sides of the second and third appendages. At 10 hours this bifurcation is completed for both pairs of appendages. The latter gradually become narrower and longer. Meanwhile, a depression has formed along the middle line on the ventral side of the body—the future stomadeum or mouth. Between this depression and the anterior edge of the body a swelling occurs which is the root of the labrum or upper lip. The latter becomes more fully developed with age and shows a tendency to bend toward the ventral side of the body. A pair of minute setae or furcal spines are placed at the caudal end of the body.

About 11 hours after spawning a dark ocellus or simple naupliar eye appears at the anterior end of the body and lies slightly on the ventral surface. The labrum bends farther toward the ventral side, obscuring the root of the stomadeum. Soon after the ocellus appears the embryo commences an oscillatory movement within the egg.

In about 12 hours after spawning the embryonic membrane is broken by the embryo which spreads its first and second antennae within the egg membrane. Several hours later the egg nauplius breaks the egg membrane and emerges.

FIRST NAUPLIUS

The first nauplius measures from 0.30 to 0.34 mm. in body length and from 0.16 to 0.20 mm. in greatest body width. Length of body of the nauplius was taken between the apical and caudal ends; the furcal spines were not included in the measurements. Width of body was taken at the point of greatest width along the dorsal surface.

The dark-brown opaque body of the nauplius possesses a somewhat pyriform shape from a dorsal or ventral aspect and has a moderate ventral flexure about midway of the body observed from a lateral aspect. It is unsegmented. (See fig. 3.)

An ocellus, or simple eye of dark coloration, lies on the medial ventral surface of the body close to the anterior margin. This ocellus persists in the larva through the
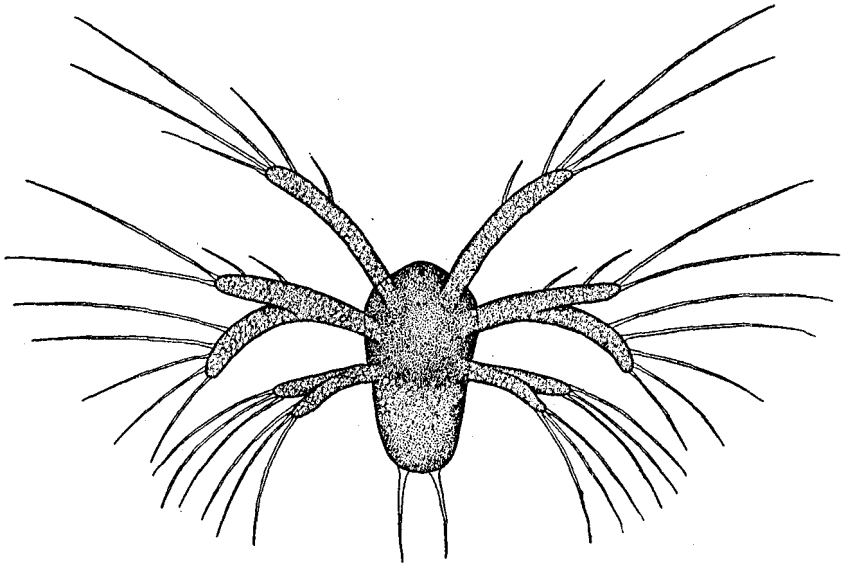

FIGURE 3.—First nauplius of *Penaeus setiferus.* Length 0.30 mm. Ventral aspect.

protozoea stages and probably also occurs in the mysis stages. It enables the nauplius to respond to light stimuli.

A half-spherical flaplike labrum, or upper lip, lies ventrally about the middle of the body and tends to protrude outward at the ventral flexure.

A pair (1+1) of spines half the length of the body extend out from the posterior margin of the body.

There are three pairs of appendages, the first and second antennae and the mandibles. These appendages of natatory function appear as stout, unsegmented, club-shaped structures, blunt at the end, and are capable of rapid movement.

The first antenna is uniramous, about three-quarters of the length of the body, and bears two moderate lateral, two long and one moderate terminal setae.

The second antenna is as long or longer than the first antenna and is biramous. The endopod, or inner ramus, bears two moderate lateral and two long terminal setae. The exopod, or outer ramus, is somewhat longer than the endopod and bears a series of five long setae placed along the lateral and apical margins.

The mandible is biramous, much shorter than the other appendages, and bears three long terminal setae on both the endopod and exopod.

Yolk granules fill the body of the nauplius and are used as a source of food supply. No internal structure was observed under the microscope.

The nauplius begins to swim immediately after emergence from the egg. Movement is produced by means of the three pairs of appendages and is erratic, darting and spasmodic. Müller (1863), in his description of the first recognized peneid nauplius, stated that a man floating perpendicularly in the water, with widespread arms and slender willow branches in each hand, striving to work himself upward, would furnish a notion of the peculiar movement by which the nauplius and protozoea may be recognized at the first glance amongst hundreds of other small crustacea. Hudinaga (1935), describing the movements of the nauplius of *P. japonicus*, states that the second antenna is the most effective appendage in locomotion, that movement is fairly swift, and effected by the appendages rolling the body around in a zigzag fashion. When at rest, the nauplius keeps the dorsal side down and stays in a perpendicular position in the water with the appendages kept aslant upwards.

In still water the nauplius of *P. setiferus* may remain suspended in the water or may lie quietly on the bottom for some 30 seconds or more before a series of rapid beats of the appendages enables the nauplius to zigzag off in a forward direction. Movement has a duration from approximately 5 to 15 seconds, after which the larva maintains a rest somewhat longer than the active period. Agitation of the water generally induces immediate movement of normal duration and intensity. A positive, although probably complicated reaction to light stimulus was noted for the nauplius. A similar phototropic response was noted by Hudinaga. This response to light in the open ocean probably brings the nauplius toward the surface of the sea from the deeper water layers where the eggs occur.

The nauplius of *P. setiferus* lives well in small glass containers holding about six tablespoonfuls of sterile sea water and molts within a few hours into the second nauplius. The nauplius appears quite hardy for it was frequently found alive in the plankton samples long after most other organisms, such as copepods, had perished. The first nauplius was obtained both by hatching several eggs and from the plankton.

TABLE 1.—*The body segments and paired appendages of the larva of the shrimp,* Penaeus setiferus *with the chief function of the appendage and time of functional appearance* [1]

No.	Somite	Appendage	Chief function of appendage	Appendage appearance
1	Ophthalmic	Eyestalk	Visual	Second protozoea.
2	First antennal	First antenna	Natatory in nauplius and protozoea, sensory in mysis.	First nauplius.
3	Second antennal	Second antenna	do	Do.
4	Mandibular	Mandible	Natatory in nauplius, masticatory in protozoea and mysis.	Do.
5	First maxillary	First maxilla	Masticatory	First protozoea.
6	Second maxillary	Second maxilla	do	Do.
7	First thoracic	First maxilliped	Natatory, masticatory	Do.
8	Second thoracic	Second maxilliped	Natatory in protozoea, masticatory in mysis.	Do.
9	Third thoracic	Third maxilliped	Masticatory	First mysis.
10	Fourth thoracic	First pereiopod	Natatory in mysis	Do.
11	Fifth thoracic	Second pereiopod	Natatory	Do.
12	Sixth thoracic	Third pereiopod	do	Do.
13	Seventh thoracic	Fourth pereiopod	do	Do.
14	Eighth thoracic	Fifth pereiopod	do	Do.
15	First abdominal	First pleopod	do	Second mysis.
16	Second abdominal	Second pleopod	do	Do.
17	Third abdominal	Third pleopod	do	Do.
18	Fourth abdominal	Fourth pleopod	do	Do.
19	Fifth abdominal	Fifth pleopod	do	Do.
20	Sixth abdominal	Uropod	do	Third protozoea.
21	Telson	Wanting	do	Do.

[1] All appendages except eyestalk, first antenna, mandible, and pleopods are biramous. Mandible is biramous in naupliar stages. All body segments are differentiated by the third protozoea.

SECOND NAUPLIUS

The second nauplius measures from 0.32 to 0.34 mm. in body length and from 0.16 to 0.18 mm. in greatest body width. The shape of the body is generally similar to that of the first nauplius with the exception that a slight medial notch appears at the posterior margin of the body. (See fig. 4.) There are now two pairs of posterior marginal spines as the result of the appearance of a weak outer spine on each side of the slight furcal process. Faint anlages of the fourth to seventh pairs of appendages frequently are visible near the midline on the ventral surface of the body. The first antenna generally possesses two long and one short terminal setae, two moderate setae on one lateral margin, and one moderate seta on the opposite lateral margin.

The second antenna has the endopod bearing another moderate terminal seta, making a total of three terminal and two lateral setae. The exopod also bears another moderate terminal seta, making a total of six in the series. It appears that after each
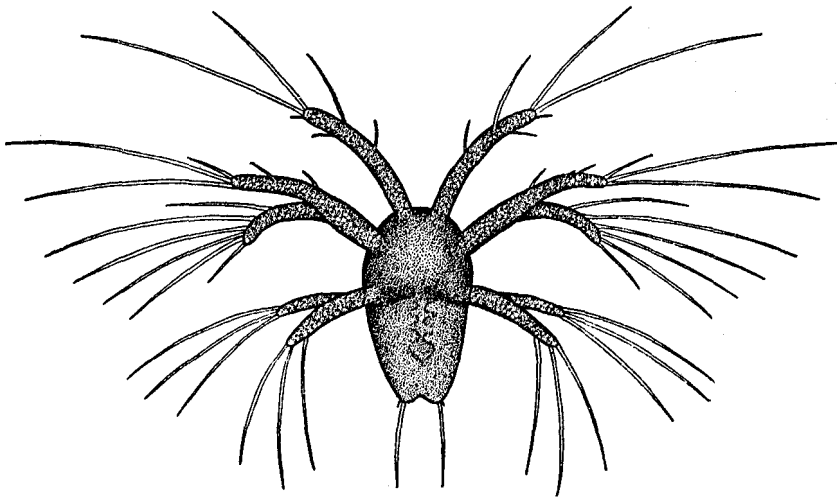

FIGURE 4.—Second nauplius of *Penaeus setiferus*. Length 0.34 mm. Ventral aspect.

naupliar molt the number of setae on the exopod of the second antenna increases by one. This character, together with a progressive increase in the number of furcal spines, appears constant and assists greatly in the differentiation of the various naupliar stages. (See table 2.) Table 2 also shows the progressive increase in the number of setae on the exopod of the second antenna and in the number of furcal spines after each naupliar molt. The range in body length and in the greatest body width are given in millimeters; measurements were made in 0.02-mm. units; based on 61 specimens obtained from the egg or plankton.

TABLE 2.—*The nauplius of* Penaeus setiferus

Stages	First	Second	Third	Fourth	Fifth
Setae on exopod	5	6	7	8	9
Furcal spines	1+1	2+2	3+3	5+5	7+7
Body length	0.30 to 0.34	0.32 to 0.34	0.36 to 0.40	0.38 to 0.44	0.46 to 0.56
Body width	.16 to .20	.16 to .18	.14 to .16	.16 to .18	.16 to .20
Number of specimens	2	6	13	26	14

Hudinaga (1935) also found a progressive increase in the number of setae on the exopod of the second antenna and in the number of furcal spines in the six naupliar

stages of *P. japonicus.* Apparently there exists no variation in the number of setae or spines within a single naupliar stage in this Japanese shrimp. Herz (1933) found that the setation at each stage in the six naupliar stages of *Balanus crenatus* was definite. However, Bassindale (1936) suggested that the sizes of the nauplii of barnacles and possibly the setation of the naupliar appendages is subject to variation from place to place for the same species. As noted later in the case of the nauplii of *Eusicyonia stimpsoni,* there appears to be a certain variation in furcal spine count in some naupliar stages of this American peneid shrimp.

There are three setae on both exopod and endopod of the mandible throughout the naupliar stages of *P. setiferus.*

Fine cilia are now evident on the longer setae of the appendages, giving a plumose or feathered appearance to the setae under high magnification. Most setae are ciliated in all later larval stages. (See fig. 12.)

Hudinaga (1935) noted that the second naupliar molt occurred in *P. japonicus* about 6 hours after hatching.

One specimen of the second nauplius of *P. setiferus* was obtained by hatching an egg; others were taken from the preserved plankton.
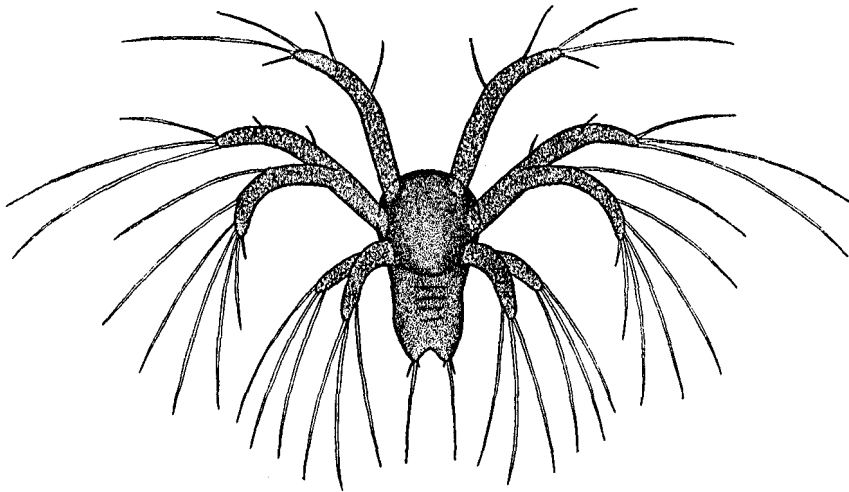
FIGURE 5.—Third nauplius of *Penaeus setiferus.* Length 0.38 mm. Ventral aspect.

THIRD NAUPLIUS

The third nauplius measures from 0.36 to 0.40 mm. in body length and from 0.14 to 0.16 mm. in greatest body width.

The body becomes more elongated posteriorly, the posterior marginal furcation more acute, and the body mass somewhat less opaque. (See fig. 5.)

The furcal spines increase to 3+3 by the addition of a weak inner spine on each furcal process.

The setation of the appendages remains practically the same with the exception that another short terminal seta is acquired on the exopod of the second antenna, making a total of seven.

The third molting of *P. japonicus* occurred about 11 hours after hatching, according to Hudinaga.

The third nauplius of *P. setiferus* was obtained by hatching one egg and from the preserved plankton.

FOURTH NAUPLIUS

The fourth nauplius measures from 0.38 to 0.44 mm. in body length and from 0.16 to 0.18 mm. in greatest body width.

The body becomes much more slender and is incurved posteriorly. Two frontal sense organs or papillae are present on the anterior margin of the body. (See fig. 6.)

Four pairs of appendages, the fourth to seventh body appendages, appear externally on the ventral surface of the body. These appendages are concealed by the cuticle in the third nauplius. Each appendage is biramous, the endopod being longer than the exopod. The appendages constitute the rudiments of the first and second maxillae and the first and second maxillipeds. They remain unfunctional until the protozoea stages.

The labrum which has become somewhat larger after each molt becomes more pointed posteriorly.
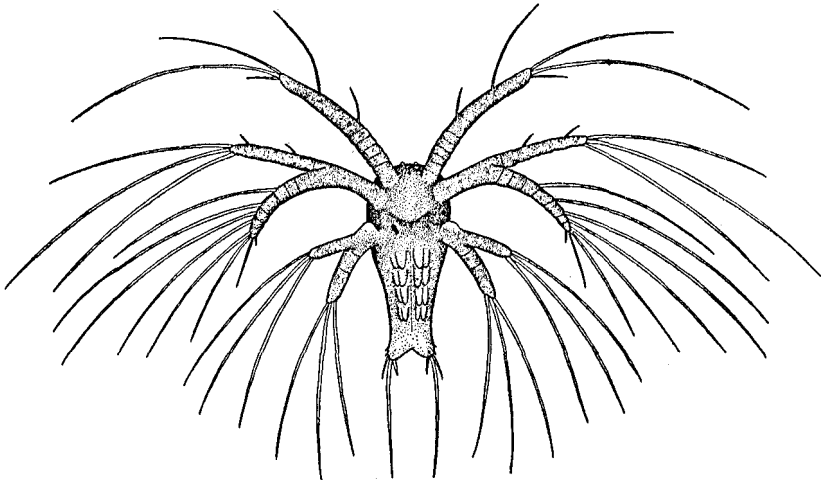

FIGURE 6.—Fourth nauplius of *Penaeus setiferus*. Length 0.44 mm. Ventral aspect.

The furcal spines increase to 5+5 by the addition of two pairs of weak spines on each outer margin of the furcal process.

The setation on the appendages remains constant with the exception that another short terminal seta is added to the exopod of the second antenna, making a total of eight. The first two pairs of antenna may show a number of indistinct joints or segments. The first antenna appears to have five segments at the proximal end of the appendage beside a long distal segment. The second antenna appears to have about eight segments on the exopod. All segments are indistinct and difficult to distinguish accurately.

A whitish somewhat globular swelling occurs on the inner side of the protopod or basal section of the mandible.

The fourth molt of the nauplius of *P. japonicus* occurred about 16 hours after hatching according to Hudinaga.

The fourth nauplius of *P. setiferus* was obtained only from preserved plankton, no larva from the egg being secured.

FIFTH NAUPLIUS

The fifth nauplius measures from 0.46 to 0.56 mm. in body length and from 0.16 to 0.20 mm. in greatest body width. The average body length is about 0.50 mm.

The body becomes quite slender posterior to the mandibles but still possesses a ventral flexure and concavity posterior to the labrum. The rudiment (posterior rim) of a carapace or dorsal shield becomes visible as a transverse fold about midway of the body on the dorsal surface. The pair of frontal sense organs become larger. (See fig. 7.)

The first and second maxillae and the first and second maxillipeds appear larger and are clearly biramous. They now possess short terminal setae.

The labrum is comparatively large and is more pointed posteriorly.

The furcal spines increase to 7+7 by the addition of the spines on the inner margin of each furcal process.

The setation of the first antenna may be increased by the addition of several short lateral setae placed near the terminal setae and by a small seta placed laterally proximal to the base of the appendage.
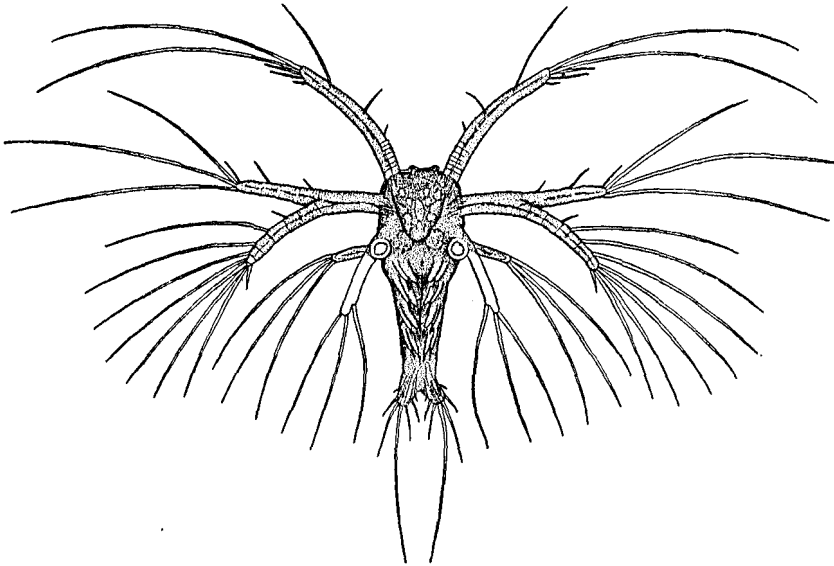

FIGURE 7.—Fifth nauplius of *Penaeus setiferus*. Length 0.56 mm. Ventral aspect.

The setation of the second antenna is increased by another short terminal seta on the endopod, making a total of four. The exopod also gains a short lateral seta, making a total of nine.

The swelling at the base of the mandible is very pronounced and shows a spherical masticatory surface. The latter appears concave and has an inner rim lined with saw-like teeth. The musculature of the endopod of the mandible is withdrawn into the basal portion of the appendage, leaving the endopod transparent and apparently functionless.

The fifth nauplius is usually less opaque than the previous four naupliar stages owing to the gradual exhaustion of internal yolk upon which the larva has sustained growth.

The molt following the fifth naupliar stage (fifth naupliar molt) brings the shrimp larva into the first protozoea stage. Although Hudinaga (1935) found six stages of the nauplius in *P. japonicus*, there appear (on the basis of rearing experiments of three species of American *Penaeidae*) to be only five stages of the nauplius in these species. As the five naupliar stages of *P. setiferus* show the various developmental characters

in about the same sequence as the six stages of *P. japonicus*, it is difficult to determine where the possible loss of one naupliar stage of *P. setiferus* might occur in the series if it is assumed that six naupliar stages are the normal number among the *Penaeidae*. On the basis of the descriptions of the nauplii of *P. japonicus*, perhaps the first two stages of this species may be combined in the first stage of *P. setiferus*.

It is significant that the first nauplius of both species of *Penaeus* have five setae on the exopod of the second antenna and a single pair of furcal spines. The last nauplius stage has seven pairs (7+7) of furcal spines (in both species) but the number of setae on the exopod of the second antenna appear to differ. As indicated by the setation formulae of the naupliar stages of two other *Penaeidae* described in this report, a difference in the numerical relation between the furcal spines and the setae on the exopod of the second antenna occurs among the nauplii of the various species.

Hudinaga (1935) noted that the fifth naupliar molt of *P. japonicus* occurred about 23 hours after hatching of the egg. In *P. setiferus* the entire naupliar period was passed through within 24 to 36 hours. No food is ingested during the naupliar stages of development.

The fifth nauplius of *P. setiferus* was obtained for examination only from preserved plankton with the exception of one specimen reared to the first protozoea.

FIRST PROTOZOEA

The first protozoea of *P. setiferus* measures from 0.80 to 1.14 mm. in body length based on the examination of 35 specimens. The body length of the first protozoea extends from the anterior margin of the carapace to the tip of the forked tail. Subsequent larval stages were measured for body length from the tip of the rostrum to the tip of the forked tail or telson.

The body has undergone a pronounced morphological change since the fifth nauplius primarily owing to the further development and functional use of the first and second maxillae and the first and second maxillipeds; to the formation and use of jaws, mouth, oesophagus, stomach, intestine, and anus; to the development of a flexible, partially segmented abdomen; and to the formation of a carapace, or dorsal shield attached to the tergites of the body segments anterior to the second maxillae. The body lacks pigmentation and is nearly transparent. (See fig. 8.)

The carapace is considerably depressed, rounded anteriorly but nearly square posteriorly. It tends to bend downward and cover laterally the mouth parts and the basal portions of the maxillipeds. It possesses no spines or other protuberances and shields the body loosely. The carapace measures 0.46 mm. in length and 0.36 mm. in greatest width on a first protozoea with a body length of 0.86 mm.

An ocellus is still present while a pair of sessile compound eyes is shielded dorsally by the anterior portion of the carapace. Frontal sense organs are lacking.

The labrum, or upper lip, is considerably smaller than in the naupliar stages. The anterior edge is now sharply pointed while the posterior edge is rounded and covers a section of the mandibles. A labrium, or lower lip, is developed during the naupliar stages but cannot be distinguished without dissection either in the nauplius or protozoea.

The first antenna is a uniramous appendage, consisting of three segments. The basal segment is divided, however, into five subsegments, the latter fusing into a single basal segment in the third protozoea. The second or middle segment is the longest and has two short and one moderate setae along the lateral margin. The distal segment has four setae at the tip, one much longer than the rest, and a mod-

erate seta on the lateral margin near the tip. The setae are quite similar in arrangement and number to those on the fifth nauplius.

The second antenna remains biramous and is as long or longer than the first antenna. The protopod, or basal portion of the appendage, is typically divided into two segments. The endopod consists of two segments; a distal segment bearing four long terminal setae and a proximal segment bearing two short separate lateral setae together with a pair of moderate setae arising from a notch at the articulation with the distal segment. The proximal segment is the longer of the two. The endopod is somewhat shorter and weaker than the exopod. The exopod consists of 9 to 10 segments. The exact number is obscure in most instances. A latero-distal series of 10 moderate to long setae is present, an increase of one lateral seta compared to the number on the fifth nauplius. Five setae occur on the distal segment and one on each successive segment. Two short setae are present on the outer lateral margin.

Gurney (1926) noted that the proximal seta is borne by the third joint (from base) and the second on the fifth joint, the fourth having none. This position probably
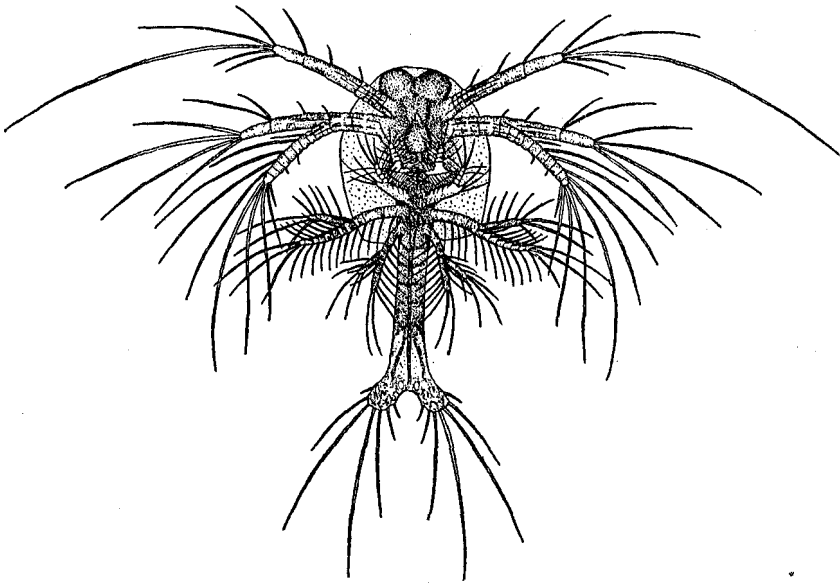

FIGURE 8.—First protozoea of *Penaeus setiferus*. Length 0.90 mm. Ventral aspect.

occurs in the protozoea described in this report although not placed accordingly in the illustrations because of the indistinct segmentation.

The mandible is modified into a flattened plate with a serrated edge on the inner margin. The movement of the serrated edges of the two mandibles has a scissorlike masticating effect on ingested particles of food. Both endopod and exopod have been temporarily lost. The mandibles are largely concealed by the labrum and the thick setae on the maxillae.

The first maxilla consists of a protopod of two segments, an endopod of three or four segments, and an exopod of a single segment. The protopod has a lobe or endite on the inner margin of each segment, each lobe bearing about four setae. The segments of the endopod form a slender palplike structure and each segment, except the distal segment, has a pair of setae along the inner margin. The distal segment has four setae. Several outer lateral setae are also present on the endopod.

The exopod or scaphognathite consists of a small lobe bearing about two setae and is not separated from the protopod by any evident articulation.

The second maxilla has a protopod with the inner margin divided into four small lobes or endites, each lobe bearing two inwardly directed setae. The endopod is composed of four (possibly five) segments, each provided with at least a pair of setae. Four setae occur on the distal segment. The exopod or scaphognathite is knoblike, somewhat similar to that of the first maxilla, and bears three setae. The second maxilla is larger than the first. Both maxillae, often termed "lower jaws," assist in the selection of food materials.

The first maxilliped is an elongate, biramous structure, apparently useful to the protozoea in locomotion. The protopod is composed of two segments and a row of four setae. The endopod appears to be composed of nine segments, each segment excepting the distal one bearing a pair of setae. The distal segment has four setae at the tip. The exopod is shorter than the endopod and is composed of a single segment that bears about four lateral and four terminal setae.

The second maxilliped is considerably smaller than the first. The protopod has two segments and bears four setae on the lateral margin. The endopod consists of five segments and bears five setae along one lateral margin and two setae on another lateral margin. The distal segment has three terminal setae. The exopod consists of a single segment with about seven setae placed along the lateral margin and at the tip.

Traces of the thoracic somites, posterior to the second maxillipeds, are faintly discernable but there are no evidences of appendages. The abdominal somites are not differentiated at all.

The bifurcation of the tail is much stronger than in the fifth nauplius. The median notch made by the bifurcation is semiovate. The size and shape of this notch afford diagnostic characters of considerable value. The furcal spines remain the same in number (7+7) as in the fifth nauplius.

The internal anatomy of the first protozoea is somewhat obscure, although the alimentary canal is clearly visible in live larvae. Superior to and around the ocellus lies the cerebral or cephalic ganglion, probably giving off nerves to the eyes and the antennae. A chain of nerve ganglia probably extends the length of the body.

The alimentary canal consists of an oesophagus, stomach, and intestine, and extends from the mouth or stomadeum (placed dorsal to the mandibles) the length of the body to the anus, which opens somewhat ventrally at the apex of the notch at the posterior end of the body. The liver consists of two large equal lateral lobes, one lying on each side of the stomach, dorsal to the mandibles and mouth.

A heart and associated blood vessels are situated immediately below the carapace, slightly posterior to the liver and above the intestine.

A pair of elongated tubelike structures, possibly muscle fibers, occur in the posterior region of the body, one lying on each side of the intestine. Two pores appear, one on each side of the anus.

Locomotion of the first protozoea is effected chiefly by the natatory first and second antennae and, to some degree, by the first and second maxillipeds. Swimming is considerably slower than in the naupliar stages and is usually continuous. The normal beat of the antennae approximates 40 per minute, and is much slower than in other species. The protozoea appear to respond positively to light. The bottom of a glass dish illuminated by a strong light usually attracts them. They respond negatively to gravity, however, for they otherwise avoid the bottom. Touch-

ing the protozoea lightly with a needle always induces acceleration in the rate of locomotion. They frequently interrupt the swimming activity to flex the abdomen several times.

Immediately after attaining the first protozoeal stage, the larval shrimp commences to ingest suspended food particles, almost continuously. The food in the laboratory consisted largely of microscopic green algae and diatoms, although considerable matter of unknown identity was also ingested. Much care had to be exercised to introduce only small amounts of algae for the plumose setae on the protozoea easily became entangled by any particles of sediment. The accumulation of foreign matter on the setae, especially around the mouth parts, frequently prevented movement and eventually caused the larva to die by starvation. Herrick (1909) noted that a primary cause of death for artificially reared lobsters is the accumulation of sediment on the hairs of the appendages, interfering with the locomotion of the larva and sending it to the bottom, thus cutting off its supply of food. The protozoea always emitted long filaments of excrement that also tended to bind the appendages and slow down normal movement. These long filaments of excrement were recognized by Hudinaga (1935) as constituting a major factor in the high mortality of the protozoea of *P. japonicus* in confinement.

Most first protozoea of all species reared died before reaching the second protozoeal stage. This condition was largely caused by the difficulty in preventing the sedimentation of the larva correlated with the inability of the latter to obtain food. Proper apparatus for maintaining a gentle current in small glass dishes plus the addition of only pure cultures of diatoms or microscopic algae to the sterile sea water would greatly cut down the mortality of the protozoea in any future experiments in rearing young shrimp.

As the protozoea is nearly transparent, the rapidity of passage of food particles through the body can be readily observed. Observations indicated that microscopic green algae passed through the alimentary canal within 15 to 30 minutes. The obtainment of suspended food is apparently accomplished only while swimming and by the movements of the maxillae and maxillipeds in drawing a current of water to the mouth. The setae on the maxillae serve to eliminate particles of food unsuited to the larva.

The first protozoea of *P. setiferus* was obtained by hatching four eggs and rearing the larvae through the naupliar stages. Additional material was secured from preserved plankton.

SECOND PROTOZOEA

The second protozoea measures from 1.3 to 1.7 mm. in body length, based on the examination of 45 specimens.

The carapace extends posteriorly to cover the fifth to sixth thoracic somites. It has developed a slender frontal process or rostrum which is somewhat decurved and extends forward to the distal articulation of the first antenna. The carapace also has on its anterior margin a large supra-orbital spine on each side of the rostrum, directed forward and reaching about halfway of the rostrum. The carapace tends to fit the body more closely, the posterior dorsal margin having a shallow sinuosity. (See fig. 9.)

The pair of compound eyes are now stalked, movable, and free from the carapace. They extend to approximately the tip of the rostrum when flexed forward.

The labrum, mandibles, first and second maxillae, and first and second maxillipeds remain essentially the same in structure as in the first protozoea. The setae on the natatory appendages, however, tend to become shorter. There is an additional

seta on the lateral margin of the exopod of the second antenna, making a total of 11 in the latero-distal series.

Rudimentary buds of the pair of third maxillipeds and the following five pairs of pereiopods are evident. All thoracic somites and the first five abdominal somites can be distinguished.

Rudiments of the uropods appear under the cuticle posterior to the fifth abdominal somite.

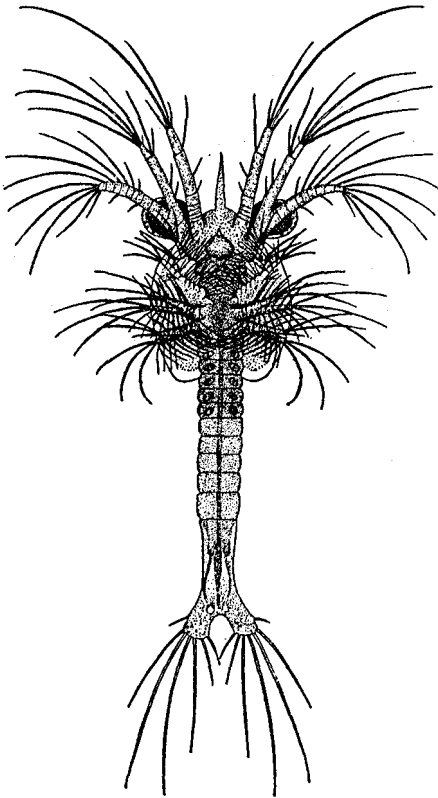The number of spines on the furcal process at the tail remain at 7+7.

FIGURE 9.—Second protozoea of *Penaeus setiferus*.
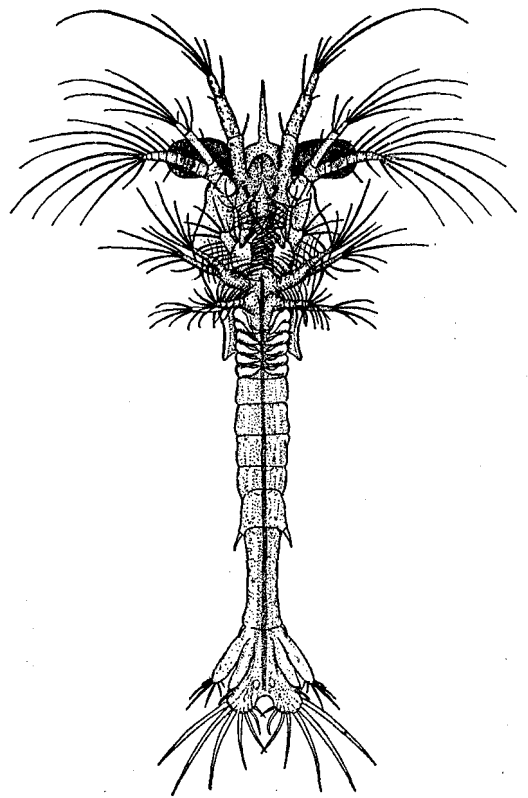Length 1.8 mm. Ventral aspect.

FIGURE 10.—Third protozoea of *Penaeus setiferus*.
Length 2.3 mm. Ventral aspect.

The second protozoea was obtained only from plankton, usually found together with first and third protozoeal stages. No larvae could be reared from the egg.

THIRD PROTOZOEA

The third protozoea measures from 2.2 to 2.6 mm. in body length, based on the examination of 17 specimens.

The carapace and the various appendages from the first antennae to the second maxillipeds remain essentially the same as in the first and second protozoea. An additional seta is added however to the exopod of the second antenna, making a total of 12. (See figs. 10 to 13.)

The third maxillipeds now appear externally but are rudimentary in structure and functionless. They are biramous, both exopod and endopod bearing several short setae. The exopod is slightly longer than the endopod.

Five pairs of pereiopods are also externally differentiated although rudimentary. They are biramous but lack setae. The exopod is again longer than the endopod in all cases.
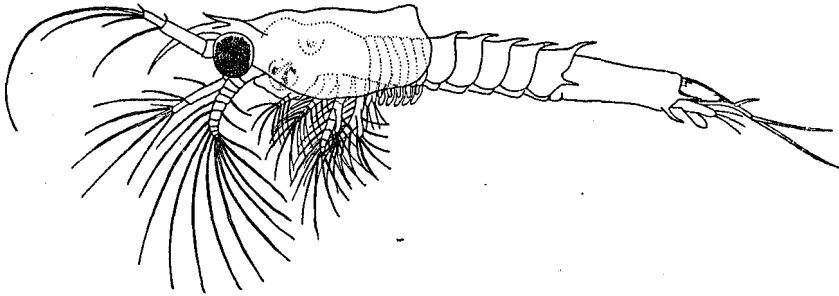

FIGURE 11.—Third protozoea of *Penaeus setiferus*. Length 2.4 mm. Lateral aspect.

A backwardly directed dorso-median spine occurs on the posterior margin of the first to fifth abdominal somites, the spine on the fifth somite being the largest. The fifth abdominal somite had a backwardly directed spine on each postero-lateral margin.
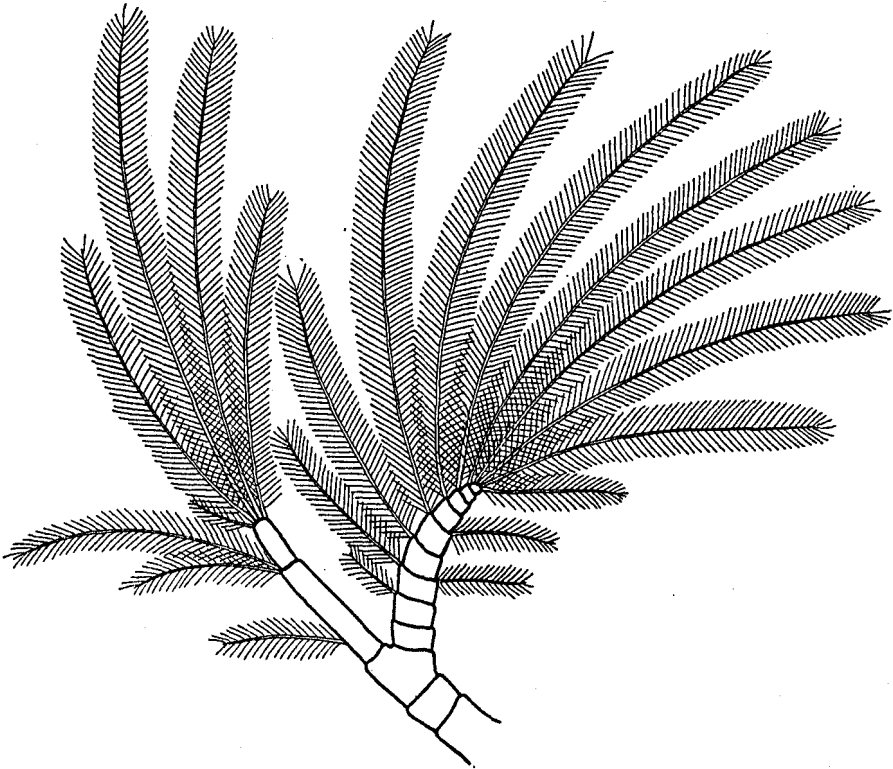

FIGURE 12.—Second antenna of third protozoea of *Penaeus setiferus*, showing ciliated nature of setae.

The sixth abdominal somite has a spine on each postero-lateral margin and also a long spine at each postero-ventral angle of the somite.

A pair of biramous uropods appear externally from the ventro-posterior margin of the sixth abdominal somite. The uropods extend to the apex of the notch in the tail or telson. The outer branch of each uropod is the larger and bears six terminal setae. The sixth abdominal somite is now separated from the telson and all body somites are completely differentiated.

The spines on the telson have increased to 8+8 by the addition of an inner short spine on each furcal process.

The third protozoea was obtained in plankton. Earlier protozoeal stages and mysis stages usually accompanied the third protozoea.

FIRST MYSIS

The first mysis measures from 3.2 to 3.8 mm. in body length, based on the examination of eight specimens.

The body of the first mysis shows remarkable development of the thoracic appendages, the latter taking over the natatory function of the antennae. The cephalic and thoracic parts become united to form the cephalothorax while the abdominal somites, particularly the sixth, are greatly elongated. (See figs. 14, 15.)

The carapace covers the body segments anteriorly to the last thoracic somite. The rostrum is slender, slightly decurved, and extends to the tip of the eye. The supra-orbital spines are not so pronounced as in the third protozoea, now reaching forward not more than a quarter the length of the rostrum. A pair of small hepatic spines appear, one on each side of the carapace, to the rear of the eye, and slightly set back from the anterior margin of the carapace. The antero-ventral margin of the carapace is sharply spined. The postero-dorsal surface of the carapace is incurved, permitting the carapace to fit the body more closely.

The first antenna is composed of three basal segments and a short, branched structure, the future flagella, now rises from the end of the distal segment. Four to five tactile setae occur at the tip of the larger outer branch of the flagella. Tactile setae also oc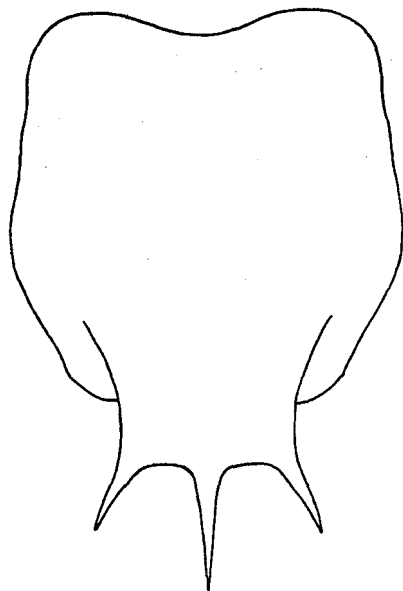cur along the inner margin of the third segment and at the articulations of the segments on the outer margin. The first antenna is now tactile rather than natatory in function.

FIGURE 13.—Carapace of third protozoea of *Penaeus setiferus*, showing form of rostrum and supraorbital spines. Dorsal aspect.

The second antenna shows considerable change from the third protozoea. There is a protopod of two segments, an exopod consisting of a flattened, unsegmented, antennal scale and an endopod consisting of an unsegmented rodlike flagellum. The endopod is shorter than the exopod, and bears about four short terminal setae and usually a pair of short setae arising from the same notch on the lateral margin as in the protozoea. The exopod has a notch on the outer lateral margin from which a single long seta rises and has, on the inner lateral margin and at the tip, a series of 11 long setae. The statement by Bate (1888) that the antennal scale is of value in helping to maintain the animal upright when swimming and, preventing it from falling into an inverted position, appears justified by observations on the movements of the mysis of *Eusicyonia* and *Trachypenaeus* at St. Augustine.

The labrum, mandibles, maxillae and maxillipeds are essentially the same in structure as in the protozoeal stages. However, the exopod or scaphognathite of the first maxilla appears reduced or wanting while that on the second maxilla appears more elongated and larger.

The third pair of maxillipeds are much longer than the first two pairs. Each maxilliped consists of a protopod of 2 segments, an endopod of 5 segments, and an exopod of 1 segment. Lateral and terminal setae are present on the endopod and short terminal setae occur on the exopod.

Five pairs of biramous pereiopods are well developed with functional exopods. Each pereiopod has a protopod of two segments, an endopod of one or more indistinct segments, and an exopod of a single segment. The exopod is at least twice as long as the endopod, and bears about five long terminal setae. The endopod of the first three pairs of pereiopods is stout, bears about three terminal setae, and shows a rudimentary chela. The endopod of the last two pairs of pereiopods is smaller, bears several setae, and is nonchelate. The pereiopods form the principal means of locomotion of the larva. An exceedingly rapid whirling motion of the long exopods enables the mysis to swim ahead in a semivertical position with the anterior region of the body elevated somewhat.

Gills are not yet developed.

Paired rudimentary buds of the pleopods appear on the first to the fifth abdominal somites, varying somewhat in degree of development among different individuals.

The sixth abdominal somite is greatly elongated and is approximately as long as the five preceding abdominal somites.

The first two abdominal somites have lost their dorso-median spines and similar spines on the third and fourth somites are reduced in size compared to those on the third protozoea. The fifth and sixth abdominal somites each possess a dorso-median spine on the posterior margin and also a spine on each postero-lateral margin. The sixth abdominal somite has a spine at each postero-ventral edge and also a weak median ventral spine at its posterior end.

FIGURE 14.—First mysis of *Penaeus setiferus*. Length 3.2 mm. Ventral aspect.

The biramous paired uropods each possess an unsegmented protopod bearing a small spine along the lateral and ventral margins. The exopods and endopods are elongated lamellae. The exopod has a weak spine on the outer distal margin and a series of seven short setae extend from this spine to the tip. Another series of nine somewhat longer setae extend from the tip along the inner margin of the exopod. The endopod is smaller than the exopod and bears a few short terminal setae.

The telson is elongated, nearly oblong, with a deep median incision in its posterior margin. A pair of small lateral spines and seven pairs of stronger terminal spines occur on the telson. The anus opens on the ventro-medial surface at the base of the telson between the basal segments of the uropods.

The first mysis was obtained only in plankton with protozoeal and postlarval stages.

SECOND MYSIS

The second mysis measures from 4.0 to 4.4 mm. in body length, based on the examination of four specimens.
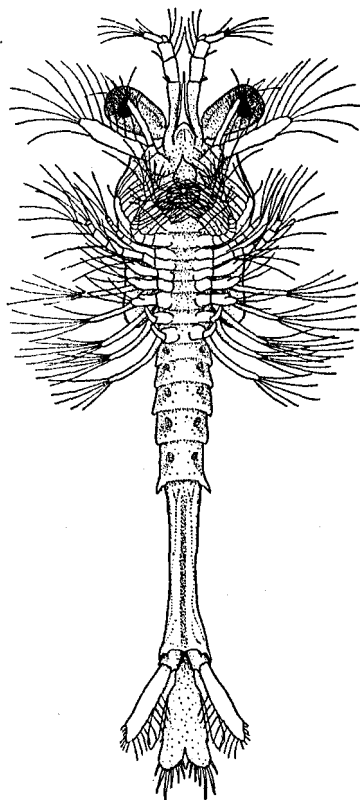
The carapace fits the cephalothorax more closely and extends posteriorly to cover all thoracic somites. The supra-orbital and hepatic spines remain. The hepatic spines tend to move somewhat posteriorly and lower on the carapace due to the change of contour of the latter. The rostrum is nearly horizontal, extends slightly beyond the eye, and bears a single weak dorsal spine near its base. (See fig. 16.)
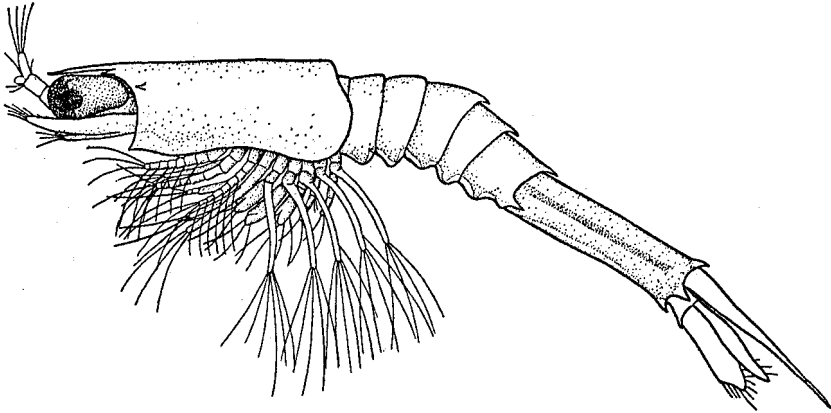
FIGURE 15.—First mysis of *Penaeus setiferus*. Length 3.2 mm. Lateral aspect.

The first antenna remains essentially the same as in the first mysis stage with the exception that the terminal flagella are longer and more nearly the same length.

The second antenna also remains the same with the exception that a weak spine appears on the ventro-anterior margin of the protopod.

The maxillae and maxillipeds remain essentially the same as in the first mysis.

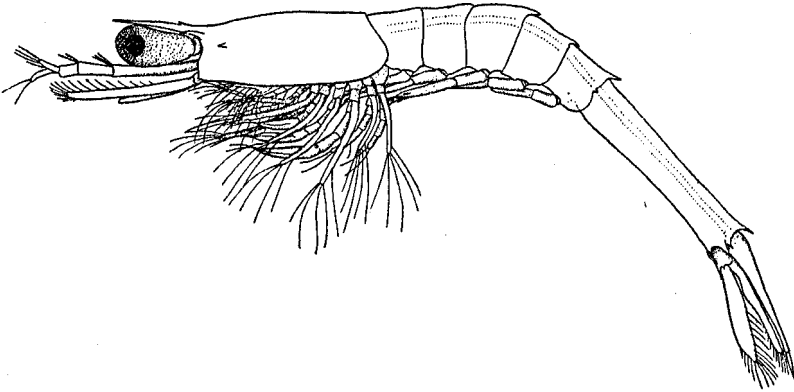The five pairs of pereiopods have reached their full larval development. The

FIGURE 16.—Second mysis of *Penaeus setiferus*. Length 4.0 mm. Lateral aspect.

exopods lack segmentation while the endopods are divided into five segments each. The former remain elongated and still serve as the principal organs of locomotion. The chelate endopods have enlarged considerably since the first mysis and the third endopod is by far the largest. The two distal segments of the endopods of the first three pairs of pereiopods, the propodus and the dactylus, are now clearly modified into scissorlike chela. The fingers of these chelae are of equal length.

Rudimentary gills appear on the thoracic somites but their number and arrangement were not determined.

A pair of pleopods appear on each of the first five abdominal somites. Each pleopod is uniramous (exopod only occurring), consists of three segments, and has a few short terminal setae. The pleopods aid in the forward movement of the mysis.

The dorsal and lateral spines on the abdominal somites remain the same as in the first mysis although generally reduced in size. The median-ventral spine on the sixth abdominal somite is larger. There is now present another postero-lateral spine on the inner margin of the sixth somite.

The uropods are slightly longer than in the first mysis and are used in conjunction with the telson to propel the larva backwards.

The telson is nearly oblong, the tip nearly square with a shallow median incision. The spines on the telson consist of three on each lateral margin and five pairs distally. All furcal spines have undergone a reduction in size since the protozoea stages.

The second mysis was obtained from plankton usually containing other larval and postlarval *P. setiferus*. One planktonic specimen, taken at St. Augustine, was reared to the first postlarva.

FIRST POSTLARVA

The first postlarva of *P. setiferus* measures approximately from 4.0 to 5.0 mm. in length.

The principal change in body structure, following the molt of the second mysis, is the disappearance of the natatory exopods from the five pairs of pereiopods. The
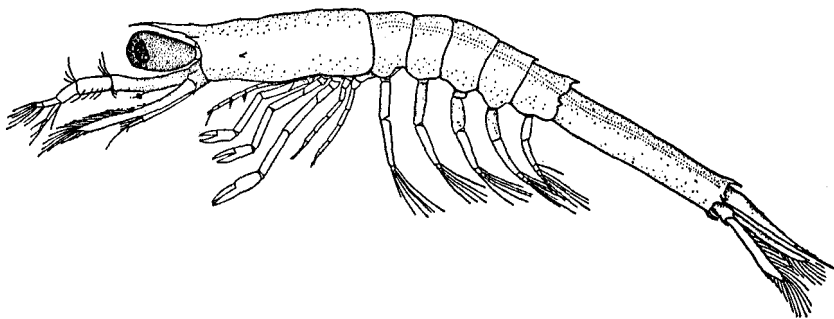

FIGURE 17.—First postlarva (postmysis or sicyonine) of *Penaeus setiferus*. Length 4.2 mm. Lateral aspect.

first three pairs of pereiopods are chelate, the third pair being the longest and extending forward nearly to the tip of the eye. The last two pairs are more weakly developed than the rest. The absence of the exopods changes the method of locomotion of the young shrimp. Forward swimming is now produced by the movement of the uniramous pleopods. The pereiopods act as walking legs and are the chief locomotor appendages after a demersal life is adopted by the young shrimp. (See fig. 17.)

The mouth parts are largely concealed by the carapace and are drawn in close to the body. The third pair of maxillipeds are as long, however, as the last two pairs of pereiopods.

Spines are present on the body somites in nearly the same arrangement as in the second mysis with the exception that the supra-orbitals are much reduced in size, the hepatics are placed more posteriorly and ventrally, and the median dorsal spine on the third abdominal somite is absent.

The first postlarva occurred in the plankton with larval and second post-larval *P. setiferus*. One first postlarva was obtained from a planktonic second mysis.[3]

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[3] The first postlarva may also be termed the first postmysis or first sicyonine stage. (See Burkenroad, 1934a, 1934b, 1939.)

SECOND POSTLARVA

The second postlarva of *P. setiferus* measures from approximately 4.5 to 6.0 mm. in length.

The disappearance of various minor larval characters is noted in this stage. The rostrum shortens to about half the length of the eye. A second dorsal spine appears posteriorly to the basal rostral spine and lies on the dorsal ridge about midway from
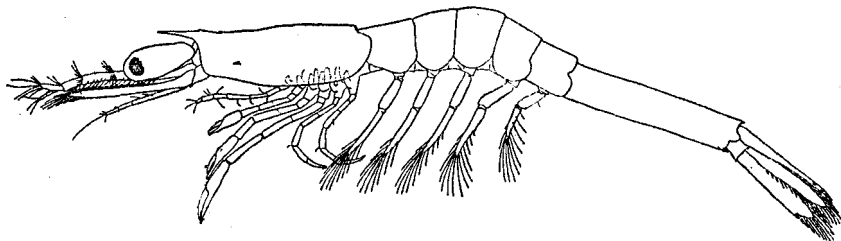

FIGURE 18.—Second postlarva of *Penaeus setiferus*. Length 4.8 mm. Lateral aspect.

the antero-lateral margin of the carapace to the hepatic spines. The supra-orbital spines have disappeared. (See fig. 18.)

Spines disappear from the abdominal somites with the exception of the median postero-dorsal and the pair of postero-ventral spines on the sixth abdominal somite.

DISTRIBUTION

EGG

Certain investigators, including Weymouth, Lindner and Anderson (1933), and Burkenroad (1934a), have discussed the probable time and place of spawning of *Penaeus setiferus*, basing their opinions principally on the inshore distribution and seasonal occurrence of mature adult shrimp off the coasts of Louisiana and Georgia. The scarcity of spermatophore-bearing females in inshore areas would indicate that spawning occurs largely in the deeper offshore waters (outer littoral areas) in which commercial or experimental trawling for shrimp has been negligible. The period of spawning apparently extends from early spring through midsummer, indicated by the seasonal occurrence of limited numbers of mature adult shrimp in inshore waters and by the presence of young demersal shrimp in estuarine areas. The presence of a planktonic postlarval penaeine of undetermined identity in the inshore oceanic waters off the coast of Louisiana was also believed by Viosca (1920) to indicate an offshore spawning habitat.

Other corroborative evidence to indicate a general offshore spawning habitat is now afforded through plankton collection of eggs, larvae, and postlarvae of *P. setiferus* from the coasts of Louisiana, Georgia, and Florida.

The eggs of *P. setiferus* were secured in small numbers only at St. Augustine Inlet, Fla. This localization appears to have been caused largely by the demersal character of the egg and the resultant inadequacy of the plankton sampling. It appears likely that in open sea where the eggs are probably spawned on or close to the sea bottom they necessarily remain near the bottom and are thus out of reach of the ordinary types of plankton-collecting gear.

Plankton collections at St. Augustine and Ft. Pierce, Fla., were made, however, largely in the narrow channel or inlet inside the barrier shoals separating the open ocean from the estuarine rivers. The oceanic water on flood tide strikes the shoals at the entrance to the inlet and is forced into the restricted channel with considerable velocity. This tidal movement of water consequently tends to mix the oceanic

plankton normally stratified in surface and bottom areas. The current in the inlet is always strong during flood tide and appears to keep peneid eggs and other demersal organisms in suspension and hence available for capture by the plankton nets.

This mixture of surface and bottom oceanic plankton in St. Augustine Inlet was clearly indicated by the collection of the many eggs of several other species of *Penaeidae* in St. Augustine Inlet although surface plankton collections made from 1 to 3 miles offshore, over several years, failed to secure a comparable number of shrimp eggs of any one species.

Despite the normal demersal existence of the peneid egg, the eggs of several species of *Penaeidae* were taken in limited numbers at sea off the coasts of Louisiana, Georgia, and Florida. However, in most instances the eggs were secured in net hauls made close to the bottom, or at least at considerable distance below the surface of the sea.

The eggs of *P. setiferus* were taken in St. Augustine Inlet on five separate dates from April 13 to 30, 1936, and on July 20, 1936. They were secured only on the flood
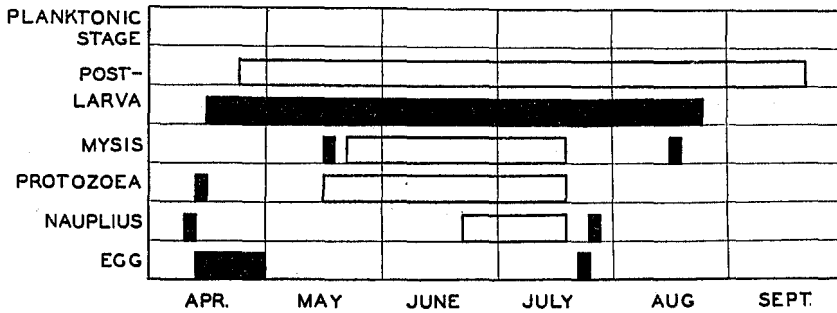

FIGURE 19.—Seasonal distribution of the planktonic eggs, larvae, and postlarvae of *Penaeus setiferus*. Solid areas represent collections along the South Atlantic coast, chiefly at St. Augustine, Fla.; clear areas represent collections off the Louisiana coast, chiefly off South West and Barataria Passes.

tide and were in late stages of development both in morning and midafternoon collections. Hudinaga (1935) found that spawning of *P. japonicus* occurs in most cases between midnight and 4 a. m. and appears to be independent of tidal phase. Assuming a similar nocturnal spawning period for *P. setiferus*, it is evident that eggs spawned sometime during the night would reach advanced developmental stages during the following day, providing the hatching period, as in the case of *P. japonicus*, occupied about 14 hours.

It is of considerable significance that the presence of the eggs of *P. setiferus* in the plankton on July 20, 1936, coincided with the capture of many mature adult shrimp off St. Augustine Inlet by commercial fishermen during the same week. Examination of the catch of these commercial shrimp on July 20 showed the presence of full (ripe) spermatophores in the males and nearly ripe (brownish) ovaries in the females. Similar schools of mature *P. setiferus* were noted off Fripp Breakers, S. C., in June 1935, and off St. Catherines Inlet, Ga., in May 1934, although no eggs were taken in surface oceanic plankton in these localities at the time.

It appears certain that the spawning of *P. setiferus*, as indicated by the limited occurrence of the eggs at St. Augustine Inlet, occurs not only at sea but probably largely in offshore areas. Other data on the distribution of larval and postlarval *P. setiferus* substantiate this statement. However, it is now definitely known that occasional schools of adult shrimp approach the coast and spawn close to inlets. The eggs may be transported into estuarine areas in small quantities, but compared to the probable enormous production of eggs in offshore waters the inshore production is almost negligible.

NAUPLIUS

The five naupliar stages of *P. setiferus* were usually taken in plankton, together with later larval and postlarval stages. Nauplii were secured on June 20 and 21, 1934, at three localities off the coast of Louisiana, 2 miles off South West Pass and 14 to 30 miles southeast of Barataria Pass. Nauplii were also taken on July 10, 1932, and from July 16 to 18, 1934, at points within a 7-mile radius of South West Pass and at 5 miles off Barataria Pass. The fifth naupliar stage appeared to be the most abundant in the plankton. (See fig. 19.)

The nauplius of *P. setiferus* was taken along the South Atlantic coast of the United States in fewer numbers than along the coast of Louisiana, possibly because fewer plankton collections were made in offshore waters off the South Atlantic coast, whereas the collections off the Louisiana coast were generally located in offshore waters ranging from 60 to 150 feet in depth. Nauplii were secured from 2 to 4 miles off Lighthouse Inlet and Gaskins Bank, S. C., on May 17 and 19, 1933, and on July 20, 1936, at St. Augustine, Fla.

Nauplii were also secured by hatching a series of eggs taken at St. Augustine Inlet during April and July 1936.

It is difficult to state the areas of greatest abundance of the nauplius of *P. setiferus* for it appears probable that the plankton collections were largely limited to the inner fringe of the spawning grounds. The area in which most nauplii were taken lay, however, in the relatively deep water adjacent to the Delta of the Mississippi River. Inasmuch as later larval stages of *P. setiferus* were also taken in abundance in this area, the latter probably constitutes one major locality at which the species spawns. (See table 3.)

Nauplii were taken in both surface and subsurface plankton, but the number of larvae were too meager and the methods of collection too inexact to determine with finality the vertical distribution of the larvae. It is known from the rearing experiments that the nauplius tends to move toward light and hence probably moves away from the sea bottom after leaving the egg. Careful experiments to determine the reactions of the peneid larvae to light and other physical conditions would prove most valuable.

TABLE 3.—*Seasonal and geographic distribution of planktonic* P. setiferus *along the South Atlantic and Louisiana coasts*

Date	Locality	Egg	Nau-plius	Protozoa			Mysis		Post-larva
				First	Second	Third	First	Second	
Apr. 12, 1936	St. Augustine Inlet	X							
Apr. 12, 1935	2 miles off St. Catharine's, S. C			X					
May 14, 1931	Off Louisiana coast				X				
May 25, 1931	10 miles south of Barataria Pass				X	X	X	X	X
May 1931	Off Louisiana coast		X	X	X	X	X		X
May 14, 1935	St. Augustine Inlet						X		X
June 20, 1934	14 miles south of Barataria Pass		X						X
Do	40 miles south of Barataria Pass		X	X	X	X		X	X
June 21, 1934	2 miles off South West Pass		X						X
June 29, 1935	St. Augustine Inlet							X	X
July 3, 1931	3 miles south of Barataria Pass				X				X
Do	6 miles south of Barataria Pass				X	X			X
July 8, 1932	12 miles east of Barataria Pass				X				X
July 10, 1932	5 miles east of Barataria Pass		X						
July 11, 1934	12 miles south of South West Pass			X	X				
July 15, 1934	12 miles southeast of South West Pass			X	X				X
July 16, 1934	3 miles east-southeast of South West Pass		X						
Do	7 miles southwest of Point Eads		X						
July 17, 1934	7 miles east-southeast of South West Pass		X				X		
Do	3 miles southeast of South West Pass						X	X	X
July 18, 1934	1 mile southwest of South West Pass			X	X	X	X		X
Do	3 miles west of South West Pass				X				
July 20, 1936	St. Augustine Inlet	X	X						
Aug. 5, 1936	do						X		X

PROTOZOEA

The protozoeal stages were obtained in plankton taken principally during July 1931, 1932, and 1934 off the coast of Louisiana. Protozoea occurred at 5 localities within a 7-mile radius off South West Pass and at 3 localities from 3 to 12 miles southeast of Barataria Pass. Collections of larvae were also made in May 1931 and 1934 from 6 to 12 miles south of Barataria Pass, and on June 20, 1934, about 30 miles southeast of this pass.

A single first protozoea was taken on April 12, 1935, 2 miles off St. Catherine's Inlet, Ga. This record was the only one from South Atlantic waters.

Nearly all protozoea were taken at subsurface levels, in depths ranging from 60 to 180 feet. Simultaneous plankton collections at the surface of the sea failed to secure protozoea in those areas that afforded large numbers of larvae at subsurface depths. However, the extreme complexity of currents and salinities off the delta of the Mississippi River render a discussion of the vertical distribution of peneid larvae quite impossible at the present time.

The fact that most protozoea, as well as the naupliar and mysis stages of *P. setiferus* and other species, were concentrated at definite points proximal to the Delta of the Mississippi River may substantiate the idea of Gurney (1924) who thought it probable that the larvae of decapods are not so much at the mercy of the currents as might be supposed. As Gurney remarked, it is not very unusual to find swarms of the larvae of one species in different stages of development, which seems to indicate a power of keeping together from hatching onwards, or of collecting in a suitable locality. The marked geographic concentration of the larval stages of *P. setiferus* will be compared to the wider dispersion of the planktonic postlarvae at a later point.

MYSIS

The first and second mysis stages were infrequently taken in the plankton. The occurrence of single individuals on May 14 and June 29, 1935, and on August 5, 1936, at St. Augustine Inlet provided the only inshore records. Mysis stages were most numerous off South West Pass, La., during July 1934. Other collections of mysis stages were made on May 25, 1931, and on June 20, 1934, at localities from 10 to 30 miles off Barataria Pass, La.

POSTLARVA

The entire larval period of *P. setiferus* is normally spent in the open sea. Furthermore, the second mysis molts into the first postlarva while the latter in turn generally molts into the second postlarva before the young shrimp reaches the coast line and enters the estuarine areas. Hence, the young shrimp, up to a length of approximately 7 mm. (0.25 inch), is strictly a member of the oceanic plankton and normally passes the first and part of the second postlarval stage at sea prior to adopting a demersal habitat in shallow, muddy estuarine bays and rivers.

Postlarvae, generally in the second postlarval stage, were abundant in the plankton at St. Augustine Inlet from April 15 to August 25, 1936, and over a nearly comparable seasonal period from 1931 to 1934 off the coast of Louisiana from the Delta of the Mississippi River west to Barataria Pass. Collections of planktonic postlarvae within the same seasonal period as at St. Augustine were secured off the coast of South Carolina, Georgia, and northern Florida. The first postlarval stage was generally limited to the deeper, offshore waters off South West Pass, La., and occurred in plankton with larval stages. No planktonic post larvae were taken south of St. Augustine.

The maximum seasonal abundance of planktonic postlarvae occurred during May and June at all localities. The vicinity of coastal inlets or passes, leading from the sea to estuarine waters, appeared to have the heaviest concentration of planktonic young shrimp. The incoming tidal currents brought vast quantities of postlarvae into the inlets and eventually to the nursery areas provided by estuarine bays and rivers.

GROWTH, POSTLARVAE

Data on the growth of the young of *P. setiferus* are based on rearing experiments conducted at St. Augustine during 1936. Postlarvae from 5 to 7 mm. in length were removed from the plankton and placed in aquaria. The young shrimp were extremely active at first, swimming incessantly around the aquarium, but settled within a day to the bottom to begin feeding. The bottom of each aquarium was covered with a shallow layer of estuarine bottom deposit consisting largely of fine sand and organic debris. The young shrimp grew rapidly and, at about 15 mm. in length, commenced to eat such introduced foods as raw fish, angleworms, and shrimp meal. The olfactory perception of food was most acute and the shrimp soon learned to swim to the surface of the water and take food from the fingers.

A 1-gallon circular glass bowl was used as an aquarium and was kept nearly filled with estuarine sea water that had a specific gravity of approximately 1.020 at 80° F. (21° C.). Fresh artesian-well water was added to compensate for evaporation. It was found that shrimp could be reared successfully in these bowls over an indefinite period of time provided that unconsumed food was removed and not allowed to pollute the water. Most aquaria were kept in moderate light to permit a growth of green algae. The latter were ingested in large quantities by shrimp but it did not appear to satisfy hunger.

The aquarium water was held at temperatures that fluctuated from about 75° to 90° F. (24° to 32° C.) and was not aerated. No excessive mortality of shrimp occurred provided that the postlarvae were obtained from the plankton in vigorous condition and that surplus food was removed before decomposition.

Series A consisted of two postlarvae, approximately 6 mm. in length and in the second postlarval stage, placed in an aquarium with two postlarval *P. brasiliensis*, approximately 8 mm. in length, on June 26, 1936. The young of *P. setiferus* were held until August 8, when they were preserved and found to measure 27 to 35 mm. each. The growth increment during the 43-day period of confinement was 21 and 29 mm. for these shrimp. This series provided the most reliable data on the probable rate of growth under normal conditions, for the shrimp were not overcrowded and apparently secured sufficient food.

Series B consisted of a larger concentration of shrimp in an aquarium. A total of 18 postlarvae of *P. setiferus*, approximately 6 mm. in length, were confined on June 22, 1936. These shrimp were held until August 10 when, after preservation, they were found to measure from 14 to 31 mm., with an average length of 20 mm. The growth increment was from 8 to 25 mm., with an average of 14 mm. for the 49-day period of confinement. It was evident that normal growth was restricted because of the larger population of shrimp in the aquarium and a resultant inability of some shrimp to obtain sufficient food for maximum growth. Constitutionally faster-growing shrimp tended to monopolize the introduced food supply and scare off the smaller individuals.

Series C consisted of 9 postlarvae of *P. setiferus*, about 6 mm. in length, confined on May 15, 1936, and held until August 8. These young shrimp measured from 22

to 35 mm. in length, with an average length of 29 mm. The growth increment was from 16 to 29 mm., with an average of 23 mm. for the 84-day period of confinement. It was evident that a limitation in maximum growth occurred quite independent of the period of confinement or the total amount of food consumed. The maximum growth of shrimp for the 84 days did not exceed that of Series A shrimp which were held for 43 days. It appears also that the size of the aquarium probably restricted the growth of the shrimp after a length of about 35 mm. had been attained. It has been noted that young *P. setiferus* tend to seek deeper, more saline water under natural conditions soon after a length of 30 mm. is reached. This movement into deeper estuarine or inshore oceanic waters does not appear to be necessitated by the absence of food in the shallow water, nor by temperature changes, although the latter cause a migration of shrimp from shallow estuarine areas in the winter.

If the maximum growth shown by Series A shrimp—29 mm. in 43 days—represents the normal average growth during the same period of time in a natural environment, certain observations on the age and growth of young *P. setiferus* of commercial size can be made. Weymouth, Lindner and Anderson (1933), who collected in Georgia
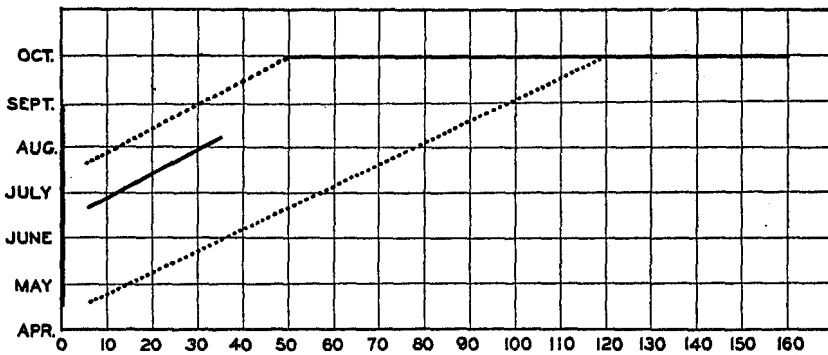

FIGURE 20.—Actual growth-rate of aquaria-held postlarval *Penaeus setiferus* (solid oblique line) compared with an assumed parallel growth-rate (dotted oblique lines) of minimum- and average-sized commercial *Penaeus setiferus* (50 and 120 mm.) taken in Georgia in October 1931 by Weymouth, Lindner and Anderson (1933). Seasonal distribution of planktonic postlarvae of *Penaeus setiferus* indicated by solid vertical line along left margin. Length given in millimeters.

waters, recorded in late July 1931 a length frequency distribution of juvenile *P. setiferus*. This distribution ranged from 70 to 110 mm. Provided these wild shrimp had the same rate of growth as shown by the captive shrimp in Series A, the date of birth for those shrimp at the modal size of the distribution (about 90 mm.) would be approximately April 1, 1931. The earliest seasonal appearance of planktonic postlarvae along the coasts of Louisiana and Florida was about April 15. (See fig. 19.) A correlation appears to exist between the known time of the earliest seasonal appearance of planktonic postlarvae of *P. setiferus* and the calculated time of arrival in estuarine waters as planktonic postlarvae of shrimp composing the early summer commercial catch.

The smallest length-frequency distribution of commercial *P. setiferus*, obtained by Weymouth et al. in Georgia waters, was secured from October 1 to 15, 1931. The minimum size of this distribution was about 50 mm. If the growth rate shown by Series A shrimp is applicable to these wild commercial shrimp, the approximate date of arrival as planktonic postlarvae in estuarine waters was about August 1, 1931. The seasonal incursion of postlarvae into estuarine waters ceases soon after the middle of August (see fig. 19) and a sharp decline in the abundance of planktonic postlarvae occurred after July 15 at St. Augustine. A close correlation thus apparently occurs

between the time of the last incursion of planktonic young shrimp into estuarine waters in early August and the calculated time of arrival of the smallest (youngest) shrimp composing a part of the October commercial fishery off the coast of Georgia.

It appears logical to assume, on the basis of the optimum growth of planktonic postlarval shrimp in confinement, that the young of *P. setiferus*, spawned offshore in late March and at the beginning of the spawning period, reach the estuarine waters as planktonic postlarvae in early April, and may enter the commercial catch at an average length of about 90 mm. (3.55 inches) by August 1; that shrimp, spawned during the peak of the spawning period in April and May, reach the estuarine waters during May and June and may comprise the greater part of the commercial fall fishery, the shrimp average 120 mm. (4.73 inches) in length by mid-October; and that shrimp spawned in late July, toward the end of the spawning period, reach the inshore waters in early August, and may enter the commercial catch in late fall or early winter.

PENAEUS BRASILIENSIS LATREILLE, THE GROOVED SHRIMP

DESCRIPTION, POSTLARVA

No larvae of *Penaeus brasiliensis* Latreille were recognized in the plankton. The smallest postlarva of this commercial shrimp measured 5.2 mm. in length and was
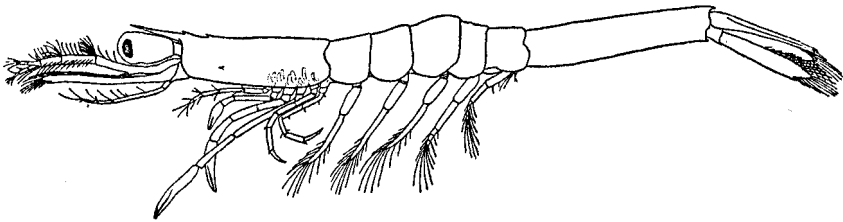

FIGURE 21.—Early postlarva (postmysis or sicyonine stage) of *Penaeus brasiliensis*. Length 5.4 mm. Lateral aspect.

taken at Ft. Pierce, Fla. It is believed that the smallest specimens of the species, taken only at Ft. Pierce, represent the second postlarval stage.[4] (See fig. 21.)

The postlarvae of *P. brasiliensis* are easily confused with the postlarvae of *P. setiferus*. As both species frequently occur together in the spring and summer littoral plankton, a differentiation is highly essential between the young of these shrimps.

There are four principal characters which separate the early postlarvae of *P. setiferus* and *P. brasiliensis*. The young shrimp at 5 mm. in length, and probably in the second postlarval stage, show the following differences when placed dorsally to each other. First, the rostrum of *P. setiferus* extends only slightly more than halfway of the eye, while that of *P. brasiliensis* extends to, or nearly to, the tip of the eye. Second, if the base of the posterior spine or tooth on the rostral ridge of one species is exactly alined with the comparable spine on the other species, it is noted that the anterior spine at the base of the rostrum on *P. setiferus* lies closer to the first anterior spine than is the case on *P. brasiliensis*. Third, the two rostral spines in *P. setiferus* are usually smaller than those in *P. brasiliensis*. Fourth, the third chelate legs of *P. setiferus*, when flexed forward, extend to, or nearly to, the tip of the eye, whereas in *P. brasiliensis* these legs are proportionally longer, extending past the tip of the eye. (See figs. 18, 21.)

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[4] Burkenroad (1939) has recently revised the *Penaeus brasiliensis* group. It would appear that the commercial shrimp, designated in this report as *P. brasiliensis*, is probably referable to *Penaeus aztecus* Ives.
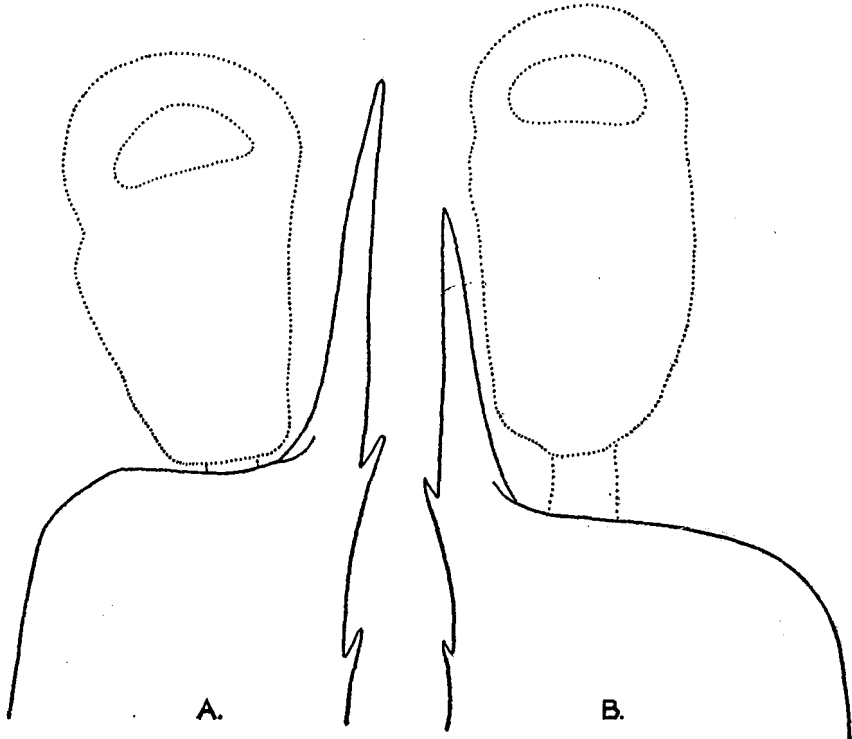
FIGURE 22.—Arrangement of rostral spines on *P. brasiliensis* (A) and *P. setiferus* (B) at 5 mm. body length.
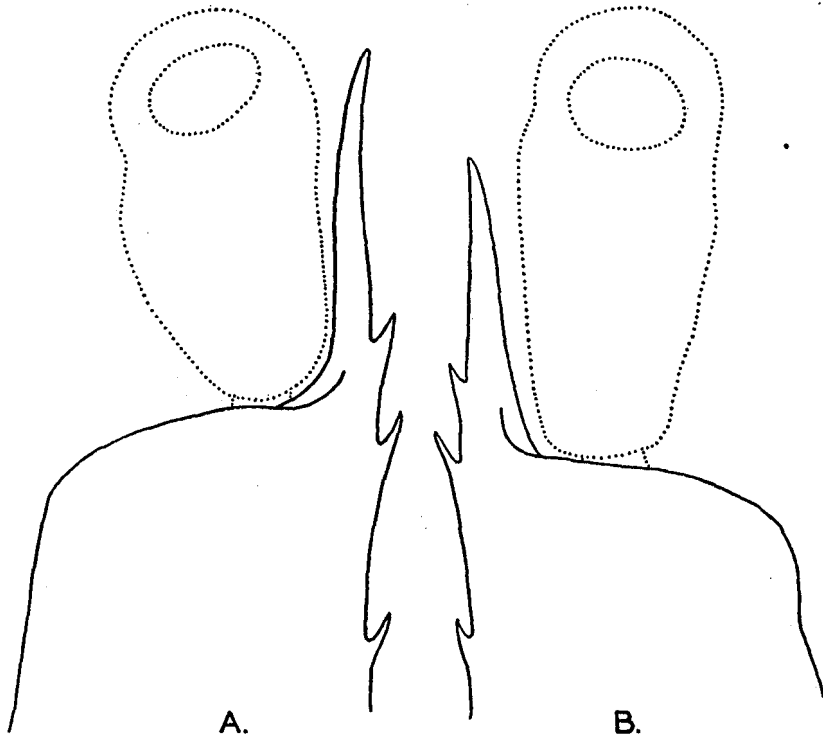

FIGURE 23.—Arrangement of rostral spines on *P. brasiliensis* (A) and *P. setiferus* (B) at 5.8 mm. body length.
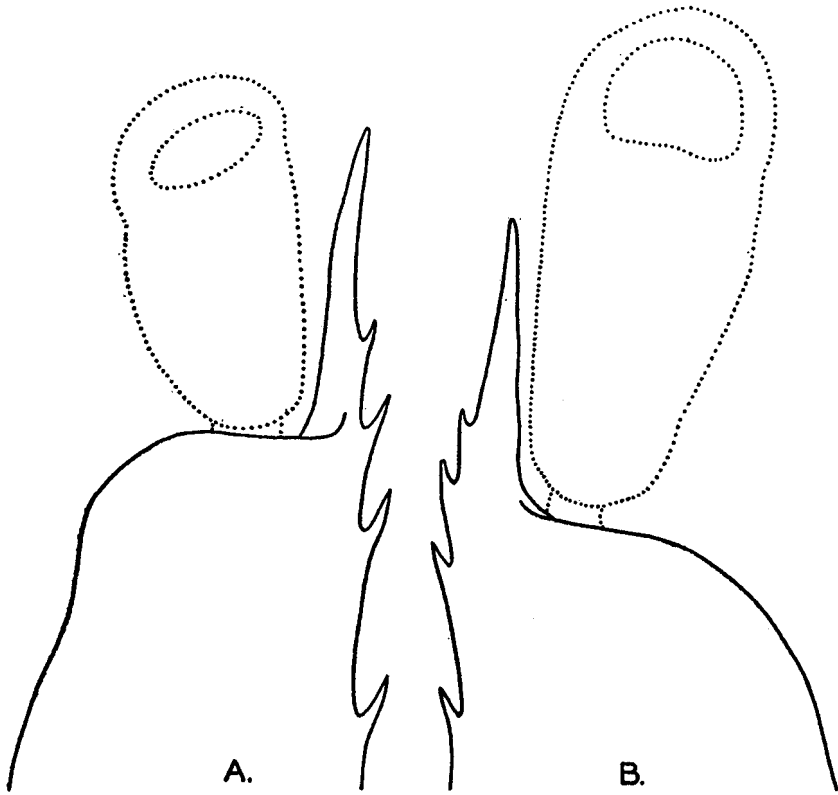
FIGURE 24.—Arrangement of rostral spines on *P. brasiliensis* (A) and *P. setiferus* (B) at 8 mm. and 7.4 mm. body length.
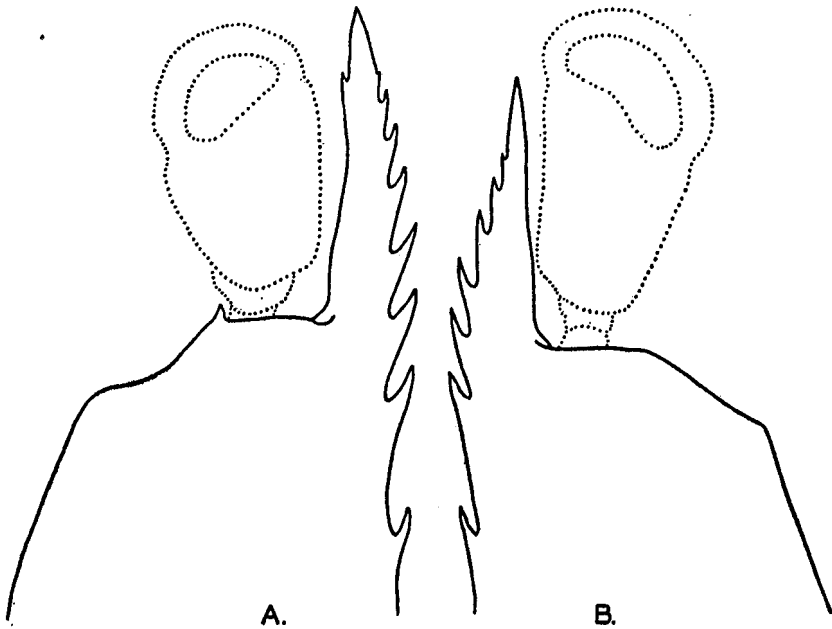

FIGURE 25.—Arrangement of rostral spines on *P. brasiliensis* (A) and *P. setiferus* (B) at 9.6 mm. body length.

Postlarvae of both species at 5.8 mm. in length and probably in the third post-larval stage have another rostral spine developed anterior to the basal spines. The relative length of the rostrum to the eye remains diagnostic, and the spacing, size, and angular formation of the three rostral spines are different in both species. (See fig. 23.)

Postlarvae of both species between 7 and 8 mm. in length, and probably in the fourth postlarval stage, have another dorsal rostral spine developed proximal to the tip. A differentiation between the two species may again be made on the basis of the relative length of the rostrum to the eye and the spacing between the rostral
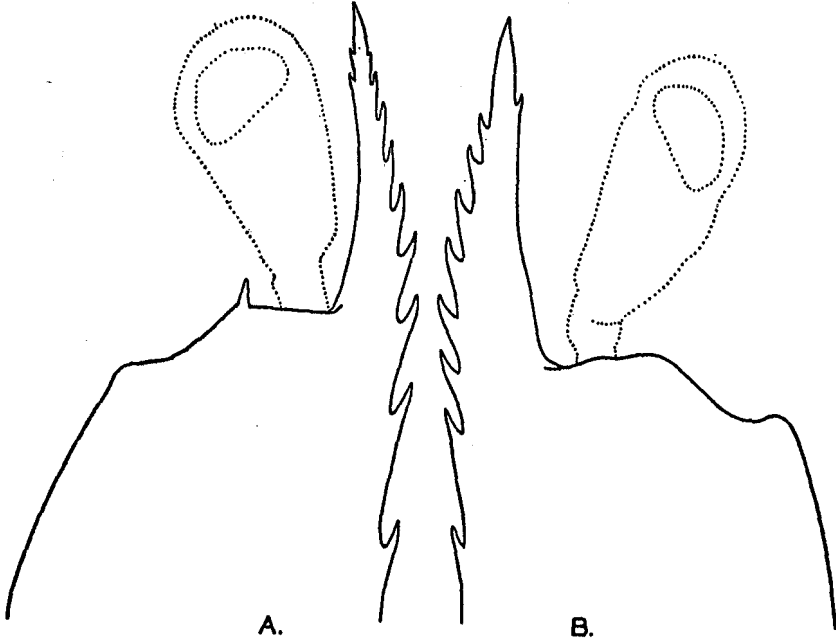

FIGURE 26.—Arrangement of rostral spines on *P. brasiliensis* (A) and *P. setiferus* (B) at 12.0 mm. body length.

spines. The fourth or distal spine of *P. setiferus* is now approximately on the same level with the third spine of *P. brasiliensis* when the posterior spines on both species are aligned. (See fig. 24.)

The postlarvae of both species between 9 and 10 mm. in length have usually adopted a bottom existence in shallow estuarine waters. Rostral spines are now developed rapidly in no apparent numerical ratio to the number of postlarval molts. The postlarval shrimp will usually possess seven dorsal rostral spines in *P. setiferus*, and from seven to eight dorsal rostral spines and one ventral rostral spine in *P. brasiliensis*. Henceforth, regardless of the exact number of spines present, the spacing between the spines remains different and will usually separate both species provided shrimp of the same approximate length are compared. (See figs. 25 to 30.)

Bate (1888) remarked that the number and arrangement of the teeth on the rostrum of the *Penaeidae* may be considered as sufficiently constant and important to be accepted as a ready and convenient guide to the determination of species. This statement certainly holds for the mysis and postlarval stages of the various species of *Penaeidae* described in the present report.
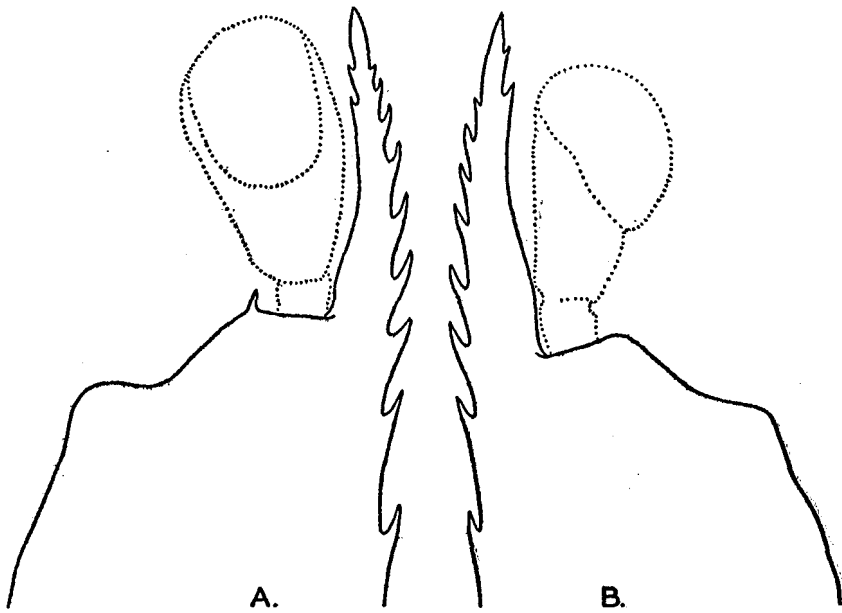
FIGURE 27.—Arrangement of rostral spines on *P. brasiliensis* (A) and *P. setiferus* (B) at 17 mm; body length.
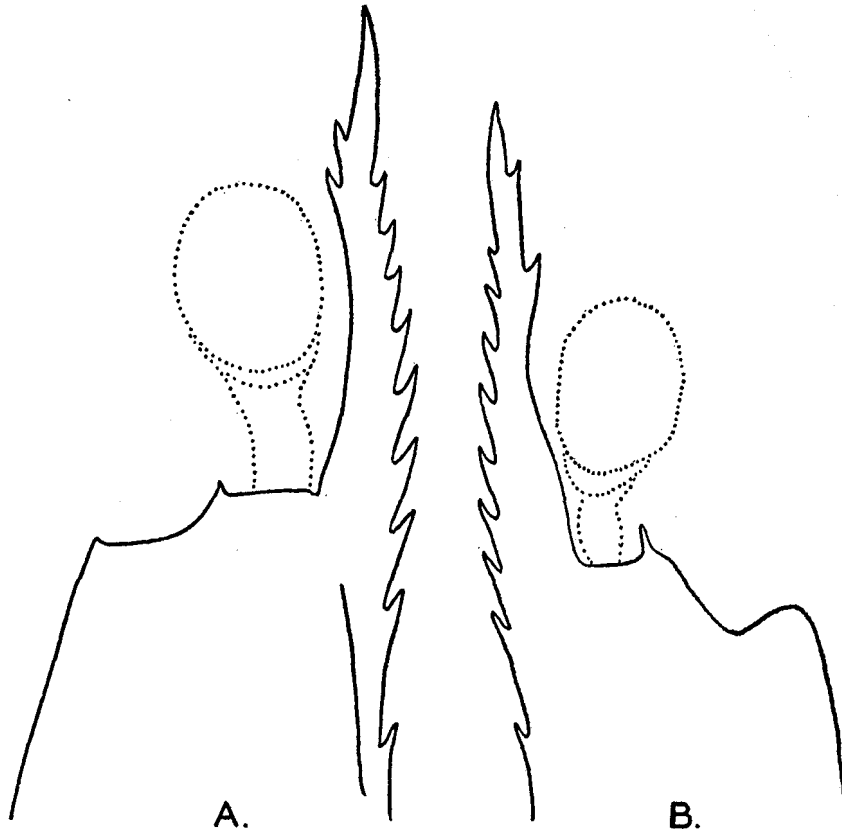

FIGURE 28.—Arrangement of rostral spines on *P. brasiliensis* (A) and *P. setiferus* (B) at 27 mm. body length.

Postlarvae of both species at 12 mm. in length have at least eight dorsal rostral spines. Nine dorsal and two ventral spines may occur on *P. brasiliensis*. One ventral rostral spine may also occur on *P. setiferus*. The difference in length of the rostrum compared to the eye no longer serves to separate the two species, but the spacing and formation of the spines remain reliable diagnostic characters.

Other specific characters appear after a length of 12 mm., to separate the young of *P. setiferus* from *P. brasiliensis*. However, the relative position of the dorsal
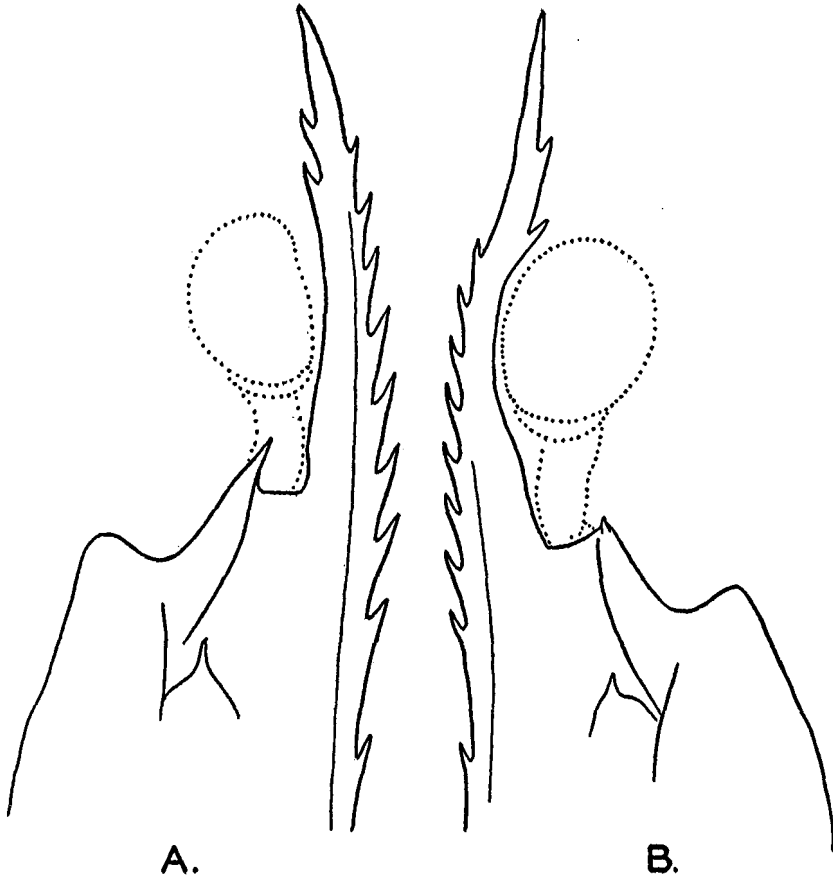

FIGURE 29.—Arrangement of rostral spines on *P. brasiliensis* (A) and *P. setiferus* (B) at 38 mm. body length.

and ventral rostral spines, to each other distinguish the two species up to adult size providing shrimp of the same length are compared. (See table 4.)

These progressive changes in rostral length and rostral spine arrangement on both *P. setiferus* and *P. brasiliensis* were observed for wild shrimp and for specimens reared in aquaria from either second or third post-larvae.

The planktonic post-larvae of both *P. setiferus* and *P. brasiliensis* are transparent and colorless except for a series of pinkish-red chromatophores extending along the ventral surface of the body, and particularly pronounced on the abdomen.
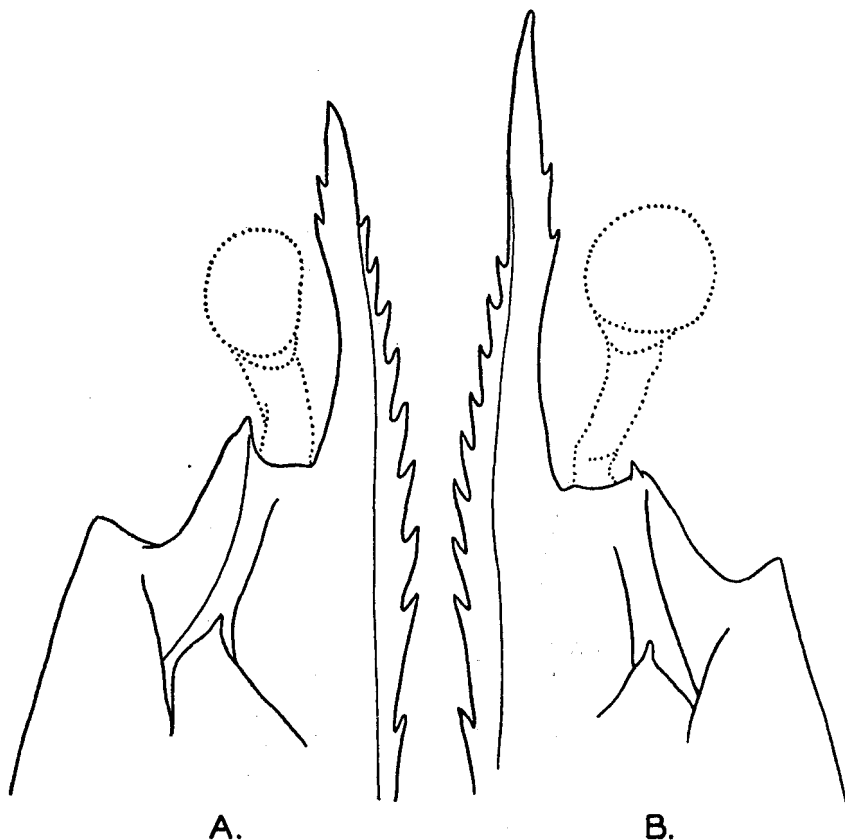
FIGURE 30.—Arrangement of rostral spines on *P. brasiliensis* (A) and *P. setiferus* (B) at adult size.

TABLE 4.—*Characters aiding in the separation of the young of* P. setiferus *and* P. brasiliensis

Size	Character	*P. setiferus*	*P. brasiliensis*
5 mm.	Third chelate leg	Not reaching beyond tip of eye	Reaching beyond tip of eye.
5 to 10 mm.	Length of rostrum	Not reaching to tip of eye	Reaching to, or nearly to, tip of eye.
5 mm. to adult	Position of rostral spines	Spaced relatively nearer to each other.	Spaced relatively farther from each other.
12 mm. to adult	Length of second antenna	Relatively long	Relatively short.
15 mm. to adult	Position of ventral rostral spines	Relatively farther apart and more distal.	Relatively nearer together and more proximal.
20 mm. to adult	Ventral postmargin of sixth abdominal somite.	Incurved	Straight.

DISTRIBUTION, POSTLARVA

Seasonal, geographic, and size distributions of the planktonic postlarvae of *P. brasiliensis* reveal an early life history differing in many respects with the closely related *P. setiferus*. The larval and early postlarval stages of both species are normally spent in the open sea and the young occur abundantly as early postlarvae in the inshore oceanic plankton. The planktonic postlarvae of *P. brasiliensis* were usually found in the same plankton with the post larvae of *P. setiferus*. The young and adults of both *Penaeidae* are undistinguished in the commercial catch although many fishermen along the South Atlantic coast recognize the young of *P. brasiliensis* and term them "brownies" because of their distinctive coloration.

Although the postlarvae of *P. brasiliensis* were found to be most abundant during spring and summer, the planktonic young, however, unlike *P. setiferus*, were also

taken during winter. (See fig. 31.) Furthermore, the postlarvae of *P. brasiliensis* occurred from Cape Romain south to Ft. Pierce, Fla., as well as at nearly all collecting points off the coast of Louisiana. The postlarvae of *P. setiferus* were not taken south of St. Augustine along the South Atlantic coast.

The planktonic postlarvae of *P. brasiliensis* were not only reduced in numbers during the winter but were usually of larger size than spring and summer shrimp. The postlarvae in summer generally ranged from 8 to 11 mm. in length, whereas in winter they ranged from 10 to 14 mm. This seasonal size variation was most evident among shrimp taken off the coast of Louisiana and at Ft. Pierce, Fla. The cause of this variation is unknown but it is probable that it indicates a more distant offshore spawning area and a more limited spawning production in winter than in summer.

The larger size distribution of planktonic *P. brasiliensis*, compared to planktonic postlarvae of *P. setiferus*, the latter seldom exceeding 8 mm., also suggests a more distant offshore spawning area for *P. brasiliensis* than for *P. setiferus*. The youngest planktonic postlarvae were secured only at Ft. Pierce during the summer of 1935. The size distribution of *P. brasiliensis* postlarvae during the rest of the year at Ft.
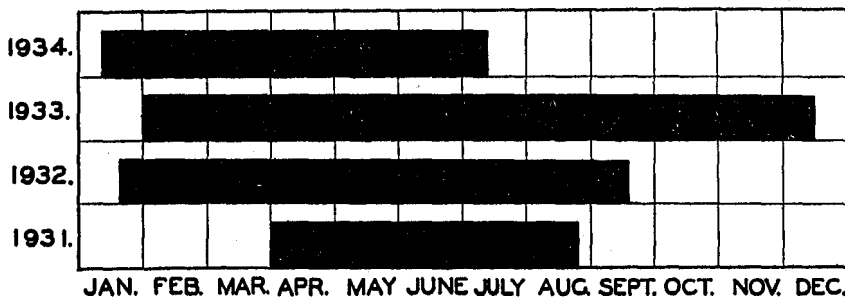

FIGURE 31.—Seasonal distribution of planktonic postlarval *P. brasiliensis* in and adjacent to Barataria Bay, La., from 1931 to 1934. Collections were not made after August 20 during 1931 nor after July 15 during 1934. Postlarvae ranged from 7 to 12 millimeters in body length.

Pierce was approximately the same as elsewhere either along the South Atlantic or Gulf coasts. Only at Ft. Pierce, supplied by the waters of the Gulf Stream, was this general uniformity of size broken. The fact that the water at Ft. Pierce Inlet is derived from much deeper oceanic areas than elsewhere in the area of collection along the South Atlantic coast indicates a more offshore and deeper spawning environment for *P. brasiliensis* than for *P. setiferus*. (See Burkenroad, 1939.)

From Ft. Pierce south, demersal young of *P. brasiliensis* were taken commonly in estuarine areas and about inlets to Ft. Lauderdale, Fla. Seine collections in July 1935 revealed the young at most inlets from Ft. Pierce to Ft. Lauderdale, indicating the direct influence of the Gulf Stream on the distribution of the planktonic postlarvae. Demersal young of *P. setiferus* were not taken at Ft. Pierce or at any point south of New Smyrna, Fla. At St. Augustine the demersal young of both species occur in about the same ratio, but north of St. Augustine the young of *P. setiferus* far exceed in abundance the young of *P. brasiliensis*. It may be mentioned that *P. brasiliensis* is known to have a more northerly range than *P. setiferus* along the Western Atlantic coast, occurring as far north as Massachusetts. This distribution may be caused by the shrimp entering the Gulf Stream off the Florida coast and being carried to more northerly points than *P. setiferus* swims by its own effort.

It appears that the young of *P. brasiliensis* remain at sea in the oceanic plankton during larval and the first, second, and third postlarval stages. The occurrence of

planktonic postlarvae as large as 14 mm. in length in winter indicates that possibly the fourth and fifth postlarval stages may also be spent at sea as a result of a more offshore spawning area in winter than in summer, the young taking a longer time to reach the coast line.

The general complexity of the geographic distributional problem of the planktonic postlarvae of *P. brasiliensis* along the South Atlantic coast cannot be understood in the absence of data on the exact spawning areas of the species. Even if the spawning areas were defined, there will remain the most interesting problem of the distribution of the postlarvae to all points along the coast line at a more or less constant size according to season.

GROWTH, POSTLARVAE

Data on the growth of the postlarvae of *P. brasiliensis* were secured in 1936 simultaneously with the data on the growth of young *P. setiferus*. The planktonic postlarvae, 7 to 9 mm. in length, are somewhat hardier than those of *P. setiferus*, prior to removal from the plankton, and generally remain vigorous long after most other planktonic organisms perish. The young shrimp swims almost incessantly about the aquarium for 1 or 2 days after capture, and does not settle to the bottom to begin feeding as promptly as *P. setiferus*. The rate of swimming of the postlarvae is often about an inch per second, over a period of several minutes, before a short rest period ensues and the shrimp drops momentarily to the bottom. After settling to the bottom to begin feeding, the young shrimp often bury their bodies in the sand while at rest. The young are extremely sensitive to changes in light intensity and to vibrations. If sufficiently alarmed, the shrimp frequently jump from the water and strike the glass cover of the aquarium.

Series A consisted of two postlarvae, approximately 8 mm. in length, placed in an aquarium with two *P. setiferus* on June 26, 1936. These shrimp were preserved on August 8 and measured 20 and 32 mm., with a growth increment of 12 and 24 mm., respectively, during the 43-day period of confinement. The growth corresponds quite favorably with that of young *P. setiferus*. A differential growth of considerable magnitude occurred between these two postlarval *P. brasiliensis* as in the case of the two postlarval *P. setiferus*.

Series B consisted of three postlarvae, approximately 8 mm. in length, isolated in an aquarium on June 22. One shrimp was preserved 39 days later and measured 23 mm., with a growth increment of 15 mm. The remaining shrimp were preserved on August 10 and measured 24 and 29 mm. each, with a growth increment of 16 and 21 mm., respectively, during the 49-day period of confinement.

Series C consisted of eight postlarvae, approximately 8 mm. in length, isolated in an aquarium on April 1. All shrimp were preserved on August 8 and measured from 21 to 36 mm., with a growth increment of 14 to 28 mm. during the 130-day period of confinement. The fact that these shrimp lived and grew for 4 months in less than a gallon of nonaerated sea water testifies to their hardiness and adaptability.

Rearing experiments were also made that show that the postlarvae, regardless of the length at capture (7 to 14 mm.), drop to the bottom of the aquarium to commence feeding soon after confinement. As a result of this adopted demersal life, aquarium-held young, at a length of about 14 mm., are quite different in appearance from planktonic shrimp taken at the same length. The body is far more robust, the pigmentation more developed, and the changes in length of rostrum and rostral spine formation most pronounced among the confined shrimp. This observation would

indicate that the planktonic postlarvae do not receive sufficient (if any) food while at sea as a member of the plankton, but must wait until a bottom existence is possible before the commencement of active juvenile feeding.

Owing to the fact that planktonic postlarvae arrive in estuarine areas throughout the year, collections of young shrimp by seine and trawl, along the coasts of both Louisiana and Florida, show an extended size distribution at all times. Late summer and early fall collections of young, however, appear to have a growth rate similar to *P. setiferus*.

The young shrimp generally move into deeper warmer water in winter throughout the northerly range along the South Atlantic coast, but from New Smyrna to Ft. Lauderdale, Fla., the young shrimp are found in estuarine areas throughout the year.

It appears on the basis of the observations of aquarium-held shrimp, and the absence of early postlarval stages on the sea bottom, that the planktonic postlarvae of *P. brasiliensis*, like those of *P. setiferus*, do not settle to the bottom to begin a demersal existence until shallow estuarine waters have been reached. This change from a planktonic surface existence to a demersal habitat quite definitely does not depend on the length or on any particular postlarval stage, but apparently is effected entirely after distribution from oceanic spawning areas to inshore estuarine areas has been accomplished. Whether this distribution is caused largely by current, by the active swimming of the postlarvae, or by both agencies cannot be determined. Neither can the type of reaction be determined which sends the planktonic shrimp to the bottom after shallow water has been reached.

TRACHYPENAEUS CONSTRICTUS STIMPSON

DESCRIPTION

EGG

Eggs of *Trachypenaeus constrictus* Stimpson were taken abundantly in the plankton at St. Augustine Inlet and to some extent at other localities along the South Atlantic coast. The eggs were isolated in glass dishes in the laboratory, hatched at air temperatures, and the resultant larvae reared through five naupliar stages, three protozoeal stages, and through the first mysis stage. Simultaneously, protozoea were taken in the plankton and reared through the second mysis stage. The latter was also obtained in plankton and reared to a postlarval length of 15 mm. Reared post-larvae were then linked to a series of young *T. constrictus* taken in plankton and to a collection of juvenile shrimp in the United States National Museum attributed to *T. constrictus*.

The egg of *T. constrictus* is demersal but is considerably lighter than the egg of *P. setiferus*. It is readily rendered buoyant by moderate current agitation. The egg is spherical and was the largest peneid egg recognized in the plankton. Measurement of the diameter of 200 unselected eggs, removed from preserved plankton, shows a size distribution ranging from 0.28 to 0.56 mm., with a strong modal diameter between 0.40 and 0.44 mm. The shrinkage of the egg after preservation was found to be within the standard unit of measurement (0.02 mm.). (See figs. 32, 33.)

The egg possesses a thin, transparent membrane that in living and preserved eggs reflects a purplish-blue color under the microscope. The color was quite similar to that observed for the egg membrane of *P. setiferus*.

Most eggs were taken in late embryonic development and usually hatched within 12 hours after capture.   Some plankton collections contained eggs in 2-, 4-, 8-, and 16-cell stages.   None of the earlier developmental stages were found in time to be removed from the plankton and isolated for observation purposes.

The development of the egg of *T. constrictus* probably proceeds according to the general plan described for *P. japonicus* by Hudinaga (1935).   The nature of this
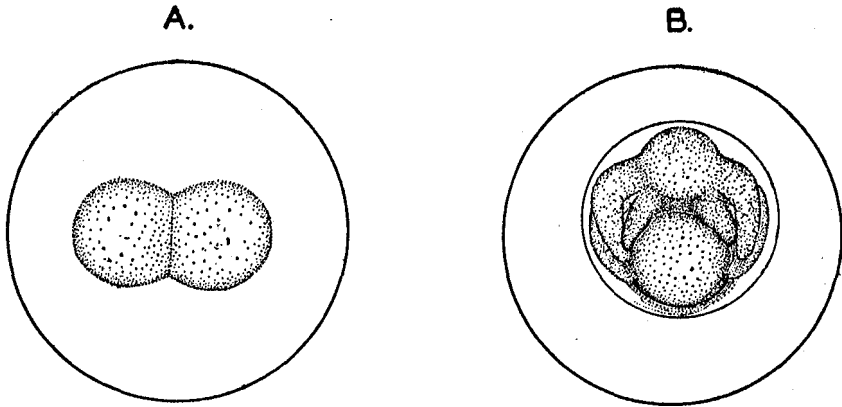

FIGURE 32.—Egg of *Trachypenaeus constrictus*.   Diameter 0.42 mm.   (A) 2-cell stage; (B) early embryo stage, ventral aspect.

development is given in summary under the description of the egg of *P. setiferus*. The much larger size of the egg of *T. constrictus* compared to that of either *P. setiferus* or *P. japonicus* enables the egg nauplius to spread the appendages to a greater degree within the egg and to move about more actively within the egg membrane.

The size of the egg nauplius, prior to hatching, is approximately the same as in *P. setiferus*.   The body length generally ranges from 0.24 to 0.26 mm.   Several
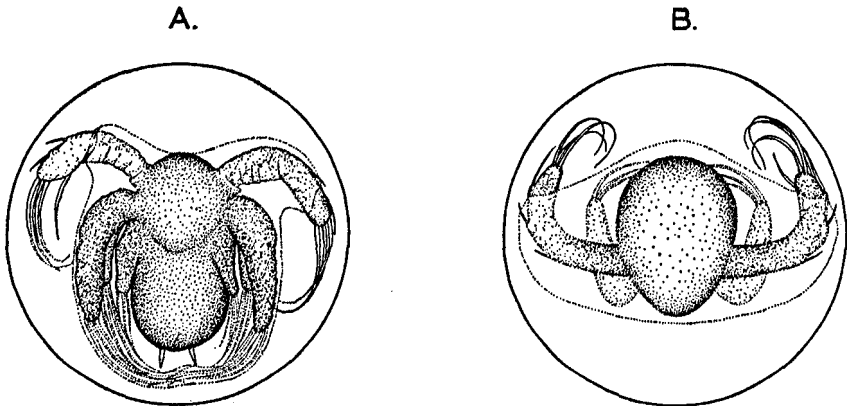

FIGURE 33.—Egg of *Trachypenaeus constrictus*.   Diameter 0.42 mm.   (A) late embryo stage, ventral aspect; (B) late embryo stage, anterior aspect.

hours before hatching the egg nauplius commences to force its appendages out of the embryonic membrane and to move around freely within the egg membrane.   However, unlike the condition observed in *P. setiferus* and *P. japonicus*, little pressure appears to be exerted by the egg nauplius on the membrane, the latter apparently disintegrating and splitting open after a certain period of time.   It is evident from the comparative sizes of the egg nauplius and the egg that little direct pressure can be exerted by the appendages upon the membrane.

It was noted in many instances that the egg nauplius failed to escape from an unruptured egg membrane and consequently passed through a series of naupliar molts within the egg. So far as could be determined considering the abnormality of the larva, a stage corresponding to the first protozoea was attained on two occasions within the egg through the apparent failure of the membrane to split open and allow the escape of the first nauplius. Efforts were frequently made to free the advanced larva from the egg membrane but all larvae died within a few hours after liberation. Lack of agitation of the water with the resultant accumulation of material on the egg membrane appears to be a possible factor preventing the escape of the nauplius.

FIRST NAUPLIUS

The first nauplius of *T. constrictus* measures from 0.24 to 0.26 mm. in body length and 0.12 mm. in greatest body width. The length of the first nauplius is somewhat
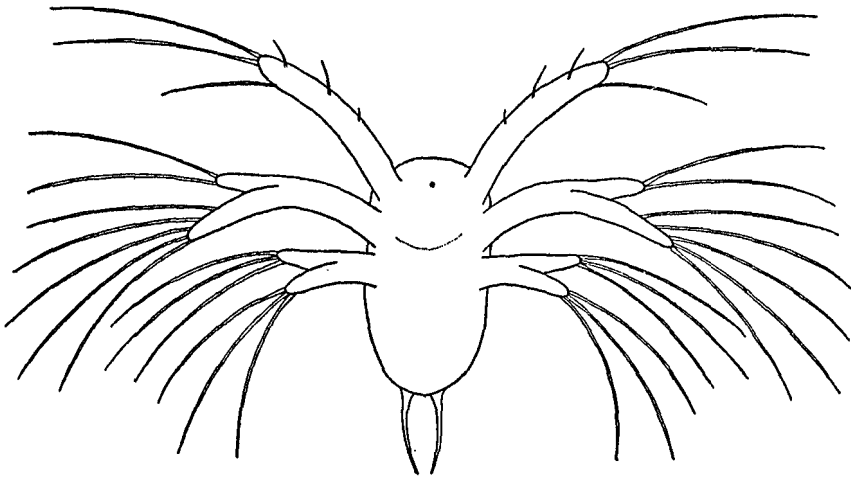

FIGURE 34.—First nauplius of *Trachypenaeus constrictus*. Length 0.26 mm. Ventral aspect.

smaller than that of the first nauplius of *P. setiferus* despite the larger egg of *T. constrictus*. (See fig. 34.)

The nauplius of *T. constrictus* closely resembles, in general appearance at comparable stages of development, the nauplii of *P. setiferus* and *E. stimpsoni*. Notwithstanding a general fundamental body morphology probably existing among all naupliar larvae of the *Penaeidae*, certain specific differences appear which usually serve to differentiate the nauplii of *P. constrictus* at comparable stages of development from the other peneid nauplii described in this report. Differences in the relative body length and width, in the number of setae on the exopod of the second antenna, and in the number of furcal spines, serve to separate most naupliar stages of the three species of *Penaeidae* considered. (See tables 2, 5, and 6.) Bassindale (1936) found that the naupliar larvae of three species of English barnacles could be separated partly by size and by setation as well as by other characters.

The first nauplius of *T. constrictus* possesses the same number of setae on the exopod of the second antenna (five) and the same number of furcal spines (1+1) as the first nauplius of *P. setiferus*. It is principally by the somewhat shorter body length and the considerably narrower body width that the two nauplii can be distinguished. The length of the third appendage of *T. constrictus* is somewhat shorter in proportion to the length of the body than in *P. setiferus*. (See figs. 3 and 34.)

The first nauplius was secured by hatching one egg and from plankton. Although all five naupliar stages of *T. constrictus* were obtained by hatching planktonic eggs, the number secured was small. This condition was caused by the fact that the nauplius cannot be observed in detail while alive and by the fact that little knowledge was then available concerning the number of different naupliar stages which existed. Without the benefit of series of naupliar stages obtained by rearing experiments from specific types of peneid eggs, the classification of some fifteen different nauplii, representing three species of *Penaeidae*, would have been almost impossible.

SECOND NAUPLIUS

The second nauplius of *T. constrictus* measures from 0.26 to 0.32 mm. in body length and 0.12 mm. in greatest body width.

The second nauplius is distinguished from the first nauplius by an increase in the number of setae on the exopod of the second antenna to six and in the number of furcal spines to 2+2. (See fig. 35.)
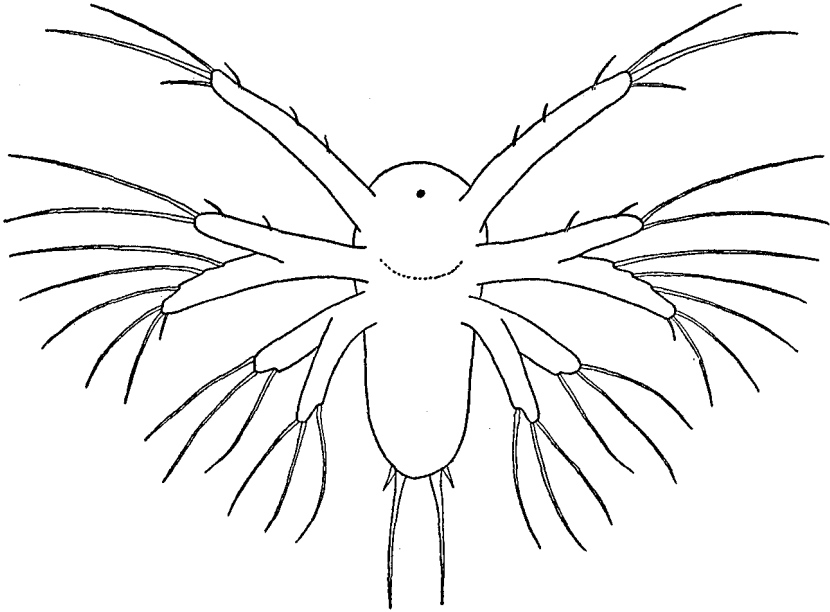

FIGURE 35.—Second nauplius of *Trachypenaeus constrictus*. Length 0.28 mm. Ventral aspect.

The same differences that distinguish the first nauplius from that of *P. setiferus* are also applicable to the second nauplii of both species. A stronger outer pair of furcal spines are present in *T. constrictus* than in *P. setiferus*. Only two terminal setae appear on the endopod of the second antenna of *T. constrictus* compared with three setae in *P. setiferus*.

The second nauplius was secured by hatching six eggs, and from plankton.

THIRD NAUPLIUS

The third nauplius measures approximately 0.36 mm. in body length and about 0.14 mm. in greatest body width.

The third nauplius is distinguished from the second nauplius by an increase in the number of setae on the exopod of the second antenna to 7, and in the number of furcal spines to 5+5. (See fig. 36.)

Differences in body proportions remain diagnostic between *T. constrictus* and *P. setiferus*. Shorter terminal setae are present on the appendages of *T. constrictus* than on *P. setiferus*. The greater increase in the number and size of the furcal spines in *T. constrictus* also distinguishes this species from *P. setiferus*. A globular swelling
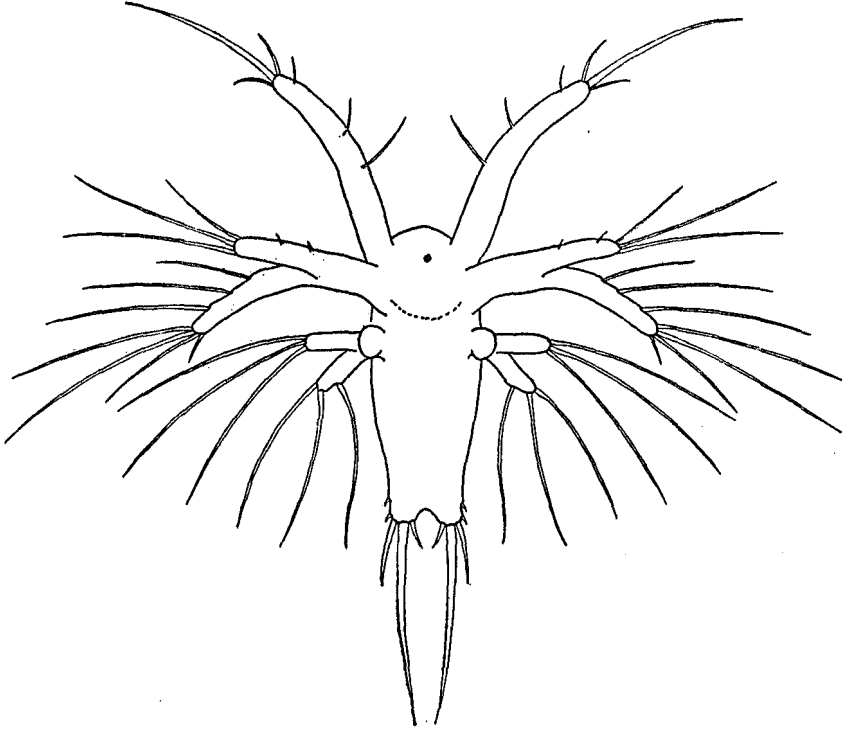

FIGURE 36.—Third nauplius of *Trachypenaeus constrictus*. Length 0.36 mm. Ventral aspect.

is formed at the base of the third appendage, this formation not becoming evident until the fourth naupliar stage of *P. setiferus*.

The third nauplius of *T. constrictus* was secured by hatching one egg, and from plankton.

FOURTH NAUPLIUS

The fourth nauplius of *T. constrictus* measures from 0.38 to 0.42 mm. in body length and 0.14 mm. in greatest body width.

The fourth nauplius is distinguished from the third nauplius by an increase in the number of setae on the exopod of the second antenna to 8, and in the number of furcal spines to 6+6. Biramous rudimentary pairs of the fourth to seventh body appendages appear, while a deep sulcus, or notch, is formed at the postero-medial margin of the tail, forming a furcal process. (See fig. 37.)

The furcal spines are more numerous and stouter in the fourth nauplius than in the comparable stage of *P. setiferus*. No sense organs appear, as are found in the latter species. The third appendages are much reduced in length compared to those of *P. setiferus*.

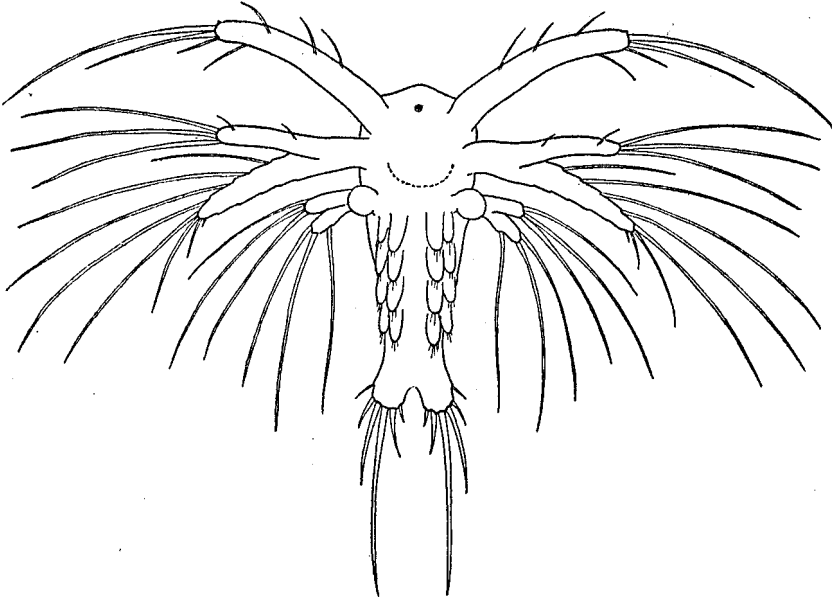The fourth nauplius was secured by hatching one egg, and from plankton.

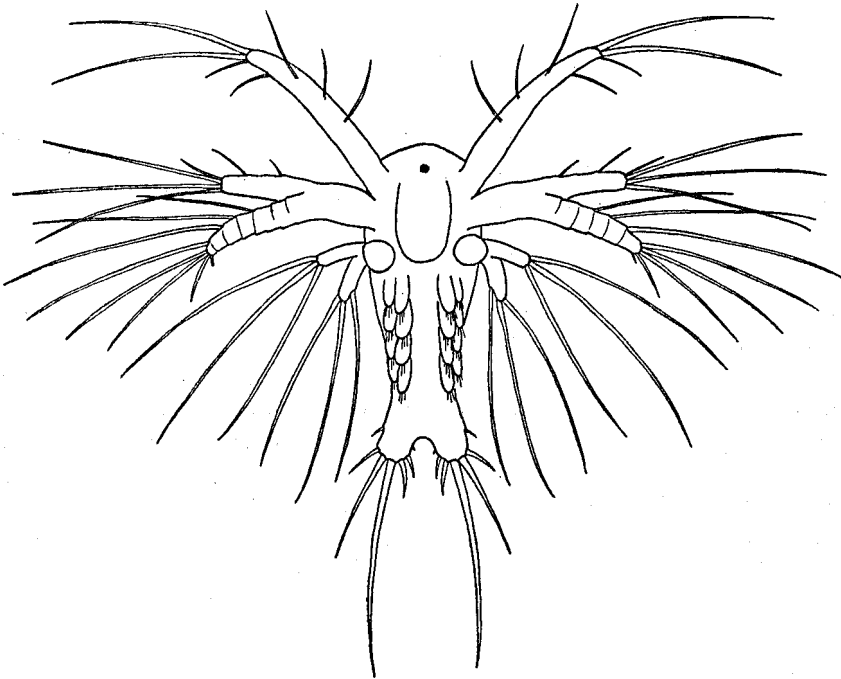FIGURE 37.—Fourth nauplius of *Trachypenaeus constrictus*. Length 0.36 mm. Ventral aspect.

FIGURE 38.—Fifth nauplius of *Trachypenaeus constrictus* Length 0.42 mm. Ventral aspect.

FIFTH NAUPLIUS

The fifth nauplius of *T. constrictus* measures from 0.40 to 0.44 mm. in body length and 0.14 mm. in greatest body width.

The fifth nauplius is distinguished from the fourth nauplius by an increase in the number of furcal spines to 7+7. There are also four terminal setae developed on the endopod of the second antenna instead of three as in the preceding stage. (See fig. 38.)

The body length and width are much shorter for this species than for *P. setiferus*. The outer pair of furcal spines are placed more anteriorly on the lateral margins of
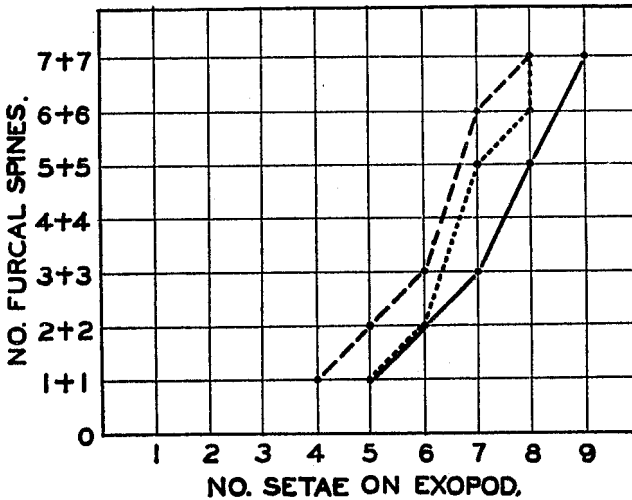

FIGURE 39.—The number of furcal spines and number of setae on the exopod of the second appendage of the five naupliar stages of *P. setiferus* (solid line), *T. constrictus* (short dash line), and *Eusicyonia stimpsoni* (long dash line).

the furcal process in *T. constrictus* than in *P. setiferus*. The behavior of the nauplii of both species at all stages is quite similar, and the naupliar stages of *T. constrictus*, as in *P. setiferus*, are passed through within 36 hours. Food is not taken by the nauplius.

The fifth nauplius was obtained by hatching one egg, and from plankton.

TABLE 5.—*The nauplius of* Trachypenaeus constrictus

[Showing the progressive increase in the number of setae on the exopod of the second appendage and in the number of furcal spines after each naupliar molt. The range in body length and in greatest body width are given in millimeters; measurements were made in 0.02 mm. units. Based on 30 specimens, 10 of which were reared from the planktonic egg]

Stage of nauplius	First	Second	Third	Fourth	Fifth
Setae on exopod	5	6	7	8	8
Furcal spines	1+1	2+2	5+5	6+6	7+7
Body length	0.24–0.26	0.26–0.32	.36	0.38–0.42	0.40–0.44
Body width	.12	.12	.14	.14	.14
Number reared	1	6	1	1	1

FIRST PROTOZOEA

The first protozoea of *T. constrictus* measures from 0.60 to 0.82 mm. in body length based on 12 specimens reared from the eggs, and from 0.70 to 1.0 mm. in length based on 40 specimens taken in plankton along the South Atlantic coast. An additional 20 specimens, taken off the coast of Louisiana and attributed either to *T. constrictus* or to *T. similis*, have a range in length from 0.70 to 0.90 mm.

It has been found impossible to distinguish any significant differences between the larval material of *Trachypenaeus* from the coast of Louisiana and the South Atlantic coast. Inasmuch as *T. similis* is the predominant species in Louisiana (Burkenroad, 1934a), specific differentiation must await further studies.

The metamorphosis from the fifth nauplius to the first protozoea is accompanied by the same striking morphological changes as described for *P. setiferus*. The presence in the first protozoea of natatory first and second antennae, a flattened pair of mandibles used in mastication, first and second maxillae used in straining and selecting food, and first and second maxillipeds most useful in locomotion, affords sufficient
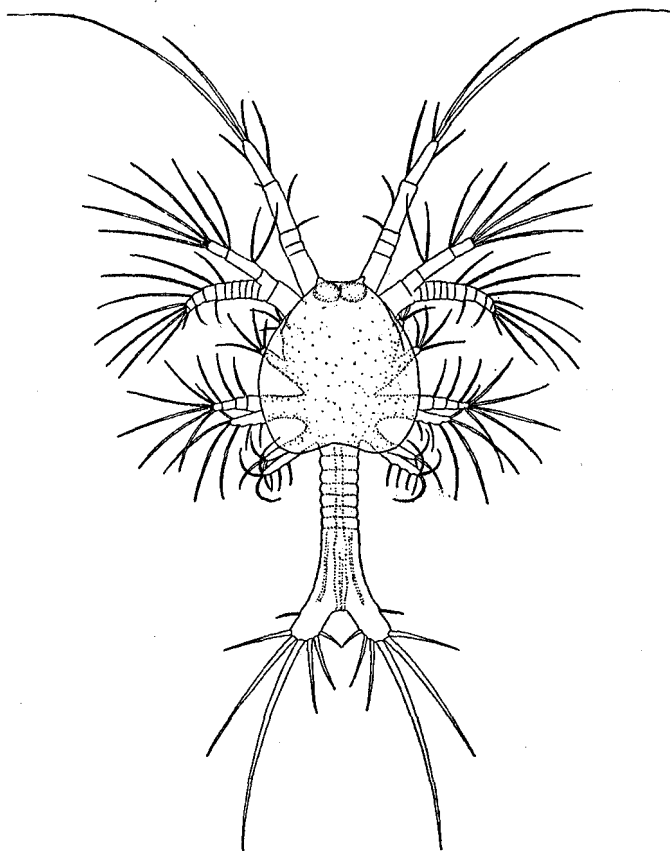

FIGURE 40.—First protozoea of *Trachypenaeus constrictus*. Length 0.72 mm. Dorsal aspect.

distinction between the two larval stages. A carapace covers the anterior part of the body and the bases of all differentiated appendages. The posterior end of the body shows a strong furcal process that possesses 7+7 well-developed spines. (See fig. 40.)

The first protozoea further possesses a double pair of long setae on the lateral margin of the endopod of the second antenna, while the number of setae on the exopod of the second antenna increases to nine in the latero-terminal series. Two short setae appear on the outer lateral margin of the exopod. Segmentation of the antennae is quite clear and is similar to that noted for *P. setiferus*.

There are certain consistent morphological differences which separate the first protozoea of *T. constrictus* from the first protozoea of *P. setiferus*. The second antenna of *T. constrictus* is much shorter than the first antenna, whereas in *P. setiferus*

the two appendages are of nearly equal length.   Two pairs of lateral setae are present on the endopod of the second antenna of *T. constrictus*, whereas only a single pair (arising from the same lateral notch) is found on *P. setiferus*.   The angle of the notch at the postero-medial margin of the tail is broader and somewhat deeper in *T. constrictus* than in *P. setiferus*.   (See figs. 8 and 40.)

SECOND PROTOZOEA

The second protozoea measures from 1.0 to 1.2 mm. in body length based on two specimens reared from eggs, and from 1.06 to 1.5 mm. in length based on 46
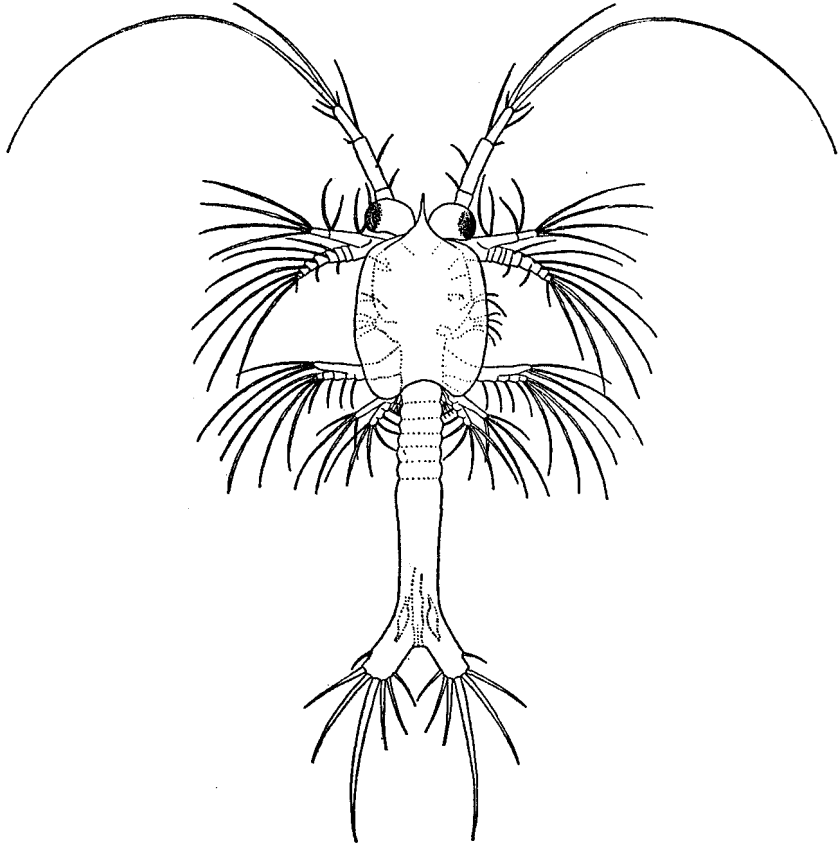

FIGURE 41.—Second protozoea of *Trachypenaeus constrictus*.   Length 1.28 mm.   Dorsal aspect.

specimens taken in plankton along the South Atlantic coast.   A length range from 1.1 to 1.48 mm. was noted for 20 specimens of *Trachypenaeus* sp. taken off the coast of Louisiana.

The second protozoea shows the typical body metamorphosis described for the second protozoea of *P. setiferus*.   The compound eyes become stalked, a short rostrum becomes differentiated at the anterior median margin of the carapace, all thoracic somites are distinct and the body becomes more elongated posteriorly.   (See fig. 41.)

The same differences noted between the first protozoea of *T. constrictus* and *P. setiferus* are also applicable to the second protozoea of both species.   Other constant differences include a much shorter rostrum and the greater development of the third maxillipeds on *T. constrictus*.   No supra-orbital spines are present on the carapace, in contrast to the strong pair found on *P. setiferus*.   (See figs. 9 and 41.)

THIRD PROTOZOEA

The third protozoea measures from 1.5 to 1.6 mm. in body length based on two specimens reared from eggs, and from 1.4 to 2.2 mm. in length based on 28 specimens taken in plankton along the South Atlantic coast. An additional 12 specimens of *Trachypenaeus* sp. from the coast of Louisiana have a length range from 1.76 to 1.92 mm.

The metamorphosis from the second to the third protozoea shows the same general changes as occurred in *P. setiferus*. The latero-terminal series of setae on the exopod of the second antenna increases to 10. The last 5 thoracic somites become
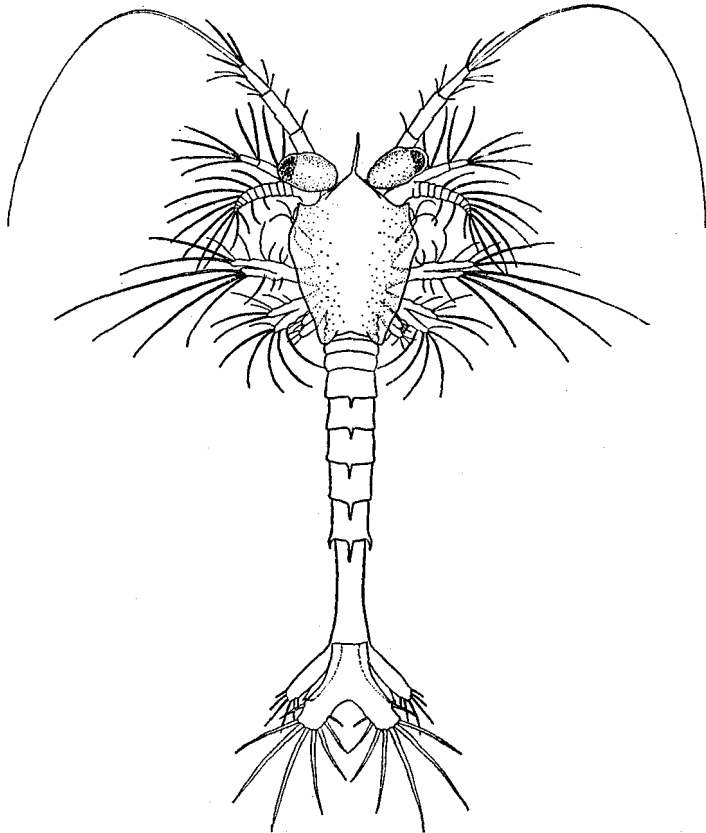

FIGURE 42.—Third protozoea of *Trachypenaeus constrictus*. Length 1.9 mm. Dorsal aspect.

more consolidated and bear paired rudimentary appendages. The abdominal somites and the telson are differentiated but lack appendages, with the exception that the pair of biramous uropods appear from the ventral base of the sixth somite. The number of furcal spines increases to 8+8. (See fig. 42.)

The differences separating the first and second protozoea of *T. constrictus* from comparable stages of *P. setiferus* remain to separate the third protozoea of both species. In particular, the size and shape of the notch in the telson are strikingly different in the two species. Postero-dorsal and postero-lateral spines are absent on the sixth abdominal somite but postero-dorsal median spines are present on the first five somites and a pair of postero-lateral spines are present on the fifth somite of the third protozoea of *T. constrictus*. The first antenna of *T. constrictus* bears an extremely long terminal seta. (See figs. 10 and 42.)

FIRST MYSIS

The first mysis of *T. constrictus* measures from 1.9 to 2.6 mm. in length based on three specimens reared from the third protozoeal stage, and from 2.1 to 3.4 mm. in length based on 52 specimens taken in plankton along the South Atlantic coast. Five mysis of *Trachypenaeus* sp. from the coast of Louisiana had a length range from 2.8 to 3.2 mm.

A metamorphosis occurs from the third protozoeal to the first mysis stage in *T. constrictus* quite comparable to *P. setiferus*. The first and second antennae of the protozoea become greatly reduced in size and altered in structure in the mysis, losing their natatory function. The development of five pairs of biramous thoracic append-ages, or pereiopods, in the first mysis produces a new method of locomotion. The endopods of the first three pairs of pereiopods are faintly chelate. A pair of strong supra-orbital and a pair of weak sub-orbital spines appear on the anterior margin of the carapace. The rostrum now extending beyond the tip of the eye carries a single dorsal spine, slightly forward of the anterior margin of the carapace. Postero-dorsal spines are lacking on the first to third abdominal somites while postero-lateral spines are also lacking from the fifth abdominal somite. The postero-dorsal spine on the
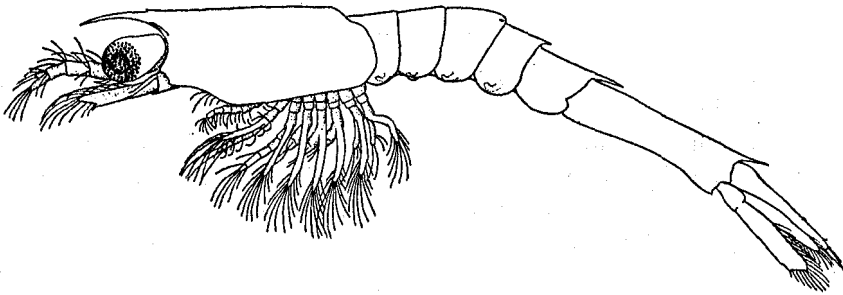

FIGURE 43.—First mysis of *Trachypenaeus constrictus*. Length 2.8 mm. Lateral aspect.

fifth somite is strongly developed while a similar spine occurs on the sixth abdominal somite. (See fig. 43.)

The variation in development and arrangement of the spines on the abdominal somites will distinguish the first mysis of *T. constrictus* and *P. setiferus*. The rostrum of *T. constrictus* possesses a dorsal spine which is lacking in *P. setiferus*. The hepatic spines are absent in the former and present in the latter. Lateral spines on the fifth abdominal somite are also absent in former species and present in the latter species. (See figs. 15 and 43.)

SECOND MYSIS

The second mysis measures from 3.4 to 4.6 mm. in length based on 34 specimens taken in plankton along the South Atlantic coast. A length range from 3.2 to 3.6 mm. was noted for 14 specimens of *Trachypenaeus* sp. taken off the Delta of the Mississippi River.

The development of uniramous paired pleopods on the first to fifth abdominal somites, the enlargement of the endopods of the pereiopods with the first three pairs chelate, the addition of two dorsal spines on the rostral ridge, and the disappearance of the supra-orbital and sub-orbital spines provide the chief differences between the second and first mysis stages. Certain characters may occasionally overlap into the

two stages.   The pleopods are frequently developed in some specimens to a greater extent than in other specimens in the same mysis stage.   (See fig. 44.)

The second mysis of *T. constrictus* and *P. setiferus* are distinguished by the presence of three rostral spines in the former species and one spine in the latter, by the absence of supra-orbital and hepatic spines and by a longer postero-dorsal spine on
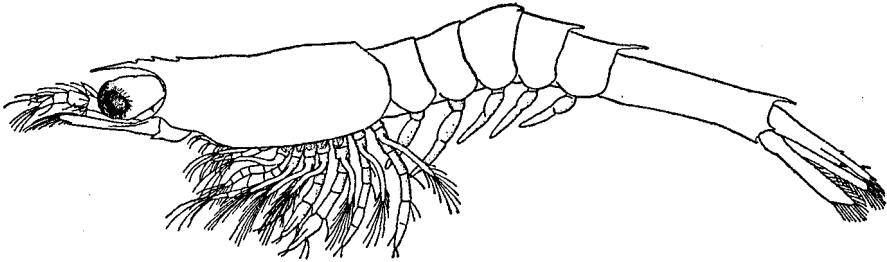
FIGURE 44.—Second mysis of *Trachypenaeus constrictus*.   Length 4.0 mm.   Lateral aspect.

the fifth abdominal somite in the former, and by a shorter sixth abdominal somite on *T. constrictus*.   (See figs. 16 and 44.)

POSTLARVA

The first postlarva of *T. constrictus* measures from about 3.8 to 4.7 mm. in length based on five specimens reared from the second mysis stage.

The change from second mysis to first postlarva is fundamentally similar to the metamorphosis occurring between comparable stages of *P. setiferus*.   The flagellum of the second antenna is elongated, being composed of about fifteen segments and extending far beyond the antennal scale and the first antenna.   The spines on the
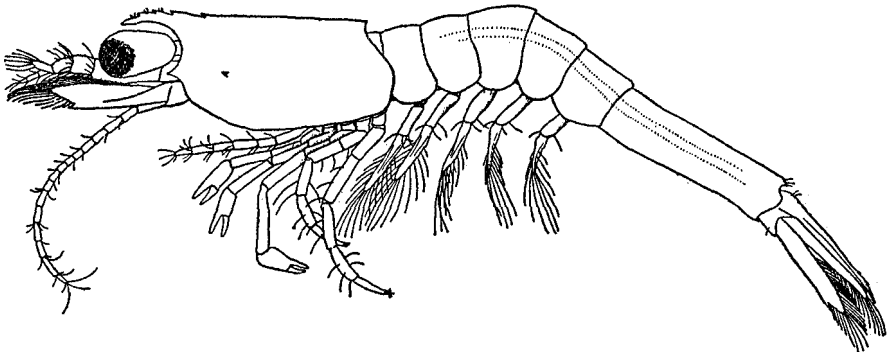
FIGURE 45.—First postlarva of *Trachypenaeus constrictus*.   Length 3.8 mm.   Lateral aspect.

rostral ridge increase to four.   The rostrum is shorter than the eye and is moderately decurved.   A strong spine, probably referable to the sub-orbital, is present on the anterior margin of the carapace.   The exopods of the pereiopods are lacking, of course, while the endopods have become modified into walking legs.   The first three pairs of pereiopods are chelate, the third pair being the longest.   The fourth and fifth pairs are nonchelate, but, unlike either *P. setiferus* or *P. brasiliensis*, are much elongated and strongly developed, the fifth pair probably being the largest of all the pereiopods. The postero-dorsal spines on the fourth and fifth abdominal somites of the mysis stage are lost while a similar spine on the sixth somite is much reduced in the first postlarva.   The pleopods are further developed and bear long terminal setae.   (See fig. 45.)

The early postlarva is separated from the early post larvae of *P. setiferus* and *P. brasiliensis* by the shorter, stouter, and decurved rostrum, by the much longer flagellum, by a broader antennal scale, and by proportionally longer fourth and fifth pereiopods. (See figs. 17, 21, and 45.)

The postlarvae of *T. constrictus* tend to bury themselves in the bottom sand of an aquarium to a much greater extent than *P. setiferus* or *P. brasiliensis* and are consequently much less active. The greater development of the fourth and fifth pairs of pereiopods is perhaps associated with this habit of the postlarvae to burrow in the mud or sand.

The only previous research on the larvae of North American *Penaeidae* was conducted by Brooks (1882). There has hitherto been no material available to compare with a series of peneid larvae briefly described by Brooks and believed by him to represent *P. brasiliensis*. It is now evident that the series of young reared by Brooks are probably referable to *T. constrictus* rather than to *P. brasiliensis*. Diagnostic characters do not appear in the descriptions by Brooks until the "Penaeus" stage is discussed. The description states: "The scale of the antenna becomes broad and triangular, the flagellum is greatly elongated and is divided into twelve joints." It is known that the early postlarvae of both *P. setiferus* and *P. brasiliensis* do not possess so elongated a flagellum, whereas the first postlarva of *T. constrictus* has a long flagellum of at least 12 joints or segments. An examination of the unpublished drawings, by Brooks, of these larval and postlarval shrimp also indicate that the probable identity is *T. constrictus*.

Brooks mentioned that the time elapsing between the first protozoea and the first postlarvae was approximately 3 weeks. This period of development agrees well with the composite series of larvae and postlarvae reared at St. Augustine in 1936.

DISTRIBUTION

EGG

The eggs of *T. constrictus* were taken in the plankton at St. Augustine Inlet from April 13 to August 3, 1936, and over a nearly comparable period of time in 1935 at the same locality. The common occurrence of the eggs of *T. constrictus* in the incoming tidal current from the sea would indicate the presence of spawning adults in the vicinity of the inlet. There are no data available to indicate the degree of concentration of spawning adult shrimp off the inlet. Collections by commercial trawls, from time to time, have shown a small population of *T. constrictus* along the South Atlantic coast of the United States. However, the species, owing to its small size, may escape through the trawl. Observations on the postlarvae in aquaria indicate that the species hides in the bottom deposit to a much greater extent than either young *P. setiferus* or young *P. brasiliensis*. Quite possibly the species is largely passed over by the trawls and not adequately represented in the catch. (See fig. 46.)

Eggs were also taken in limited quantity at other localities along the South Atlantic coast from Cape Romain to Ft. Pierce. It was the first type of peneid egg recognized in the plankton (Pearson, 1935) and proved more abundant at sea than the eggs of the other species of *Penaeidae*. This greater offshore abundance may be due to the greater buoyancy of the eggs. The larger perivitelline space of the egg renders the latter much lighter than the smaller eggs of *P. setiferus* and *E. stimpsoni*, in which the embryo occupies nearly the entire egg sphere. This greater buoyancy of the egg of *T. constrictus* was clearly demonstrated by simple agitation of the small

amount of sea water containing the eggs of all three species of shrimps. As the greater portion of the plankton along the South Atlantic coast was secured from surface areas, this greater buoyancy of the eggs was naturally reflected in the more abundant catch.

The seasonal distribution of the eggs along the South Atlantic coast was quite similar to that observed at St. Augustine Inlet, with the exception that eggs were taken at Ft. Pierce both during the summer and winter. This offshore distribution extended from April 8 at Cape Romain, S. C., and April 13 at Cape Canaveral, Fla., to August 13 at St. Augustine and to December 17 at Ft. Pierce. The absence of the eggs at or north of St. Augustine after August indicates a spawning period extend-
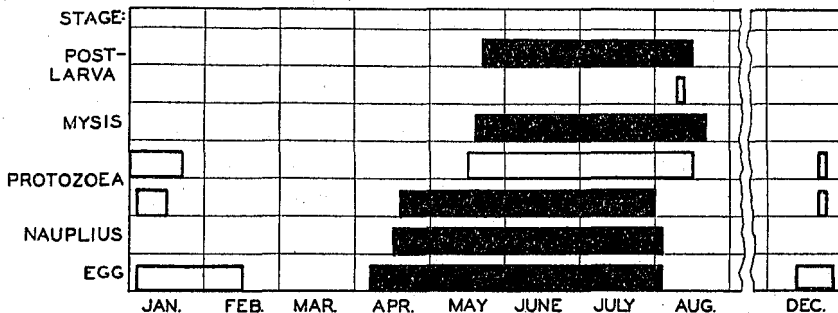

FIGURE 46.—Seasonal distribution of the planktonic eggs, larvae, and postlarvae of *Trachypenaeus constrictus* along the South Atlantic coast. Solid areas represent collections chiefly at St. Augustine, Fla.; clear areas are collections at Fort Pierce, Fla.

ing over the warm months of the year for this area. The occurrence of eggs at Ft. Pierce throughout the year probably indicates a year-round spawning at this locality.

NAUPLIUS

The seasonal distribution of the naupliar stages of *T. constrictus* at St. Augustine Inlet follows closely that of the egg, which extended from April 13 to August 3 in 1936. Although the nauplius frequently hatched in the laboratory soon after removal of the egg from the plankton, it did not occur in the natural environment in the same abundance as the egg. The presence of late naupliar stages in the plankton was rare despite the abundance of eggs.

The general scarcity of all larval stages of *T. constrictus*, excepting the mysis stage at St. Augustine Inlet, together with the observation that juvenile and adult shrimp of the species are largely oceanic in habitat, suggest that distribution of eggs and early larvae in estuarine areas is purely accidental and may not permit survival of the young. After distribution into estuarine areas, eggs and early larvae of all the *Penaeidae* are unavoidably carried over shallow tidal flats where tidal current is weak. It may be possible that the eggs and larvae are dropped to the muddy bottom at slack water and are consequently unable to survive. Both eggs and early postlarvae were found to be easily smothered to death when placed in an aquarium with a mud or silt bottom deposit.

It may be noted that although plankton was secured both from surface and bottom at St. Augustine Inlet, at a depth of 25 feet, nauplii and protozoea were as rare at one level as at the other. Furthermore, although plankton was secured on both incoming and outgoing tides, eggs and most larvae were taken only on the incoming, or flood tide. This fact appears significant for, if any eggs and larvae do survive a slack-water period, after being brought into the estuarine areas, their capture during ebb tide should be anticipated. Nauplii, hatching from the eggs carried into the

estuarine areas, would remain planktonic for at least a day after hatching and should be taken on ebb tide as well as flood tide. This was not the case, however, for ebb tide always showed a dearth of larvae as well as a decrease in the number of eggs compared with the preceding flood tide.

It is suggested that both the planktonic eggs and larvae of *T. constrictus* may fail to survive when brought into estuarine areas from the spawning areas in the open sea by tidal current. A similar condition may also exist in *P. setiferus* whenever it occurs that eggs and larvae are brought into shallow estuarine areas before a demersal stage (postlarval) is acquired.

A study was not made on the seasonal or geographic distribution of the naupliar stages of *T. constrictus* along the South Atlantic coast, other than at St. Augustine Inlet.

PROTOZOEA

The protozoeal stages of *T. constrictus* were taken in plankton along the South Atlantic coast from Stono Inlet, S. C., to Ft. Pierce, Fla. Collections of protozoea were made from April 12 to August 17 at many localities from South Carolina to St. Augustine, Fla., and in December, January, and May at Ft. Pierce. Protozoea attributed to *Trachypenaeus* sp. were taken off South West Pass, La., during June and July. The eggs and other larval stages of the species were frequently taken in the same plankton with the protozoea.

MYSIS

The mysis stages of *T. constrictus* were secured in the plankton from Stono Inlet, S. C. to Cape Canaveral, Fla., from April 9 to August 10. Collections at Ft. Pierce, Fla., were made throughout the year. Mysis attributed to *Trachypenaeus* sp. were taken during June and July off the coast of Louisiana. Most Gulf of Mexico collections were secured off South West Pass, although mysis were taken once in Barataria Bay.

The mysis stages were abundantly taken in St. Augustine Inlet, although earlier larval stages were rare. The mysis were reared in aquaria up to 15 mm. in postlarval length. Normally the mysis swam around the aquarium, usually seeking the brighter side. The larva, as it approached the molting period, usually swam or hovered near the bottom, continually ingesting fine particles of material stirred up by the movement of the maxillipeds and pereiopods. Immediately after molting, the postlarva promptly buried itself in the mud or sand, leaving eyes and antennae exposed.

POSTLARVA

The postlarvae of *T. constrictus* were taken occasionally in the plankton at St. Augustine Inlet from May 22 to October 10, the lengths of the young ranging from 4 to 16 mm. Although the mysis stages were common in plankton along the South Atlantic coast, only on one occasion was a postlarva secured. This fact, contrasted with the abundance at sea of planktonic postlarvae of *P. setiferus* and *P. brasiliensis*, reflects the observations on aquaria shrimp that indicated a prompt change from a planktonic mysis to a demersal postlarval existence. The occasional occurrence of postlarvae at St. Augustine Inlet was probably the result of the young shrimp becoming caught in the rapid tidal current and being unable to reach the bottom. It was often noted that juvenile *P. setiferus* and *P. brasiliensis* also swam off the bottom when brought into the swift channel of a coastal inlet.

Postlarvae of *Trachypenaeus* sp. were occasionally taken off the coast of Louisiana. The young were usually secured in a bottom dredge, or in plankton nets towed near the bottom, off the Delta of the Mississippi River.

PARAPENAEUS LONGIROSTRIS (LUCAS)

DESCRIPTION

FIRST PROTOZOEA

An incomplete series of larval and postlarval *Penaeidae*, including the first protozoea to the first postlarva, was taken in plankton off the Delta of the Mississippi River in relatively deep inshore water. This series has been tentatively identified as *Parapenaeus longirostris* (Lucas) on the basis of characters found in the first postlarva, particularly the presence of a pterygostomial spine. Although Monticelli and Lo
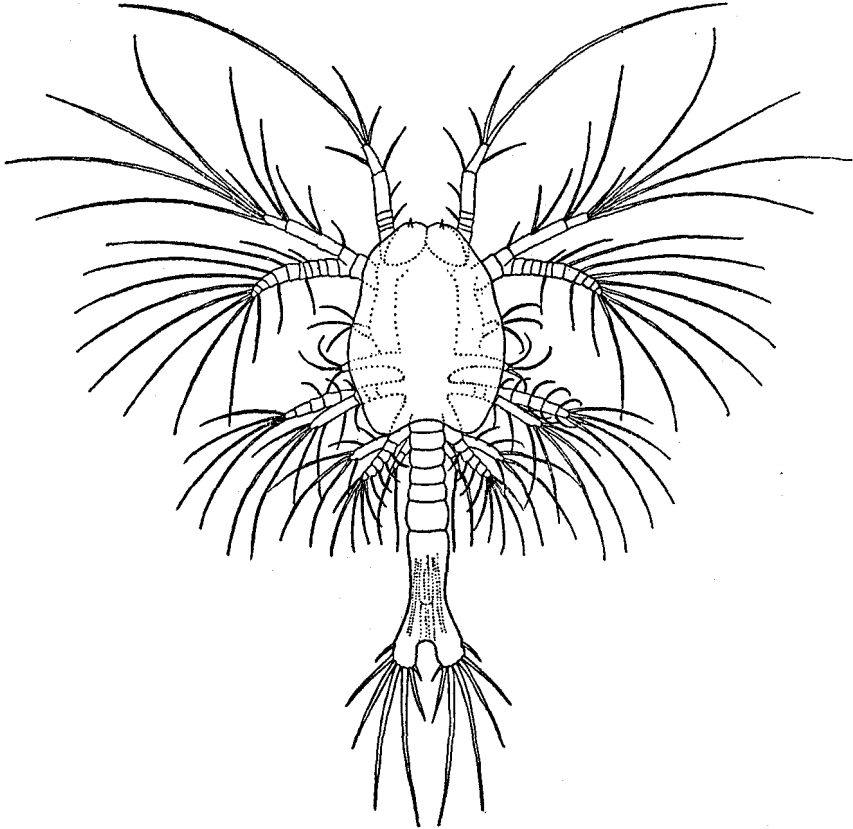

FIGURE 47.—First protozoea of *Parapenaeus longirostris*. Length 0.96 mm. Dorsal aspect.

Bianco (1901) described some larval stages of *P. longirostris* (*Penaeus membranaceus*), the account is not illustrated and difficulty was found in obtaining a clear idea of the larvae that would be useful from a comparative standpoint.

The first protozoea measures from 1.0 to 1.28 mm. in length, based on five specimens taken in plankton. It was the largest peneid first protozoeal stage obtained. (See fig. 47.)

The first protozoea of *P. longirostris* possesses the same fundamental morphology described for the comparable stage of *P. setiferus* and *T. constrictus*. Certain diagnostic features appear, however, to separate the species from the two other peneids throughout the larval stages of development.

It is separated from the first protozoea of *P. setiferus* by the presence of two pairs of lateral setae on the endopod of the second antenna, each pair originating at a differ-

ent notch on the lateral margin, and a single proximal lateral seta. Further, the first protozoea of *P. longirostris* has a pair of small, pointed projections on the antero-dorsal side of the carapace, slightly back from the frontal margin of the latter. Although these projections may be frontal organs, they appear to be rudiments of the supra-orbital spines which appear strongly developed in the succeeding larval stage. (See figs. 8 and 47.)

The first protozoea of *P. longirostris* is distinguished from the comparable stage of *T. constrictus* by a much smaller notch at the posterior margin of the tail and by the
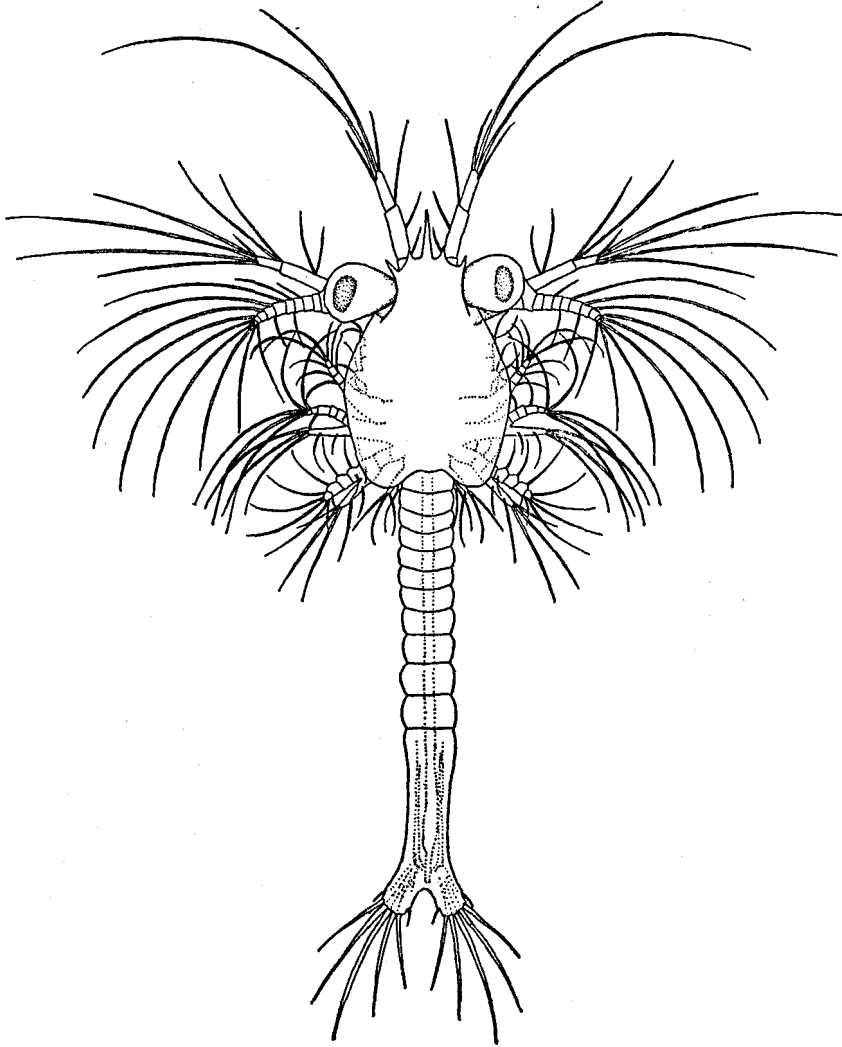

FIGURE 48.—Second protozoea of *Parapenaeus longirostris*. Length 2.0 mm. Dorsal aspect.

nearly equal length of the first and second antennae. The third maxillipeds are developed to a greater degree than in first protozoea of either *P. setiferus* or *T. constrictus* and are not developed simultaneously with the five pairs of pereiopods as in the latter two species. (See figs. 40 and 47.)

SECOND PROTOZOEA

The second protozoea measures from 1.7 to 1.9 mm. in length, based on three specimens taken in plankton with other protozoeal stages.

The metamorphosis from the first to the second protozoea is accompanied by the same general changes as described for *P. setiferus* and *T. constrictus*. The second protozoea shows a pair of stalked compound eyes; a rostrum extending nearly to the distal segment of the first antenna; two pairs of supra-orbital spines, the outer pair being the strongest; and the division of all thoracic and all but the sixth abdominal somites. The five pairs of pereiopods appear as budlike structures. The third maxillipeds are further developed. (See fig. 48.)

The second protozoea of *P. longirostris* is distinguished from the comparable larval stage of *P. setiferus* by the presence of two pairs of supra-orbital spines, compared to a single pair in the latter species, by the presence of two pairs of lateral setae on the endopod of the second antenna and by the longer and better developed third maxillipeds in the former species. (See figs. 9 and 48.)

The second protozoea likewise is distinguished from the comparable stage of *T. constrictus* by the presence of two pairs of supra-orbital spines, compared to the absence of such spines in the latter species; by the nearly identical lengths of the first and second antennae in *P. longirostris* compared to the greater length of the first antenna of *T. constrictus;* and primarily by the much smaller and narrower notch at the posterior margin of the tail of *P. longirostris*. (See figs. 41 and 48.)

FIGURE 49.—Third protozoea of *Parapenaeus longirostris*.
Length 2.7 mm. Dorsal aspect.

THIRD PROTOZOEA

The third protozoea measures from 2.3 to 2.6 mm. in length, based on 16 specimens taken in plankton with first and second protozoeal stages.

The typical changes in morphology from the second protozoea to the third protozoea show the differentiation of all abdominal somites and the telson, the development of uropods, and the appearance of postero-dorsal spines on the first five abdominal somites and a pair of postero-lateral spines on both the fifth and sixth abdominal somites. The pereiopods are differentiated, although rudimentary, as in the third protozoea of *P. setiferus*. (See fig. 49.)

The third protozoea is distinguished from the comparable stages of *P. setiferus* and *T. constrictus* by the same characters as separate the second protozoea of all three species. (See figs. 10, 42, and 49.)

Gurney (1924) described a number of larval stages of a peneid attributed to *Parapenaeus*. There are many similarities between the stage II (fig. 8) of the *Parapenaeus* described by Gurney and the third protozoea of *Parapeneaus longirostris* (fig. 49) described in this report. The two pairs of forwardly pointing teeth (supra-
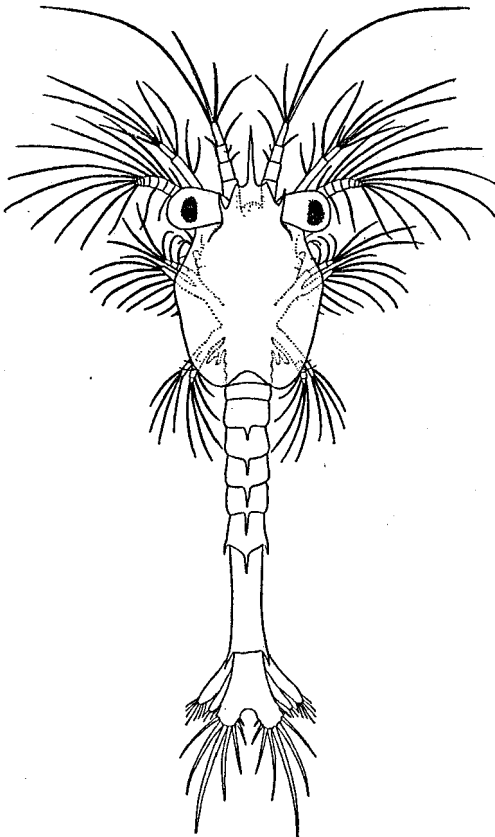
orbital spines) at the anterior margin of the carapace, and the number of spines on the abdominal somites, are comparable for both forms and would apparently indicate at least generic relationship.

FIRST MYSIS

The first mysis measures from 3.3 to 3.8 mm. in length, based on four specimens taken in plankton with protozoeal stages.

The characteristic changes from the third protozoea to the first mysis occur in *P. longirostris* as described in the other species of *Penaeidae*. The first and second antennae, losing their previous natatory function, become modified into tactile and balancing structures. The rostrum becomes greatly elongated, extending beyond the tip of the antennular flagella. The rostrum is slender, decurved distally, and bears two strong dorsal spines; the proximal spine placed on the level with the frontal margin of the carapace. A single pair of strong supra-orbital spines remain while small hepatic spines now occur on the carapace. The antero-ventral margin of the
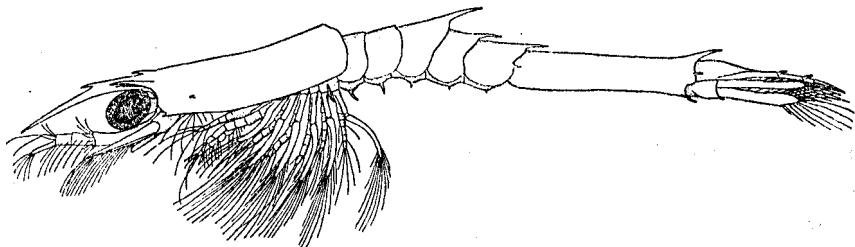

FIGURE 50.—First mysis of *Parapenaeus longirostris*. Length 3.6 mm. Lateral aspect.

latter ends in a sharp spine. Biramous pereiopods are well-developed and bear long setae. The endopods of the pereiopods are divided into seven segments but the first three pairs do not appear chelate distally. (See fig. 50.)

A strong spine appears on the postero-dorsal margin of the third abdominal somite, followed by weaker postero-dorsal spines on the fourth to sixth somites. Postero-lateral spines are present on the fifth and sixth abdominal somites, while a postero-ventral spine occurs on the sixth somite.

A mysis stage described by Gurney (see fig. 9) shows many characters found in the first mysis of *P. longirostris* (see fig. 50), figured and described in this paper.

A small spine appears medially on the sternite of the last thoracic and the first to fifth abdominal somites. The sternal spines on the first and second abdominal somites are the largest. The ventral margin of the pleuron of the first to fifth abdominal somites is finely serrated. The sixth abdominal somite is as long as or longer than all preceding abdominal somites.

The mysis of *P. longirostris* is readily distinguished from all other mysis stages described in this report by the elongated rostrum and by the elongated postero-dorsal median spine on the third abdominal somite.

The mysis stages of *P. longirostris* show a distinct type of larval development from the other species of *Penaeidae*. The mysis is apparently made up of four distinct stages instead of the customary two stages. These four stages cover a length range of the larva from 3.6 to 8 mm., extending well over the size at which the other *Penaeidae* have passed into the postlarvae. The cause for this extended mysis period is not clear. The fact that the species is almost entirely oceanic, being rarely taken in

estuarine areas, has perhaps resulted in a more prolongated planktonic larval period than in the case of those species dependent on reaching shallow estuarine water at postlarval stages.

SECOND MYSIS

The second mysis measures about 4.4 mm. in length, based on one specimen taken in plankton.

It is distinguished from the first mysis stage by the addition of a distal dorsal spine on the rostrum, by the weaker supra-orbital spines, by the disappearance of
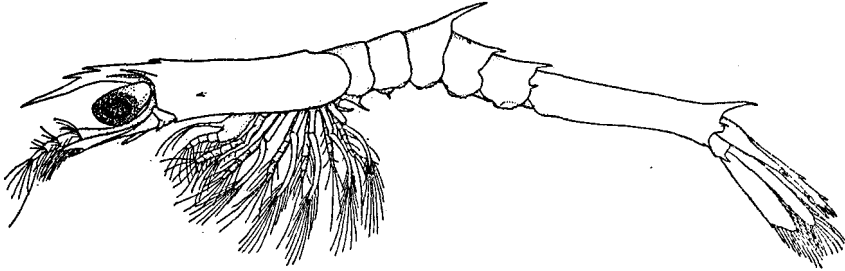

FIGURE 51.—Second mysis of *Parapenaeus longirostris*. Length 4.4 mm. Lateral aspect.

the sternal spine from the third, fourth, and fifth abdominal somites, and by the somewhat weaker postero-dorsal spines on the fourth and fifth abdominal somites. (See fig. 51.)

THIRD MYSIS

The third mysis measures about 5.6 mm. in length, based on specimens taken in plankton.

It is distinguished from the second mysis stage by the addition of a distal dorsal spine on the rostrum, by a posterior migration of the proximal rostral spine to an
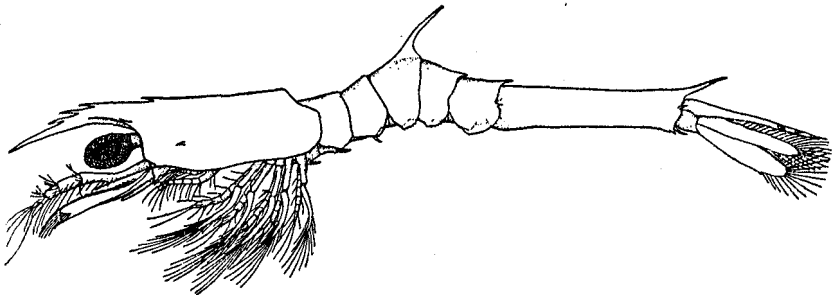

FIGURE 52.—Third mysis of *Parapenaeus longirostris*. Length 5.6 mm. Lateral aspect.

epigastric position and by the rudimentary formation of chelae on the endopods of the first three pairs of pereiopods. The supra-orbital spines persist but are greatly reduced in size. (See fig. 52.)

FOURTH MYSIS

The fourth mysis measures about 8 mm. in length, based on specimens taken in plankton.

The fourth mysis is distinguished from the third mysis stage by the addition of a distal dorsal spine on the rostrum, by the further movement posteriorly of the epigastric spine, by the differentiation of the pleopods and by disappearance of the supra-

orbital spines. The endopods of the first three pairs of pereiopods are clearly chelate. The pleopods are unique in that a short endopod is present, together with the func-
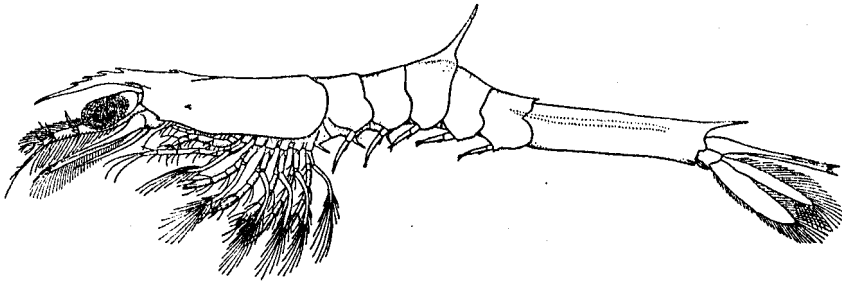

FIGURE 53.—Fourth mysis of *Parapenaeus longirostris*. Length 8.0 mm. Lateral aspect.

tional exopod. A biramous pleopod is not evident until late postlarval stage in *P. setiferus*, *P. brasiliensis*, and *T. constrictus*. (See fig. 53.)

POSTLARVA

A single postlarva of *P. longirostris*, obtained off the coast of Louisiana on July 17, 1934, measures 8.2 mm. in length.

The rostrum has become shortened but still extends beyond the eye. It bears six dorsal spines that are spaced from the frontal margin of the carapace to the tip of the rostrum. An epigastric spine lies on the dorsal carina slightly in advance of the hepatic spines. A branchiostegal or true pterygostomian spine is placed near the
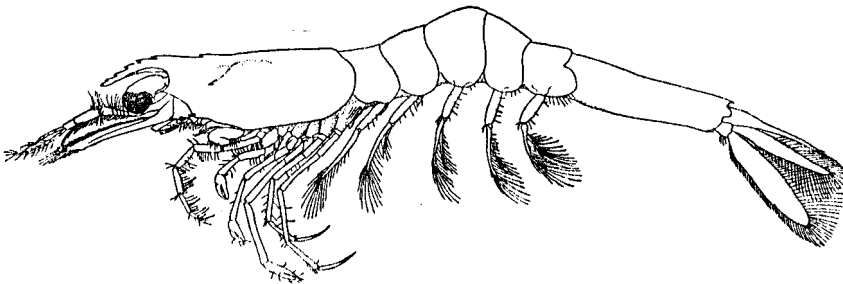

FIGURE 54.—First postlarva of *Parapenaeus longirostris*. Length 8.2 mm. Lateral aspect.

antero-inferior angle of the carapace slightly back from the margin of the latter. (See fig. 54.)

The endopods are lost from the five pairs of pereiopods. There occurs a spine on the ventro-median margin of the basal segment of the peduncle of the second antenna and the first pair of pereiopods possess a spine on the basis and ischium of each cheliped.

All spines disappear from the first five abdominal somites, but a small postero-dorsal spine persists on the sixth abdominal somite. The pleopods are biramous with the notable exception of the first pair that is uniramous. There appears a distal pair of fixed lateral spines on the telson preceded by two pairs of smaller movable spines.

Rudiments of epipodites appear on all of the five pairs of pereiopods.

DISTRIBUTION, LARVAE

The protozoeal, mysis and postlarval stages of *P. longirostris* were taken principally during July 1934, off South West Pass, La. Generally, a complete series of

larval stages was taken in the same plankton collection. A mysis was taken on May 25, 1931, about 10 miles south of Barataria Pass, La.

A single first protozoea of *P. longirostris* was taken at Ft. Pierce, Fla., in January 1936. No other record of this shrimp was obtained along the South Atlantic coast.

EUSICYONIA STIMPSONI (BOUVIER)

DESCRIPTION

EGG

Eggs attributed to *Eusicyonia stimpsoni* (Bouvier) were abundantly taken in the plankton and hatched in aquaria at St. Augustine, Fla. The larvae were usually
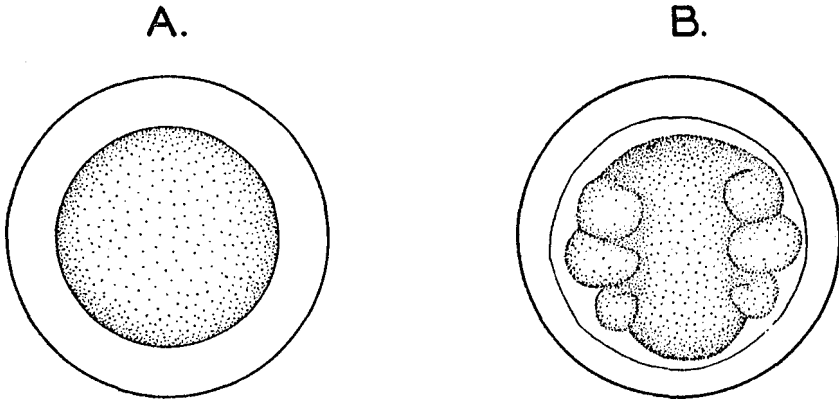
FIGURE 55.—Egg of *Eusicyonia stimpsoni*. Diameter 0.26 mm. (A) Embryo prior to differentiation of appendages; (B) early. embryo, ventral aspect.

reared to the first or second protozoeal stage and were carried through the first mysis stage in two instances. To complete the larval series, protozoeal stages were taken in plankton and reared to the second mysis stage. The generic and specific identity of this larval series has been suggested primarily by the number and arrangement
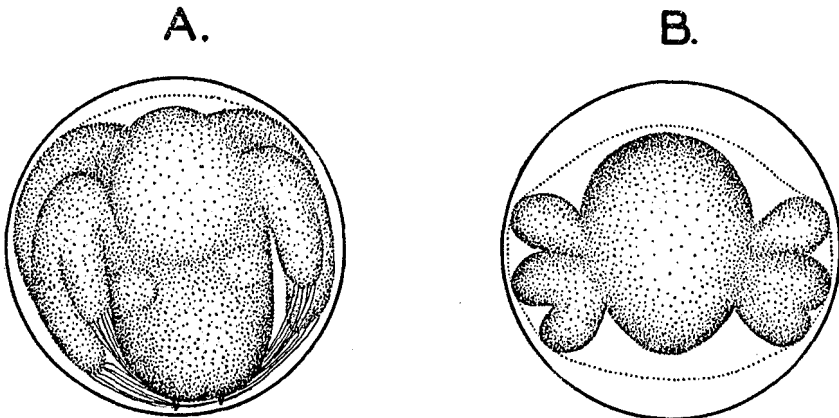
FIGURE 56.—Egg of *Eusicyonia stimpsoni*. Diameter 0.26 mm. (A) Late embryo, ventral aspect; (B) late embryo, anterior aspect.

of the rostral and postrostral spines and by the angular formation of the ventral margins of the pleura of the first to fifth abdominal somites. The confusion in the taxonomy of *Eusicyonia* in the Western Atlantic has been well brought out by Burkenroad (1934b). Assignation of specific identity has been also guided by the geographic

ranges of the closely related species, *E. stimpsoni* and *E. dorsalis*, as designated by Burkenroad.

The egg of *E. stimpsoni* is spherical, nonadhesive, and normally demersal. The eggs range from 0.22 to 0.32 mm. in diameter and in a size-frequency distribution of 70 preserved eggs a total of 54 measured 0.26 mm. The smaller-sized eggs resemble closely the eggs of the Sergestid, *Acetes*, while many eggs approximate in size those of *P. setiferus*. (See figs. 55 and 56.) Eggs of *Acetes* sp. were taken in plankton at St. Augustine and reared to the first protozoea. These eggs uniformly measured 0.22 mm. in diameter.

The eggs are rendered buoyant temporarily by agitation of the water, but are less buoyant than the eggs of *T. constrictus* and somewhat more buoyant than the eggs of *P. setiferus*. The relative size of the embryo, in proportion to the egg space, apparently determines this differentiation in buoyancy among the eggs of the three species of *Penaeidae*.

The egg of *E. stimpsoni* is separated from the egg of *P. setiferus* and *T. constrictus* both by the relative size of the embryo to the egg space and by the reddish-pink color reflected by the egg membrane of *E. stimpsoni* under the microscope. The eggs of the other two species possess a bluish coloration of the membrane.

The eggs taken in the plankton at St. Augustine Inlet were generally in late stages of development similar to the condition found for the eggs of the other *Penaeidae*. The position of the egg nauplius within the egg is distinctive for the former is not as tightly invested by the egg membrane, as in the case of *P. setiferus*, or as loosely invested as in the case of *T. constrictus*. The egg nauplius measures about 0.24 mm. in length prior to hatching.

FIRST NAUPLIUS

Five stages of nauplius were found to occur in the larval development of *E. stimpsoni*. This number is comparable to that noted for the nauplius larvae of *P. setiferus* and *T. constrictus*. Diagnostic characters appear to distinguish comparable stages of the nauplii of these three species of Penaeidae and also to separate the five successive stages of the nauplius within a single species. (See table 6.)

The first nauplius of *E. stimpsoni* measures from 0.24 to 0.26 mm. in body length and 0.12 mm. in greatest body width.

The body is ellipsoid in shape but is somewhat incurved medially and tapers to a slight degree posteriorly. It has a ventral flexure of the body like all peneid nauplii. (See fig. 57.)

The first antenna possesses one long and two moderate terminal setae and four moderate lateral setae. This number contrasts with the two long and one moderate terminal setae found on *P. setiferus* and the two long terminal setae on *T. constrictus*.

The second antenna has the endopod with the two terminal setae while the exopod bears four latero-terminal setae.

The third appendage has endopod and exopod each bearing three long terminal setae.

A pair of strong spines appears at the posterior margin of the body.

TABLE 6.—*The nauplius of* Eusicyonia stimpsoni

[Showing the progressive increase in the number of setae on the exopod of the second appendage and in the number of furcal spines after each naupliar molt. The range in body length and in greatest body width are given in millimeters; measurements were made in 0.02 mm. units. Based on 33 specimens, all reared from planktonic eggs]

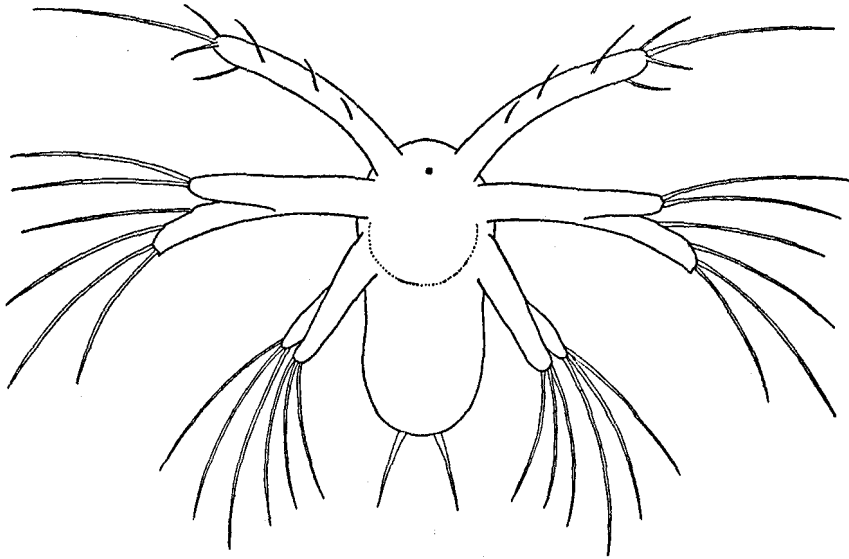| Stage of nauplius	First	Second	Third	Fourth	Fifth
Setae on exopod	4	5	6	7	8
Furcal spines	1+1	1+1	2+2	6+6	7+7
		2+2	3+3	7+7	
Body length	0.24-0.26	0.26-0.30	0.30-0.36	0.36-0.40	0.36-0.42
Body width	.12	.12	.12	.12	.14
Number reared	2	15	5	5	6

FIGURE 57.—First nauplius of *Eusicyonia stimpsoni*. Length 0.26 mm. Ventral aspect.

The first nauplius of *E. stimpsoni* is distinguished from the first nauplii of *P. setiferus* and *T. constrictus* principally by the presence of four instead of five setae on the exopod of the second antenna. The general body shape also appears different in the three species.

The first nauplius of *E. stimpsoni* was secured by hatching two eggs.

SECOND NAUPLIUS

The second nauplius measures from 0.26 to 0.30 mm. in body length and 0.12 mm. in greatest body width.

This naupliar stage is separated from the first nauplius by an increase of one terminal seta on both the exopod and endopod of the second antenna. The presence of an outer pair of short spines often occurs at the posterior margin of the body. (See fig. 58.) As suggested by Bassindale (1936), in the case of the variation of setae in barnacle nauplii, the variations in the number of furcal spines, or setae, in the naupliar stages of *E. stimpsoni* are perhaps caused by the precocious development of a spine normally appearing at the next stage or to the delayed development of a spine. A difference of more than one pair of spines was not observed.

The second nauplius is distinguished from the comparable naupliar stage of *P. setiferus* by the presence of five instead of six setae on the exopod of the second antenna

and by a less tapered body posteriorly. It is further separated by a shorter body width in proportion to body length and by the absence of a sulcus, or bifurcation, at the posterior margin of the body.

The second nauplius is distinguished from the second nauplius of *T. constrictus* by the presence of five instead of six setae on the exopod and three instead of two terminal setae on the endopod of the second antenna. The absence of lateral setae on the endopod of *E. stimpsoni* may also tentatively be regarded as a diagnostic character between the two species. The presence of three terminal setae on the endopod of the second antenna separates the second nauplius of *E. stimpsoni* from the first nauplius of *P*.
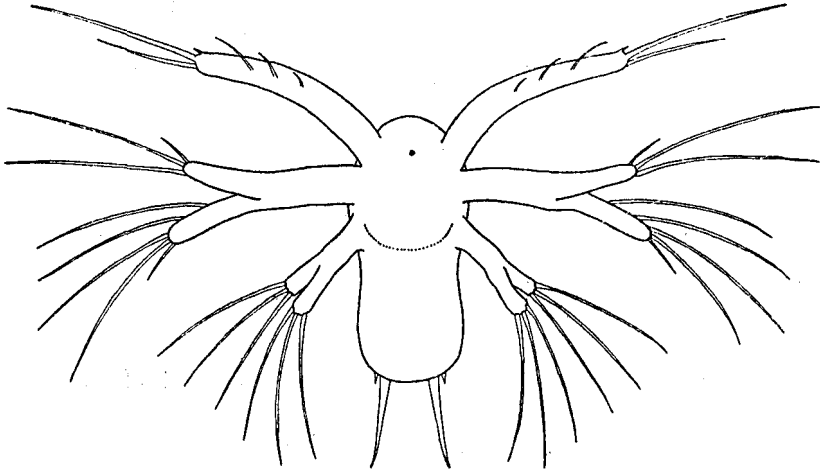

FIGURE 58.—Second nauplius of *Eusicyonia stimpsoni*. Length 0.28 mm. Ventral aspect.

setiferus and *T. constrictus* where the second pair of postero-marginal spines are absent in the former.

The second nauplius was obtained by hatching 15 eggs.

THIRD NAUPLIUS

The third nauplius measures from 0.30 to 0.36 mm. in body length and 0.12 mm. in greatest body width.

This naupliar stage is separated from the second nauplius by an increase of one terminal seta on the exopod and one terminal seta on the endopod of the second antenna. The number of spines at the posterior margin usually increases to a total of 3+3. A shallow sulcus tends to bifurcate the posterior margin of the body. (See fig. 59.)

The third nauplius of *E. stimpsoni* is distinguished from the third nauplius of *P. setiferus* by the presence of six instead of seven setae on the exopod and four instead of three setae on the endopod of the second antenna. A shallower postero-marginal notch is found on *E. stimpsoni* than on *P. setiferus*. A larger pair of outer furcal spines will separate the third nauplius of *E. stimpsoni* from the second nauplius of *P. setiferus* in addition to a difference in setation of the second antenna.

The third nauplius of *E. stimpsoni* is distinguished from the third nauplius of *T. constrictus* by the same differences in setation of the second antenna as occurs in *P. setiferus* and by the presence of two or three pairs of furcal spines in contrast to five pairs found on *T. constrictus*. The larger number of setae on the endopod of the
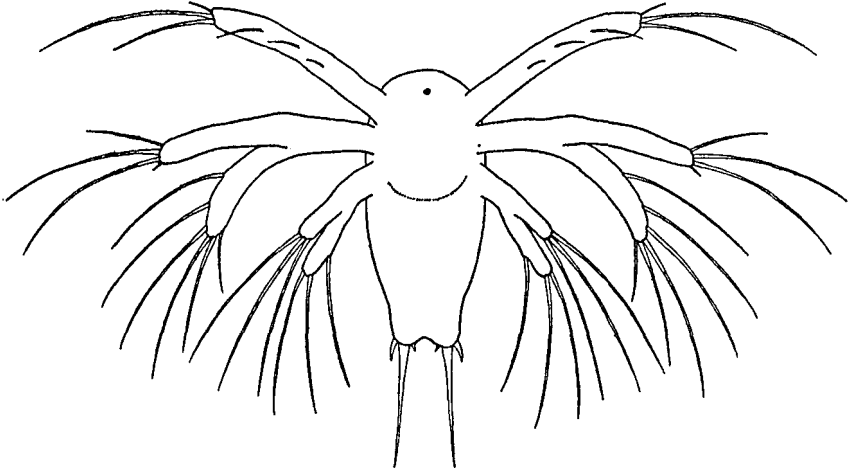
FIGURE 59.—Third nauplius of *Eusicyonia stimpsoni*. Length 0.34 mm. Ventral aspect.

second antenna of *E. stimpsoni* separates the third nauplius from the second naupliar stage of *T. constrictus*.

The third nauplius was obtained by hatching five eggs.

FOURTH NAUPLIUS

The fourth nauplius measures from 0.36 to 0.40 mm. in body length and about 0.14 mm. in greatest body width.

This naupliar stage is separated from the third nauplius by an increase of one lateral seta on the exopod of the second antenna, and by an increase in the number
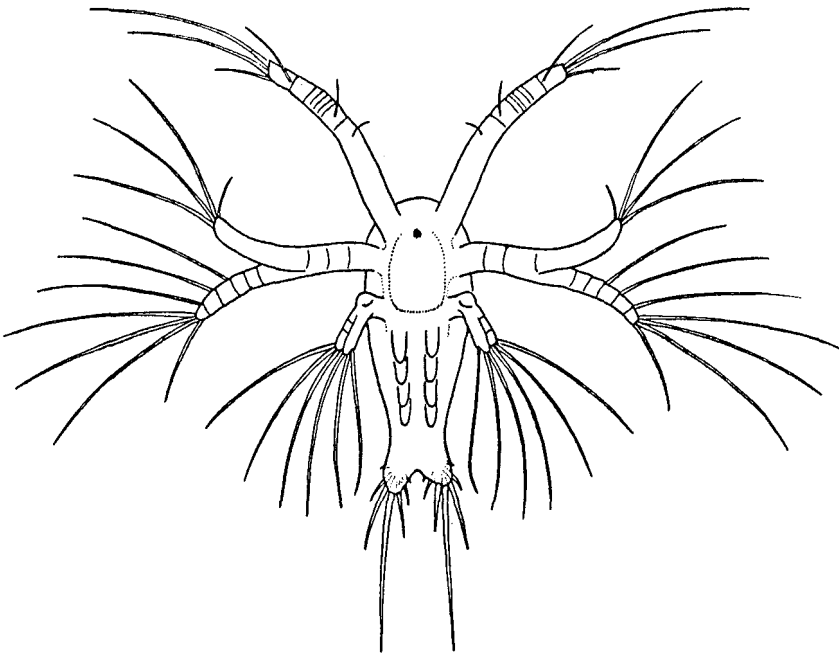

FIGURE 60.—Fourth nauplius of *Eusicyonia stimpsoni*. Length 0.38 mm. Ventral aspect.

of furcal spines either 6+6 or 7+7. The fourth to seventh pairs of body appendages appear externally developed although rudimentary. A globular swelling appears at the base of the third appendage. The bifurcation at the posterior margin of the body becomes deeper. The body shape is much constricted posteriorly. (See fig. 60.)

The fourth nauplius of *E. stimpsoni* is distinguished from the fourth naupliar stage of *P. setiferus* by the possession of seven instead of eight setae on the exopod and four instead of three terminal setae on the endopod of the second antenna, by the presence of larger and more numerous furcal spines, and by the absence of frontal sense organs.

It is distinguished from the fourth nauplius of *T. constrictus* by the possession of seven instead of eight setae on the exopod and four instead of three setae on the endopod of the second antenna, by a more moderate swelling at the base of the third appendage, and by a somewhat weaker pair of outer furcal spines.

The fourth nauplius was obtained by hatching five eggs.

FIFTH NAUPLIUS

The fifth nauplius measures from 0.36 to 0.42 mm. in body length and about 0.14 mm. in greatest width.

This naupliar stage is separated from the preceding fourth nauplius by an increase of one seta on the exopod of the second antenna, making a total of eight, and by a
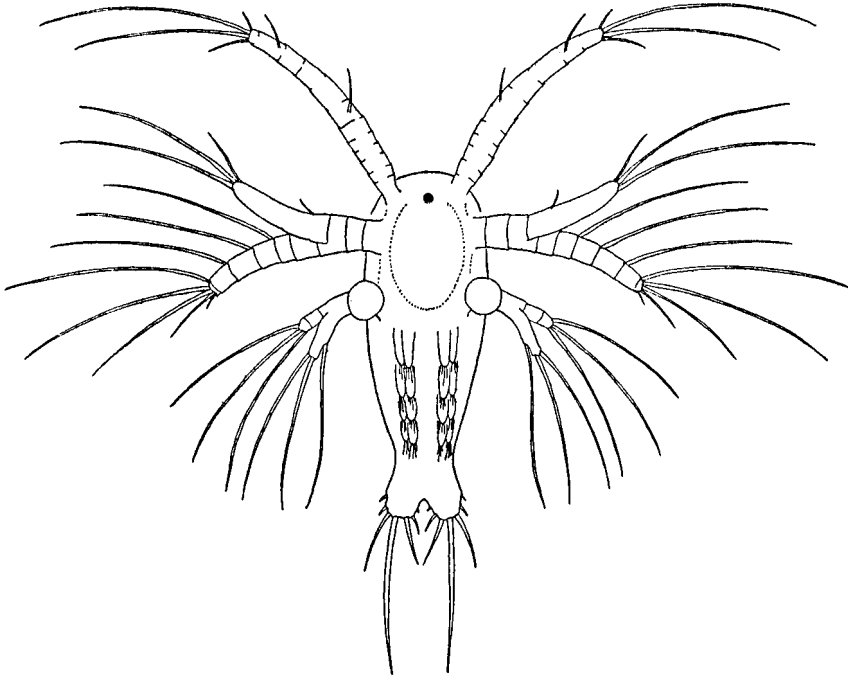

FIGURE 61.—Fifth nauplius of *Eusicyonia stimpsoni*. Length 0.42 mm. Ventral aspect.

uniform number of 7+7 furcal spines. The globular swelling at the base of the third appendage becomes enlarged. The fourth to seventh pairs of appendages are further enlarged, are biramous and bear short terminal setae. (See fig. 61.)

The fifth nauplius of *E. stimpsoni* is distinguished from the fifth nauplius of *P. setiferus* by a much shorter body length and body width, by the absence of frontal sense organs, and by the somewhat narrower notch at the posterior margin of the body.

It is distinguished from the fifth nauplius of *T. constrictus* by weaker outer furcal spines and by a somewhat narrower furcal notch. The fifth nauplius of *E. stimpsoni* closely resembles the fourth nauplius of *T. constrictus* for the somewhat weaker furcal

spines on the former appears to be the only differential character, excepting certain differences in setation that may not be reliable.

The fifth nauplius was obtained by hatching six eggs.

The naupliar stages of *E. stimpsoni*, similar to those of the other peneids, were passed through within 36 hours after the first nauplius emerged from the egg. The behavior of the nauplii of *E. stimpsoni* appeared identical to those of the other two species of *Penaeidae*.

Time or material did not permit an exhaustive study of the degree of variation in the various diagnostic characters that separate the nauplii of the three species of *Penaeidae* described in this report. All five naupliar stages of *T. constrictus* and *E. stimpsoni*, and three of the five naupliar stages of *P. setiferus*, were secured by hatching isolated eggs of each species. Although the diagnostic characters which have been described appear constant and reliable, so far as the reared nauplii show, the limited amount of reared nauplii at certain stages must necessitate a degree of caution in the evaluation of specific differences among the various naupliar stages.

FIRST PROTOZOEA

The first protozoea of *E. stimpsoni* measures from 0.70 to 0.80 mm. in body length, based on the measurements of 32 specimens reared from eggs.

The same fundamental changes in body morphology of the first protozoea are shown by this species as noted in the first protozoea of *P. setiferus*, *T. constrictus*,
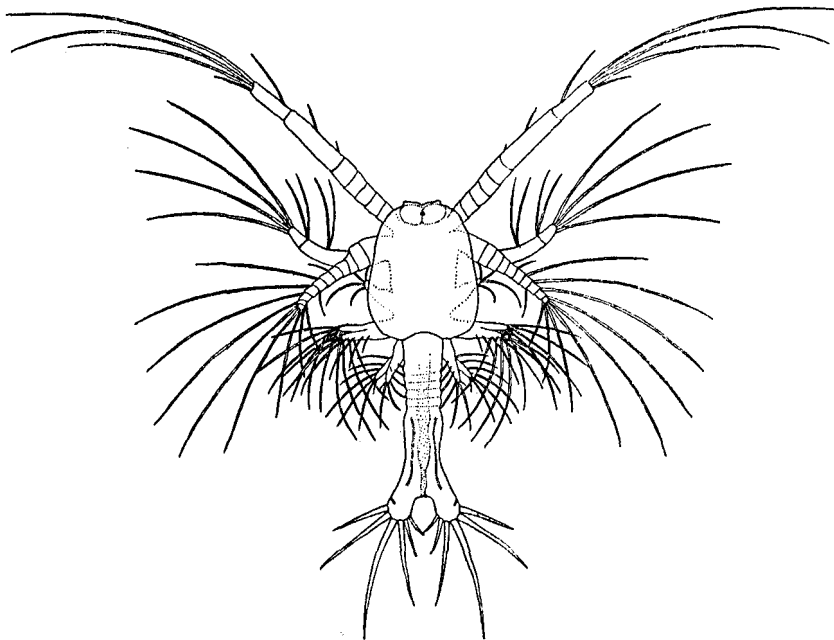

FIGURE 62.—First protozoea of *Eusicyonia stimpsoni*. Length 0.72 mm. Dorsal aspect.

and *P. longirostris*. Diagnostic differences are present, however, that separate the first protozoea of *E. stimpsoni* from the comparable larval stage of the other species of *Penaeidae*. (See fig. 62.)

The first protozoea of *E. stimpsoni* is distinguished from the first protozoea of *P. setiferus* by its somewhat smaller size, by two pairs of lateral setae on the endopod of the second antenna, and by a narrower notch at the posterior margin of the tail.

Furthermore, the second antenna is much shorter than the first antenna, whereas in *P. setiferus* both appendages are of nearly equal length.   (See figs. 8 and 62.)

The first protozoea is distinguished from the comparable larval stage of *T. constrictus* principally by the much narrower notch at the tail and by the outer pair of furcal spines placed somewhat lower on the furcal process and directed more dorsally than laterally.   (See figs. 40 and 62.)

SECOND PROTOZOEA

The second protozoea measures 1.0 mm. in body length, based on four specimens reared from eggs.

The development of stalked compound eyes, a short rostrum, and an elongated abdomen separate the second protozoea from the previous stage.   Rudiments of the pereiopods become differentiated.   (See fig. 63.)

The second protozoea is readily distinguished from the second protozoea of *P. setiferus* and *P. longirostris* by the absence of supra-orbital spines.   Furthermore, the
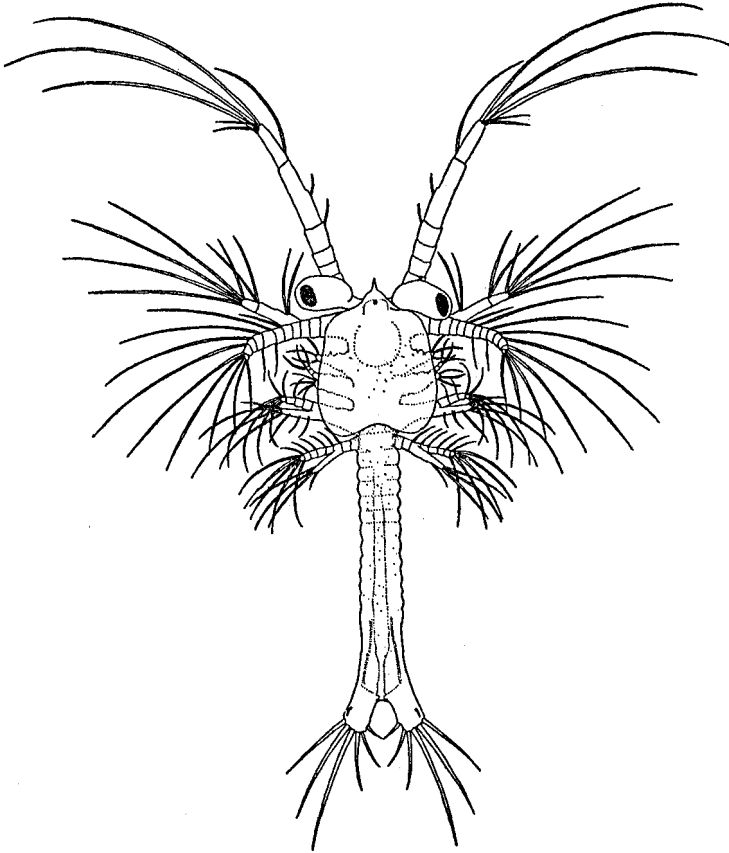

FIGURE 63.—Second protozoea of *Eusicyonia stimpsoni.*   Length 1.0 mm.   Dorsal aspect.

length of the second antenna is much shorter, compared to the first antenna in *E. stimpsoni* than in the other two species.   (See figs. 9, 41, and 63.)

The second protozoea is distinguished from the comparable stage of *T. constrictus* by the narrower notch between the posterior furcal process.   The outer marginal pair of furcal spines in *E. stimpsoni* are smaller and also directed more dorsally instead of laterally as in *T. constrictus.*

THIRD PROTOZOEA

The third protozoea measures from 1.36 to 1.68 mm. in body length, based on the measurement of seven specimens reared from eggs.

The development of biramous uropods at the base of the sixth abdominal somite and the complete segmentation of the thoracic and abdominal somites separate the
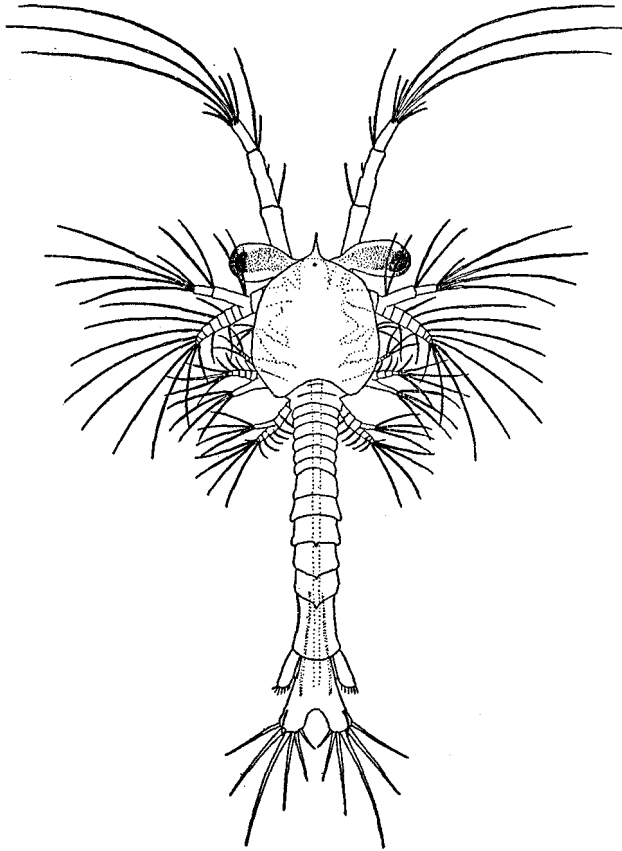

FIGURE 64.—Third protozoea of *Eusicyonia stimpsoni*. Length 1.5 mm. Dorsal aspect.

third protozoea from the preceding stage. Weak postero-dorsal spines appear on the third to fifth abdominal somites. The third maxilliped and pereiopods are rudimentary. (See fig. 64.)

The third protozoea is distinguished from the comparable stage of *P. setiferus* and *P. longirostris* by the absence of supra-orbital spines and by a difference in the number and position of the abdominal spines. (See figs. 10, 42, and 64.)

It is again distinguished from the third protozoea of *T. constrictus* by the narrower notch at the posterior furcal process, or telson, and by the absence of postero-dorsal spines on the first and second abdominal somites and postero-lateral spines on the fifth somite. The sixth abdominal somite is much shorter in *E. stimpsoni* than in the other three species of *Penaeidae*.

FIRST MYSIS

The first mysis measures from 2.0 to 2.8 mm. in body length based on five specimens, two of which were reared from eggs.

The same fundamental morphological changes from the third protozoea to the first mysis stage occur in *E. stimpsoni* as noted in the other species of *Penaeidae*. A

short rostrum is present, reaching about halfway of the eye. There are three spines on the dorsal carina of the carapace, one spine being placed anterior to the orbital margin. The carapace also has on the anterior margin weak supra-orbital, and sub-orbital spines. The antero-ventral angle ends in a sharp spine. Dorsal spines are absent on the first to fifth abdominal somites but a small postero-dorsal spine
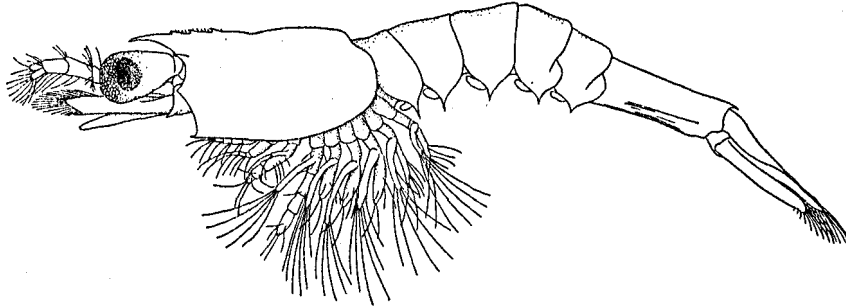

FIGURE 65.—First mysis of *Eusicyonia stimpsoni*. Length 2.4 mm. Lateral aspect.

appears on the sixth somite. The ventral margins of the pleura of the first to fifth abdominal somites end in sharp spines. Pleopods may be slightly developed. (See fig. 65.)

The first mysis of *E. stimpsoni* is distinguished from the first mysis of the other species of *Penaeidae* by the absence of dorsal spines on the first five abdominal somites, by a shorter rostrum, and by the spinous ventral margins of the pleura of the first five abdominal somites.

One first mysis was reared from the egg in 7 days and died during an attempt to molt into the second mysis 6 days later.

SECOND MYSIS

The second mysis measures from 2.8 to 3.6 mm. in body length, based on 10 specimens obtained from plankton. The most striking differences between the first
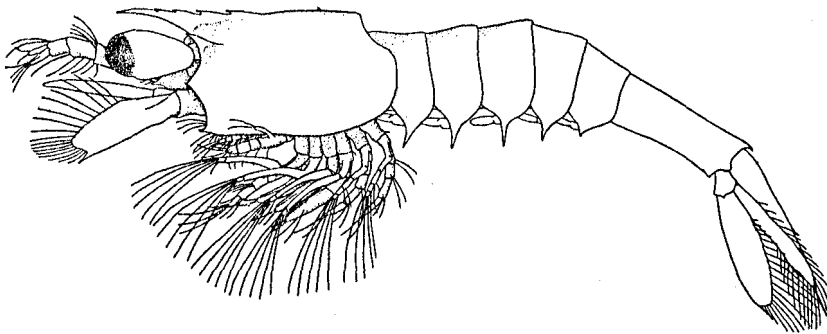

FIGURE 66.—Second mysis of *Eusicyonia stimpsoni*. Length 3.2 mm. Lateral aspect.

and second mysis are the addition of a distal dorsal spine on the rostrum, a weak spine on the posterior dorsal carina, about three-quarters the way from the frontal to the posterior margin of the carapace; the further development of the pleopods, and an increase in size of the chelate appendages of the pereiopods. (See fig. 66.)

The second mysis of *E. stimpsoni* differs from the comparable larval stage of the other *Penaeidae* by the elongated spinous margin of the pleura on the first five abdominal somites and by the short sixth abdominal somite.

The second mysis was reared from planktonic third protozoea.

DISTRIBUTION

EGG

The eggs of *E. stimpsoni* were abundantly taken in plankton at St. Augustine Inlet from March 30 to August 8, 1936. They were taken in lesser abundance from January to March 1936, and in August and September 1935 at Ft. Pierce Inlet, Fla. A small number of eggs were also taken at sea off Stono Inlet, S. C., in September 1933.

The abundance of eggs at St. Augustine Inlet, contrasted with the scarcity of eggs from areas in the open sea along the South Atlantic coast, points to the conclusion offered regarding a quite similar distribution of eggs of *P. setiferus* and *T. constrictus*. The normal demersal nature of the peneid egg brings the latter on or close to the bottom in open ocean, whereas the egg is agitated by the strong tidal current prevailing in coastal inlets and is carried above the bottom in such inlets. Plankton collection methods enable a far greater number of eggs to be secured in the inlets than in open sea.

The abundance of eggs at St. Augustine Inlet is not correlated with any recognized abundance of spawning adult *E. stimpsoni* in this area. It is probable, however, that the species escapes capture by the commercial shrimp trawls by reason of its small size and habit of remaining on the sea bottom, perhaps buried in the sand or mud. It is of interest to note also that the statement by Burkenroad (1934b) that the range of adult size within a species of the genus *Eusicyonia* is much greater than in other *Penaeidae* and that sexual maturity may be attained at a size so much less than the maximum that a rapid maturation of the eggs and a very extended adult life seem implied. Whether a rapid maturation of eggs and an extended adult life produce large quantities of eggs are unknown but are, nevertheless, possible.

NAUPLIUS

The seasonal distribution of the nauplius of *E. stimpsoni* naturally closely parallels that noted for the eggs of the species at St. Augustine. A differentiation of the nauplii of *E. stimpsoni* and *T. constrictus* in the plankton taken at sea has not been made.

PROTOZOEA

The protozoeal stages of *E. stimpsoni* were rarely taken in plankton, despite the abundance of eggs at St. Augustine and Ft. Pierce Inlets. Whether this condition
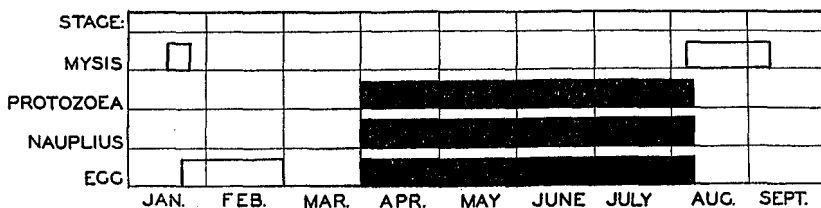

FIGURE 67.—Seasonal distribution of planktonic eggs and larvae of *Eusicyonia stimpsoni* along the South Atlantic coast. Solid areas indicate collections at St. Augustine, Fla.; clear areas are collections at Fort Pierce, Fla.

was caused by the death of the larvae if brought by tidal currents into estuarine areas is unknown. The scarcity of protozoeal and mysis stages of all *Penaeidae* in estuarine areas, compared to the abundance of several types of eggs and postlarvae, indicates either that the planktonic eggs and larvae perish if accidentally brought into the shallow estuarine waters or that the natural mortality between egg and postlarval stage is enormous in estuarine areas. (See fig. 67.)

MYSIS

Mysis stages were rarely taken in plankton at St. Augustine Inlet and were not obtained at sea either along the South Atlantic or Louisiana coasts. Both first and second mysis were rather frequently taken at Ft. Pierce Inlet during August and September 1935 and in January 1936. (See fig. 67.)

GENERAL DISCUSSION

The larval development of *Penaeus setiferus*, the common commercial southern shrimp, consists of 10 distinct stages excluding the demersal spherical egg. These stages are made up of 5 forms generally included under the name of nauplius, 3 forms included under the name of protozoea, and 2 forms included under the name of mysis. The larval development of *P. setiferus* was found to be closely paralleled by two other species of American *Penaeidae, Trachypenaeus constrictus*, and *Eusicyonia stimpsoni*.

The fact that relatively few specimens of eggs, larvae, and first postlarvae of *P. setiferus* were obtained at collection points proximal to the coast line is an indication of a general offshore spawning area. The distribution of planktonic larvae and postlarvae to inshore waters depends apparently on the duration of the larval period and on the direction and speed of the currents to which the larvae are exposed in open sea. It is logical to presume that the major spawning areas of the species are within such a distance of the coast line as to permit the young shrimp to reach estuarine areas at or soon after the second or third postlarval stage (approximately 5 to 7 mm. in length) is reached.

It is believed, on the basis of the observed growth of the larvae of *Penaeus, Trachypenaeus*, and *Eusicyonia* in aquaria, that the earliest common inshore postlarval stage of *P. setiferus* is reached within 2 to 3 weeks from the time the eggs are spawned in offshore waters. If this assumption is correct, the peak of the annual spawning season occurs during April and May, judging from the maximum seasonal abundance of planktonic postlarvae. The spawning season extends, however, from March to late August.

The exact nature of the inshore movement of larval and planktonic postlarval *P. setiferus* is unknown and cannot be determined until the complete geographic distribution of eggs and larvae, and the direction and force of prevailing ocean currents, are ascertained for both inshore and offshore waters along the South Atlantic and Gulf coasts of the United States. Whether or not spawning occurs more or less directly offshore from the inlets through which the planktonic postlarvae enter estuarine areas cannot be determined on the basis of existing data. It is highly possible that extensive coastal movement of planktonic larvae and postlarvae occurs before inshore nursery grounds are reached and the young shrimp adopt for the first time a demersal existence.

A sharp geographical boundary in the southward distribution of both planktonic and demersal young of *P. setiferus* was found to occur along the South Atlantic coast. An absence of young shrimp was noted in estuarine waters south of St. Augustine, Fla. This distribution was based on extensive seine collections of *Penaeidea* from Brunswick, Ga., to Ft. Lauderdale, Fla. South of St. Augustine and New Smyrna Inlets, young *P. setiferus* is completely replaced by young *P. brasiliensis*. The latter species extends, however, along the Atlantic coast, at least from Chesapeake Bay to Miami, Fla., although most abundant in estuarine waters from St. Augustine to Ft. Pierce, Fla.

It has been found by commercial shrimp fishermen that large numbers of adult *P. setiferus* range along the coast of Florida as far south as Cape Canaveral and Cocoa

Beach. South of the latter point, *P. brasiliensis* usually replaces *P. setiferus* in the scattered catches from this area. Observations of fishermen, confirmed by marking experiments now in progress by the Bureau of Fisheries, indicate that the occurrence of *P. setiferus* south of St. Augustine is largely seasonal; that schools of shrimp move southward along the coast in winter into areas extending from St. Augustine to Cocoa Beach, and migrate back northward in early spring probably prior to spawning. The habit of the adult shrimp to move offshore into deeper water prior to spawning, both along the South Atlantic and Gulf coasts, has aided in preventing overfishing up to the present time.

It was found that planktonic postlarvae of *P. setiferus*, when placed in aquaria, settle to the bottom within a few hours and commence feeding on detritus. Shrimp placed in aquaria lacking bottom detritus, or any source of nourishment, remain restless and die within a week. Planktonic postlarvae usually lack food material or detritus in their digestive tract but whether this indicates little or no feeding when at sea after the larval stages are passed is unknown.

No evidence was found to indicate that planktonic postlarvae of *P. setiferus* settle to the bottom at sea and gain access to estuarine areas after a demersal oceanic existence has been adopted. Collections on seabottom have failed to reveal any young shrimp of this species under about 30 mm. (1.25 in.) in length, although demersal postlarvae of *Trachypenaeus* and *Eusicyonia* have been taken on numerous occasions. Likewise, no records exist either for demersal oceanic postlarval stages of *P. brasiliensis*. In general behavior the latter species is comparable to *P. setiferus*, although reaching the estuarine waters at a larger planktonic postlarval size and occurring in the plankton throughout the year.

In conclusion it seems obvious that the factors influencing the abundance of the common shrimp. *P. setiferus*, are linked with the distribution of the young to shallow estuarine areas from offshore oceanic spawning grounds. The exact nature of this distribution must await further research.

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