Specimens of the starry flounder, Platichthys stellatus (Pallas, 1811) Girard, 1854, were collected in Yaquina Bay near Newport, Oregon, from July, 1970, to August, 1971. Fish infected with Lepeophtheirus hospitalis Fraser, 1920, were transported to Corvallis, Oregon, and maintained in a sea water system at 15°C. Isolated copepods were studied in finger bowls in non-aerated sea water which was changed several times daily.

The morphology and behavior of the ten life history stages of the parasitic copepod L. hospitalis have been described. Measurements and figures for all stages were included.

Adults are motile ectoparasites on the ventral surface of the starry flounder. They adhere with prehensile second antennae, maxillipeds, and a suction cup action produced by the arched cephalothorax. The primary food was slime, but if an abrasion or cut was present, blood was sometimes
ingested. Seasonal abundance of the parasite in Yaquina Bay seemed to be correlated with the amount of fresh water flowing through the bay.

Ovulation and egg string formation occurred simultaneously at night. At 20°C, 64 hours elapsed between ovulation and hatching. The major features of ovulation, egg string formation, embryology, and hatching have been described.

The two unsegmented naupliar stages were free-swimming, positively phototropic, and possessed three pairs of appendages: first antennae, second antennae, and mandibles all of which were used in swimming. The duration of the first naupliar stage at 20°C was seven and a half hours and at 15°C about 24 hours. For the second nauplius these times were 11 and 40 hours respectively. Mortality on the molts following each of these two stages was less than five percent and five to ten percent.

The segmented body of the copepodite possessed those appendages present on the naupliar stages, and added the post oral processes, maxillae, maxillipeds, the first two pairs of thoracic legs, and the caudal rami. This stage was free-swimming, but died in three to eight days, at 20°C, if a host was not located. Copepodites held onto the flounder with their prehensile second antennae for four to six days, at 15°C, at which time they formed attaching filaments. This process began with a series of rapid jabs
to the host substrate by the anterior cephalothorax. A droplet of frontal organ secretion appeared between copepodite and host and was pulled out into a filament which hardened immediately. At 15°C the molt to the first chalimus stage took place 36 to 48 hours after filament formation. Laboratory mortality from copepodite to first chalimus was over 95 percent.

The six chalimus stages at 20°C lasted $6\frac{1}{2}$, 5, $4\frac{1}{2}$, $2\frac{1}{2}$, 2, and 1 days respectively. The first four stages were attached by a frontal filament, the fifth was usually unattached, and the sixth was always unattached. Sexual differentiation became evident in the fifth chalimus: males possessed a sixth pair of legs, females did not. Sixth chalimus males were usually found coupled to adult females or mobile chalimus stages of either sex. The third and fourth pairs of legs appeared in the first chalimus stage. The post antennal processes and fifth pair of legs were new structures in the third chalimus, and the sternal furca was new to the fourth chalimus.

The above mentioned times, changes, and behavior were compared to that of other caligids. Possible functions for all appendages and processes previously proposed were given and it was herein suggested that the post oral process serves to protect the mouth cone.
LIFE HISTORY OF THE CALIGID COPEPOD *LEPEOPHTHEIRUS HOSPITALIS* FRASER, 1920 (CRUSTACEA: CALIGOIDA)

by

David Richard Voth

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Typed by Erma McClanathan for David Richard Voth
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I would like to thank all those individuals who provided assistance during this study. Special thanks go to Francis Takahashi for help in the catching of the infected fish, and to Dr. Roger F. Cressey of the Smithsonian Institution in Washington, D.C., who verified the species identification of *Lepeophtheirus hospitalis*.

My major professor, Dr. Ivan Pratt of the Zoology Department at Oregon State University, furnished supplies, collecting equipment, laboratory facilities, and supervision.

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LIFE HISTORY OF THE CALIGID COPEPOD LEPEOPHTHEIRUS
HOSPITALIS FRASER, 1920 (CRUSTACEA: CALIGOIDA)

INTRODUCTION

Most of the parasitic crustaceans are found among the over 4,500 described species of copepods. They are known to exist in various symbiotic relationships with numerous groups, including sponges, coelenterates, polychaetes, pelecypods, arthropods, sipunculids, echiurids, brachiopods, echinoderms, chaetognaths, hemichordates, elasmobranchs, fishes, and mammals. Many also serve as intermediate hosts for various helminths. Four orders of copepods, containing over 1,000 species, are exclusively parasitic. Fishes are the most common hosts for members of the orders Caligoida and Lernaeopodoida. These ectoparasitic "fish lice" are usually found attached to gills, fins, oral membranes, or integument.

Records of parasitic copepods by Aristotle (Wilson, 1917) describe the sufferings of the tunny and swordfish in the Mediterranean Sea due to the irritation caused by these pests. These accounts are repeated in 1554 by Salviani in Aquatilium Animalium Historiae and Rondelet in Libri de piscibus marinis (in Wilson, 1917). The genus Pennella is most probably the subject of these reports. Pennella development was first studied in 1860 and finally completed in 1905 in a series of six publications spanning 45 years,
according to Wilson (1917). In 1746 the first species of parasitic copepod was described by Linnaeus from an European carp, *Cyprinus carassius*, as "*Lerneatentaculis guatuo*." He changed this name to *Lernea cyprinacea* in his tenth edition of *Systema Naturae* (1758).

As far as could be determined, the earliest parasitic copepod life cycle to be entirely worked out is that of *Lernaeocera branchialis* (Linnaeus, 1767) Blainville, 1822. Metzger (1868) studied the adult female and noted similarities to male and female copepodites which he found on the flounder, *Pleuronectes (=Platessa) flesus*, and lumpsucker, *Cyclopterus lumpus*. He proposed these copepodites to be larval stages of adult *L. branchialis*. Utilizing Metzger's work, Claus completed the life cycle in 1868. Claus hatched nauplii from eggs, observed the molt to copepodite, and noted copepodite attachment to flounder gills by prehensile second antennae. Four molts were recorded while attached by a filament to the flounder. Sexually mature forms were seen prior to the fifth molt, after which the adults became free living. Following copulation the male died and the female attached to the final gadid fish host and underwent an extreme change of morphology. This classic life cycle work was also the first report of a parasitic copepod using an intermediate host; this fact was later found to be restricted to a few genera of the family *Lernaeidae*. 
Since 1868 numerous papers have appeared in the literature on parasitic copepod life cycles. Most of these, however, have been incomplete, vague, or very difficult to follow. In 1947 Heegaard published the complete detailed life cycles of Acanthochondria cornuta O. F. Müller, 1777) Oakley, 1927, and Caligus curtus O. F. Müller, 1785. Other life cycles recently completed include those of Lernaea cyprinacea Linnaeus, 1758, by Grabda (1963); Lepeophtheirus dissimulatus Wilson, 1905, by Lewis (1963); Nectobrachia indivisa Fraser, 1920, by Wilkes (1966); and Caligus spinosus Yamaguti, 1939, by Izawa (1969).

The following history of developmental studies will be limited to the Caligidae, the family which includes Lepeophtheirus hospitalis Fraser, 1920.

The first contribution toward an account of larval development in caligid copepods is Burmeister's (1833) description of an attached larva as the new genus Chalimus. Kröyer (1837) then suggested that Chalimus is a larval stage of Caligus or some related genus. In 1842 Goodsir gave an account of egg development and metamorphosis in Caligus, and remarked on the close resemblance of the nauplius to Lernaea. Müller (1852) found that Chalimus is simply a larval stage. On Leuciscus rutilus in the Baltic Sea he found numerous caligids, some of which were mature while others were still attached by a frontal
thread. The molting of this chalimus stage to the adult was observed. That Chalimus was only a larval caligid was further accepted by Hesse (1858), and confirmed by Nordmann (1864). Hesse (1877) further stressed the larval character of Chalimus and suggested that most copepods pass through such a stage. In spite of this, contributions as late as 1890 continued to record new species of Chalimus. Burmeister's generic name (Chalimus) has since been used as a convenient term to designate the attached larval stages of caligids in general.

Finally in 1901, Scott wrote the first real description of caligid larval development. Although extremely sparse, he published accurate drawings, and found one chalimus stage of Lepeophtheirus pectoralis and two for Caligus rapax. However, he figured three segments in the endopod of the nauplius mandible and second antenna, each of which possesses only two. The drawing of the first antenna also showed too many segments. Heegaard (1947) decided Scott probably drew a late nauplius inside of which lay the next copepodite stage thereby showing a double articulation. The fact that Scott examined limb articulation in detail is significant. His drawing of the adult mandible was the first to show that it is four-segmented, a characteristic common to all of the Caligidae.

Wilson's papers on North American Caligidae (1905,
1907, 1908) constitute the next advance. His works contain many new and correct observations, but also a number of misconceptions (Heegaard, 1947).

The fullest account of caligid development yet published came in 1905 with Wilson's work on *Caligus rapax* and *C. bonito*. However, statements like "after one or two moults" and "several moults of the chalimus period" leave one rather uncertain of the actual number of stages. The form corresponding to his "metanauplius" of 1905 is indeed called a copepodid (=copepodite) in his later publications (1911, 1915). Some erroneous copepodite comparisons are also set forth (Heegaard, 1947). Wilson (1905) did correct Scott's (1901) mistake on the number of segments in the nauplius appendages, and then incorrectly claimed the copepodite first antennae to be three-segmented. He (Wilson, 1905) observed the chalimus secreting its attaching filament to the host, but did not record details of the actual fastening.

Wilson (1907, 1908) then examined larval development in the subfamilies Trebinae, Euryphorinae, and Pandarinae. His findings agreed in general with what was known in the Caliginae, aside from minor but essential details. Of the Euryphorinae, in *Alebion glaber*, the copepodite attaches to the host by the antennae and molts to a stage comparable to that of *Caligus*, attachment throughout being by means of antennae; no frontal filament exists. In the Pandarinae,
the chalimus attaches by a pair of very short ribbon-like filaments. Heegaard (1947) again pointed out what he felt were Wilson's mistakes. However, Wilson's investigations laid the foundation for our understanding of larval development of parasitic copepods.

T. and A. Scott's work (1913) on the British Parasitic Copepods briefly summarized larval development, but did not add anything new.

In 1925 Russell described *Caligus pageti* and its development. The nauplius was characterized very briefly and the copepodite was called the first metanauplius. A short account of the "subsequent metanauplius stage" followed. Heegaard (1947) claimed the descriptions possessed mixed characteristics from various stages, and what Russell called a metanauplius feeding position was actually the filament attaching position of the copepodite. Russell (1925) depicted the remaining chalimus stages as occurring in three sizes, for which distinct appendage details are lacking.

The larval development of *Lepeophtheirus thompsoni* was described by Gurney (1934). He recorded two naupliar stages, one copepodite which attached to the host, and "three or possibly four" chalimus stages.

Without a doubt, the most complete work on caligid larval development was that on *Caligus curtus* by Heegaard in 1947. This parasitic copepod was the first to have
undergone all of its development in the laboratory. From egg to adult, all stages and their behavior were described in detail. The copepodite apparently molts to a second copepodite stage after contacting the fish host. This is followed almost immediately by a second molt to what Heegaard calls a pupal stage. The pupa is still and does not feed. After "probably four or five days" the first chalimus stage emerges. After four molts, the fifth chalimus molts to the adult.

Heegaard (1947) claimed to be the first to recognize and observe the actual fastening of the copepodite to the host. After finding a suitable spot, the first maxillipeds begin tearing and scraping away the skin of the fish. Russell (1925) thought this to be feeding activity and further described the bits of "skin flying out at the rear, much as the earth comes out between the back legs of a dog when it is digging." Eventually a burrow is made into which the head is placed. The cement gland on the "forehead" then secretes viscous drops of a slowly congealing substance which is seized by the first maxillipeds, drawn into a filament and secured to the scale or fin ray at the base of the burrow. The hardened secretion forms a solid connection. Elongation into a thread occurs with further secretion and slow withdrawal of the copepod from the filament base. The complete process is repeated after all molts except the last.
The number of stages in caligid life cycles seems to vary with the species and author involved. With the exception of Russell (1925), authors describing life cycles of caligid copepods agree only that members of *Caligus* and *Lepeophtheirus* pass through two naupliar stages before reaching the copepodite stage.

The purpose of this thesis is to present the life history of *Lepeophtheirus hospitalis* Fraser, 1920, a caligid copepod parasitizing the starry flounder, *Platichthys stellatus* (Pallas, 1811) Girard, 1854.
METHODS AND MATERIALS

Collections of *Platichthys stellatus* were made from July, 1970, to August, 1971, in Yaquina Bay at Newport, Oregon. A 12-foot aluminum boat, powered by an outboard motor, was used to pull a small otter trawl net slowly along the bottom. Flounders parasitized with *Lepeophtheirus hospitalis* were transported to Corvallis, Oregon, in styrofoam coolers and maintained in a sea water table provided with flowing filtered sea water from a 7,000 gallon sea water system. It was also possible to transport only the parasites and then replace them on flounders already present in the sea water table. Fresh frozen squid chopped into small pieces served as food for the fish. The sea water tables were in a room maintained at 15°C. Sea water temperature never varied by more than one degree from 15°C.

Copepods were removed from the host and placed in glass finger bowls. The sea water was changed at least once each 24 hours. Observations were made with both a dissecting and a compound microscope.

The duration of each of the life cycle stages was considered to be the time from one molt to the next. The time of molting was recorded. As nauplii hatched, they were put in individual glass finger bowls. Copepodites refused to attach to anything except the living host.
Attached chalimus stages were removed from flounder hosts and placed in glass finger bowls. They were fed two or three times daily by being placed on the ventral surface of a flounder for about five minutes. Larval stages were handled by grasping the attaching filament with a fine forceps. Observations on the first stage nauplius, the second stage nauplius, and the copepodite were made entirely from specimens reared in vitro. Study of the remaining life cycle stages was supplemented by observations on specimens removed from naturally infected fish.

Specimens were fixed, dissected, and mounted in a water soluble stain-mountant called CMC-S, available from General Biological Supply House, Inc.

Drawings were made with the aid of a microprojector; the finer details were added freehand following microscopic examination. Appendages were usually removed from the copepod body, mounted in CMC-S under coverslips, and drawn. The smaller appendages were drawn in situ from whole mounted specimens. All measurements were made using a measuring eyepiece. First stage nauplii, second stage nauplii, copepodites, and adults were measured alive in a film of sea water without coverslips. Measurements of the other larval stages were taken from specimens freshly mounted under coverslips in CMC-S. All length and width measurements do not include setae, attaching filaments, or marginal flanges.
Numbers followed by their range in parenthesis are an average of ten counts. The time intervals mentioned in the sections on egg string formation, embryology and hatching took place at 20°C. Periods of time given for development, molting, and between molts are for observations made under various laboratory conditions.

With the exception of the mandible of the copepodite and its following stages, each figured appendage is orientated as it would appear if the anterior end of the copepod were at the top of the page. The posterior end for each of the above indicated mandibles is the denticulated end.
DESCRIPTION AND BEHAVIOR OF LIFE HISTORY STAGES

Seasonal Abundance

Specimens of *Lepeophtheirus hospitalis* parasitizing the starry flounder of Yaquina Bay first appeared in March and April. By mid-May ovigerous females and mating pairs were common. Life cycle stages occurred throughout the summer. Abundance of adults diminished during October-November and declined to almost nothing in February-March.

Mating

Mating pairs were first observed in mid-May. At this time the female is only very slightly larger than the male. The dorsal surface of both members of a copulating pair is directed outward from the surface of the host. The male second antennae are clasped onto the genital segment of the female just in front of its anterior expansion. In ventral view, the ends of the male maxillae and maxillipeds can be seen over the lateral margins of the female genital segment, thus aiding the copulatory grasp. Although not observed, spermatophore transfer is assumed to take place by a curling under of the male genital segment placing it in close apposition to the posterior margin of the ventral surface of the female genital segment. This technique was observed with one male which attempted to fertilize a previously mated female. Coupling may last for several
days before spermatophore transfer takes place.

Egg String Formation

Ovulation and egg case formation occurred simultaneously. This 30-minute process took place only at night. Eggs are ovulated into the egg cases as the latter are exuded and elongate from the mid-posterior margins of the genital segment. Initially elliptical in shape, the eggs become flat discs as they fill the egg case (Figure 1). Each egg within the egg case is also enclosed in an individual egg membrane and is separated from its neighbor by a partition. This partition, not visible under the compound microscope, becomes evident only after hatching (Figure 2). Proximal eggs remain rounded if ovulation stops before egg case formation is finished. The number of eggs per case averaged 58 (26 to 96). The two egg cases from a given female usually contained an approximately equal number of eggs. One isolated female produced three pairs of egg strings before dying. The original spermatophores were evident at death. Egg strings were always produced in pairs; a single egg string was not formed as long as the remaining one was attached to the female. After hatching, egg cases became flaccid (Figure 2) and easily dislodged with normal swimming activity. New egg strings were produced 16 hours (10 to 25) later. Egg strings removed from the female shortly after formation
produced normal nauplii.

Embryology

Ovulated eggs are of a uniform white or yellowish color. In one to two days a fringe of clear globules developed on the edge of all eggs (Figures 3, 4) in each string. Fifty-one hours (48 to 54) after ovulation two rusty dark-red pigment spots appeared in each egg (Figure 5); at this time twitching contractions were frequent. These pigment spots were usually arranged dorso-medially along each egg string. Within a few hours each pigment spot expanded to a club-shaped figure, the blunt end of which was almost always directed toward the anterior end of the egg case (Figure 6). At this point contractions of the embryo were seen every ten seconds. The double pigment spots appeared 13 hours (6 to 23) before hatching. Sixty-four hours (56 to 69) elapsed between ovulation and hatching. Developmental details were difficult to study due to the compressed disc arrangement of the eggs within the egg string. All egg strings observed contained at least one egg that failed to develop.

Hatching

Hatching proceeds in a regular sequence in each egg string, starting with the most terminal egg and progressing to the most proximal. This hatching sequence
varied from three to nine minutes (1 to 48) between eggs. At hatching, the individual egg membrane begins to swell, causing a split or crack which usually occurs on the medial edge of the egg string case. Further expansion to a sphere bends the egg string case laterally from the longitudinal body axis. The nauplius at this point occupies about one third of the space within the swollen egg membrane (Figure 7), its appendages closely appressed to its body. Seconds later the appendages have expanded to the limits of the confining membrane. With its anterior end also against the egg membrane, a single twitch of the appendages rup-
tures the individual egg case and the nauplius darts away. The terminal portion of the empty egg string case then folds back. Individual hatching of the nauplius is always anterior end first and usually in a medial direction. In-
frequently the intact egg membrane with enclosed nauplius will fall from the egg string case before hatching. Forward swimming movements of the adult female will also hatch nauplii out of individual egg membranes. When hatching proceeds to an undeveloped egg, the proximal egg behind it swells and hatching continues normally. One egg string was observed in which the eggs were loosely packed and spherical. Nauplii hatched inside the egg string case, couldn't escape, and died inside after molting to second stage nauplii. Hatching in normal cases was 80 percent successful (50 to 99). Failure to escape egg cases was
the chief cause of naupliar mortality.

First Stage Nauplius

The first stage nauplius body (Figure 8) is 443μ (420 to 460) long by 214μ (204 to 223) wide and not quite circular in any cross-sectional plane due to a slight dorso-ventral flattening. The widest point is at the mid-body region. Yolk fills the posterior third to two thirds of the unsegmented body. No evidence of digestive tract, mouth, anus, or a definite eye is visible. Muscle strands appear very faint in the anterior portion. Pigment is diffusely concentrated anteriorly. Some individuals also possess pigment splotches posterior-laterally on the edge of the yolk mass. The rod-shaped balancers at the posterior end of the body point backward, have a slight lateral curve, and taper to their largest diameter distally.

The duration of the first naupliar stage, determined in part by the difficulty encountered in hatching, was seven and a half hours (6 to 9) at 20°C and about 24 hours at 15°C. This stage swims with a typical jerky motion for five or six hours and then becomes sluggish. When not swimming, it sinks posterior end first until the balancers contact the bottom. Alternation of swimming and sinking continues until immediately before the first molt at which time it sinks to the bottom and does not rebound when contact is made. Swimming twitches of the appendages become
progressively weaker. The actual breaking and shedding of the cuticle takes place in less than a second. Either a break occurs at the dorso-anterior end of the first naupliar exoskeleton, or a portion of the ventral exoskeleton between the appendage bases is pushed away and the second naupliar stage escapes. Mortality on the first molt is very low, less than five percent. The first naupliar stage was found to be positively phototropic.

The first antennae (Figure 9) are uniramous, indistinctly two-segmented, and terminate in two long slightly plumose setae between which arises a minute third seta. On each side at the base of these swimming setae is a very tiny marginal seta which in some individuals is lacking. The larger proximal segment is spineless. The first antenna is attached to the anterior ventro-lateral body surface.

The biramous second antenna (Figure 10) attaches posterior and immediately adjacent to the base of the first antenna. The spineless protopodite of the second antenna bears on its dorso-lateral surface a five-segmented exopodite and from the ventral lateral surface a two-segmented endopodite. From the protopodite, each segment decreases in size distally. The first exopodite and endopodite segments are spineless. The remaining four exopodite segments each has a seta on the posterio-lateral edge, the distal two being lightly plumose. The second endopodite segment is as wide as, but shorter than the first. At the
posterior base of the second of the two endopodite setae is a tiny spikelike process.

The biramous mandible (Figure 11) is attached posterior and next to the base of the second antenna. Each of the four exopodite segments bears a lightly plumose seta on the posterio-lateral edge. The first exopodite segment is indistinctly attached to the dorso-lateral surface of the protopodite. The two-segmented endopodite indistinctly attaches to the ventral lateral surface of the protopodite. Both exopodite and endopodite segments become smaller distally. Two faintly plumose setae arise from the terminal portion of the second endopodite segment; the first segment is without setae.

Second Stage Nauplius

The second stage nauplius body (Figure 12) is 494µ (466 to 512) long by 212µ (204 to 223) wide. Other than the increased length, its morphology differs very little from that of the preceding stage (Figure 8). The anterior end is more rounded than that of the first nauplius, which is slightly flattened. Body elongation occurs a second or two after escape from the first naupliar exoskeleton. Muscle strands in the anterior portion are more evident due to a decrease in the amount of yolk. The balancers are slightly larger. Older second stage nauplii show distinct segmentation and digestive tract outlines through
the exoskeleton.

The duration of the second naupliar stage was 11 hours (10½ to 12) at 20°C and about 40 hours at 15°C. It exhibits a jerky swimming motion and is positively phototropic. Behavior is similar to that of the first naupliar stage; only the more elongate body shape easily distinguishes it. As the time for molting approaches, activity is progressively reduced until the second nauplius is immobile, ventral surface up, and on the bottom of the container. At this time, leg movements and digestive tract peristaltic waves of the copepodite can be seen through the second nauplius cuticle. The naupliar first and second antennae are rigidly extended in an anterior direction. A space between the second nauplius exoskeleton and copepodite can be seen at the anterior and posterior ends of the cuticle as the copepodite struggles inside. A bulge then becomes evident at the anterior end of the old exoskeleton. Then the nauplius appendages begin to rotate until they extend posteriorly at the sides of the exoskeleton. It appears that the rotation of appendages provides enough leverage to break off the anterior portion of the naupliar exoskeleton. The edge of the old exoskeleton then forms a constricting ring which slides off the copepodite. When part way out, the copepodite "sits up" and pulls its appendages out of the naupliar appendicular exoskeleton. It continues worming its way out until free of the
naupliar cuticle. Throughout this four-minute process, the copepodite appendages are continually moving. Failure to completely escape the second naupliar exoskeleton caused a five to ten percent mortality.

The first antennae (Figure 13) differ only slightly from those of the first nauplius (Figure 9). The two segments are now nearly equal in size. The anterior ventral surface of the distal segment bears two minute spines at the base of the two long terminal setae. The minute third terminal seta present in the first nauplius between the two longer setae was not seen in this stage.

The second antennae (Figure 14) are quite similar to those found in the first nauplius (Figure 10). The spine-like process at the posterior base of the second of the two endopodite setae is more pronounced.

The mandible (Figure 15) is almost identical to the first nauplius mandible (Figure 11).

Copepodite

The molt from second nauplius to copepodite (Figure 16) involves the greatest change that occurs in any one molt. The previously unsegmented body becomes divided into a cephalothorax containing the head, a maxillipede-bearing segment, and the first pedigerous segment. Following the cephalothorax are four free segments. The first bears the second thoracic legs; the second has a pair of
spines; the third is naked; the fourth also lacks legs, but terminates in a pair of caudal rami. In addition to the appendages of the naupliar stages, the post oral processes, maxillae, maxillipeds, the first two pairs of thoracic legs, and the caudal rami are now present. The balancers of the naupliar stages are lacking.

The copepodite body is 703μ (677 to 729) long by 267μ (256 to 283) wide. The cephalothorax accounts for 451μ (440 to 473) of this length, the remaining segments totalling 252μ (223 to 269). In dorsal view, the ovoid body tapers to its smallest diameter posteriorly. In lateral view, the body is of a more flattened ovoid shape. The anterior surface of the cephalothorax is more convex than the lateral cephalothoracic margins. The rostrum is situated on the anterio-medial margin of the cephalothorax. The frontal organ, or cement gland, is located in the region of the rostrum, but was not discernible. At the posterio-lateral margins of the cephalothorax are slight indentations from which longitudinal grooves extend anteriorly about one fourth the length of the cephalothorax. The transverse cephalothoracic groove, directly above the bases of the maxillipeds, extends across most of the cephalothorax. The small amount of yolk in the anterior digestive tract disappears as the copepodite ages. Irregular in outline, the digestive tract extends from just behind the eye to the terminal anus. Purple colored
pigment is associated with the lateral edges of the digestive tract and the median region of the cephalothorax anterior to the eye. The relatively large eye consists of two tiny clear lenses located laterally on each edge of a dorsal reddish pigment spot in the anterior third of the cephalothorax.

The first free segment (Figure 16), bearing the second thoracic legs, is oval in shape, and its width is nearly twice its length. All margins are convex. The second free segment is the third pedigerous segment and at this stage bears a posteriorly-directed naked spine from each posterio-lateral corner. Almost twice as wide as long, its anterior margin is slightly concave, the lateral margins convex, and the posterior margin forms a straight line with the anterior margin of the third free segment. The posterior margin of the naked third free segment also forms a straight line with the anterior margin of the fourth. The lateral margins of the third free segment are convex; the width is three times the length. The fourth pedigerous segment at this stage shows no evidence of the fourth thoracic legs. The free fourth segment is slightly wider than long and the lateral margins are barely convex. The posterio-medial edge is bilobed on either side of a slight indentation bearing the anus. The caudal rami attach to the concave posterio-lateral margins of this segment and each ramus bears three posteriorly-directed
plumose setae. The general shape of the rami is that of a compressed oval. The convex margins are somewhat irregular in the living animal.

After freeing itself from the second naupliar exoskeleton, the copepodite exhibits uncoordinated movements for a few minutes before swimming away. Swimming is not as jerky as that of the naupliar stages. Darting and circular motions are common. Copepodites seem to be indifferent to light. If the flounder host is not contacted within an average of four and a half days (3 to 8) at 20°C, death results. Periods of rest become more frequent as the copepodite ages. When at rest, older individuals lie on the bottom ventral surface up, supported on a tripod formed of the extended first antennae and the tip of the abdomen; younger individuals rest dorsal surface up. Copepodites become very active when flounder slime is placed in the culture dish. They scuttle over the surface of the slime and the peristaltic waves of the digestive tract increase in frequency. Flounder slime also stimulates a spiral or corkscrew swimming motion. When placed on the ventral surface of the flounder, copepodites first move about slightly and then remain in one place. Undulating body movements enable them to work their way through the slime toward the skin. At this time flounder slime can be observed within the digestive tract. Peristaltic waves are now continuous. After five minutes, the
copepodites are within the slime layer and attach to the flounder skin by holding on with the second antennae. In laboratory experiments, over 90 percent of the copepodites placed on the ventral surface of flounders were not present 24 hours later. None of those placed on the dorsal surface remained there. The few individuals which successfully remained attached were almost always near the margins of the fish body. Larval stages observed on naturally infected field specimens were also predominantly near the body margins. The time between host contact and the formation of the attaching filament depends in part on the age of the copepodite. Those few copepodites which did form attaching filaments in the lab (15°C) did so between the fourth and sixth day after host contact. Formation of the attaching filament starts with a series of very rapid jabs to the surface of the host by the anterior margin of the copepodite cephalothorax. Then, with the anterior margin of the cephalothorax held tightly against the host surface, a droplet of a clear, viscous substance appears between the cephalothorax and the host. As this droplet enlarges, the copepodite slowly backs away. When the droplet reaches a certain size, the copepodite backs away in such a fashion as to pull it into a filament. The maxillae stroke the filament as it is drawn out, probably shaping it. Almost immediately the filament hardens. About five minutes elapsed from the first evidence of the droplet to
completion of filament formation, which was observed only once. At 15°C the molt to the first chalimus stage took place 36 to 48 hours after filament formation. This molt, observed only once, begins with a loosening of the old exoskeleton around the base of the filament. The cuticle then splits longitudinally in several places from the base of the filament and the first chalimus stage passes the copepodite exoskeleton off posteriorly by a series of violent movements. The mortality from copepodite to first chalimus in the laboratory (at 15°C) was over 95 percent. Since naturally infected flounders rarely had up to four attached chalimus stages per fish, field mortality is probably also quite high. With the exception of the attaching filament, the free-swimming copepodite was identical to the attached copepodite.

The first antennae (Figure 17) are attached to the antero-ventral surface of the cephalothorax just lateral to the longitudinal body axis. The anterior margin of the larger first segment is irregularly convex and bears three naked setae, of which two are medial and one distal. The more strongly convexed posterior margin is bare. These margins fold the antennae posteriorly along the curvature of the cephalothorax (Figure 16). The second segment is oval, but flat on the proximal margin where it attaches to the first segment. Most of the eleven naked setae of the second segment arise from the distal lateral edge; the
others are attached on the dorsal distal surface. The length of the second segment is twice the width.

The second antennae (Figure 18) are uniramous, composed of three indistinctly divided segments, and attach posterior and slightly medial to the base of the first antennae. The thickened cuticle of the first segment bears two posteriorly-directed knobs, the distal being more pronounced. Irregular in outline and wider than long, this segment forms a broad base for the second segment, which is drumstick-shaped. The second segment is approximately two and a half times longer than wide, tapers to its smallest diameter distally, and bears the third, prehensile segment. Most of the third segment consists of a relatively huge terminal recurving claw. A small spine is present at the base of the claw. The third segment is about one sixth the length of the second. No setae were observed on the second antennae.

The mouth cone arises from the ventral medial surface slightly anterior to the region directly opposite the eye. It consists of a movable cone of very thin cuticle within which the mandibles are located. The mouth cone is usually directed posteriorly and held against the ventral surface of the body. The mandible (Figure 19) is uniramous and composed of four almost fused segments. The articulations between segments appear as transparent lines. The first segment is rectangular and three times as long as wide.
Almost square, the second segment narrows distally. The rectangular third segment is ten times as long as wide and equals in length the first two combined. The last segment is rounded distally, serrated medially, and three times as long as wide. The lateral margin of each mandible is slightly concave.

The post oral process (Figure 20) is located just posterio-laterally from the base of the mouth cone. From the medial edge of the oval globular base a posteriorly-directed blunt process arises. The shaft length is two times its greatest width. The width of the oval base is slightly more than the length of the process. From the ventral surface of this base, three posteriorly-directed naked spines arise; one is medial to the blunt process, the other two are lateral. The two post oral processes flank the mouth cone when it is adpressed to the ventral surface.

The uniramous maxillae (Figure 21) are the first pair of recognizable appendages posterior to the mouth. They attach ventrally, posterio-lateral to the post oral processes. The length of the almost rectangular first segment is twice its width. The articulation with the second segment is irregular. The second segment is about twice the length of the first, five times as long as wide, has wavy lateral margins, and terminates in two processes of about equal length. The distal half of the lateral edge on the
pointed lateral process is serrated while the rest of its margin is smooth. The medial process is rounded terminally and all edges are smooth.

The uniramous maxillipeds (Figure 22) attach to the ventral surface of the cephalothorax just posterior and medial to the bases of the maxillae. The first segment is almost three times as long as wide and roughly rectangular. The articulation with the smaller second segment is irregular and indistinct. The second segment is almost five times as long as wide, the outer margin slightly convex, the inner margin flat, and distally it bears a pointed process which curves medially. At the base of this process on the inner margin is a five-pronged spur.

The first pair of thoracic appendages is biramous and ventrally located at the posterior margin of the cephalothorax. Separated by a sternal plate, each consists of one protopodite, one exopodite, and one endopodite (Figure 23). The protopodite is rounded, being slightly longer than wide. A small naked seta arises from the lateral margin just anterior to the exopodite. The exopodite and endopodite are approximately equal in size, each being about one third that of the protopodite. Both are slightly longer than wide, ovoid, and narrowed at their articulation with the protopodite. The mid-lateral exopodite margin bears a short naked spike-like seta; the posterio-lateral corner has a similar seta but with a
membrane on the medial and lateral edges. The third seta, next and posterior to the second, is identical except that it is almost three times as long. The fourth through seventh setae are evenly spaced along the posterior exopodite margin and are over three times the length of the third. The fourth has a membrane along the lateral surface and is lightly plumose on the medial surface. The fifth is plumose medially, but laterally only at the terminus. The sixth and seventh are plumose on both margins. The medial edge of the exopodite is bare, as is the adjacent edge of the endopodite. On the posterior margin of the endopodite are five evenly spaced plumose setae, the most lateral being two thirds the length of the other four, which are equal in length to the longest exopodite setae. The fifth plumose seta arises from the anterio-medial margin near the endopodite-protopodite articulation. It is equal in length to the other long endopodite setae. The posterio-lateral corner of the endopodite is slightly plumose.

The biramous second thoracic legs (Figure 24) are posterior to the first thoracic legs and are located on the ventral surface of the first free segment following the cephalothorax (Figure 16). The single protopodite is slightly larger than that of the first thoracic legs and is more rounded. Its single seta arises on the lateral margin just anterior to the exopodite and is plumose on
the posterior margin. Exopodite and endopodite are oval, about one fourth the size of the protopodite, and constricted slightly at their protopodite articulation. The mid-lateral margin of the exopodite bears a short stout naked seta. Seven more setae, almost evenly spaced, arise from the posterior third of the convex margin. Moving medially, the first seta is stout and naked like that on the mid-lateral margin; the second is twice the length of the first and bears a membrane on the lateral surface; the third is twice the length of the second and also bears a membrane on the lateral surface; the fourth is over twice the length of the third, stout proximally, bears a membrane on the lateral margin and is plumose on the medial margin; and the fifth, sixth, and seventh plumose setae are equal in length to the fourth. The endopodite has seven plumose setae along its medial and posterio-medial margin. All are of a length comparable to the long exopodite setae. The lateral half of the endopodite margin is bare.

The second free segment following the cephalothorax bears laterally a pair of posteriorly-directed naked spines (Figure 16) which may represent the anlage of the future third pair of thoracic legs.

First Chalimus Stage

The first chalimus bears a frontal attaching filament and the third and fourth thoracic legs in addition to those
appendages and processes of the previous copepodite stage. The cephalothorax contains the first pedigerous segment and is followed by four free segments, a situation identical to that of the copepodite. The rostrum of the copepodite is lacking.

The dorso-ventrally flattened body of the first chali-mus (Figure 25) is \(966\mu (893\text{ to }1,051)\) long by \(595\mu (552\text{ to }637)\) wide. Cephalothoracic length is \(642\mu (578\text{ to }683)\); the four following segments total \(330\mu (250\text{ to }368)\) long. The cephalothorax in dorsal view resembles an equilateral triangle with the two posterior corners broadly rounded medially, then curving sharply anteriorly for a short distance and connected in such a way as to form the concave posterio-medial cephalothoracic margin. Scattered pigment cells can be seen on the dorsal surface; grooves are lacking or very indistinct. The frontal filament is \(329\mu (283\text{ to }348)\) long and expands distally to a bilobed disc-like attaching surface; proximally, its diameter also increases as it approaches the anterior margin of the cephalothorax. The very indistinct frontal organ (Figure 25) is located near the anterior apex of the cephalothorax at the base of the attaching filament. A tubule appears to lead from this organ into the base of the filament. The eye (Figure 25) is similar in structure to that of the copepodite, but relatively smaller and more posteriorly located. Filled with flounder slime, the distinct
digestive tract (Figure 25) extends from just behind the eye to the terminal anus. The edges of the digestive tract have to a lesser extent the purple pigment which was present in the copepodite.

The lateral margins of all four of the free segments following the cephalothorax (Figure 25) are convex, those of the first two being more acute posteriorly. Anterior margins of each segment are broadly convex; posterior margins of the first three are broadly concave. The oval caudal rami (Figure 25) attach to the concave posterolateral margins of the fourth free segment on either side of a bilobed indentation bearing the anus. The junctions between the four free segments are somewhat indistinct in the living copepod. The first free segment is almost four times as wide as long and ventrally bears the second pair of thoracic legs; the second free segment is almost three times as wide as long and on the ventral surface is the third pair of thoracic legs; the third free segment is over four times as wide as long and ventro-laterally bears the fourth pair of thoracic legs; the fourth free segment is one and one half times as wide as long and the anus is found posterio-medially, the caudal rami posterio-laterally. On the posterior margin of the caudal rami are six naked setae of which the medial two and lateral three are twice the length of the remaining seta.

In comparison with the previous copepodite stage, the
first chalimus is relatively inactive. Detached individuals are immobile and remain on the bottom of the container, ventral surface up. They are able to bend the portion of the cephalothorax anterior to the first antennae ventrally so that the shaft of the attaching filament is perpendicular to the longitudinal body axis. When attached to the flounder, a bend of this type would move the copepod body to the surface of the fish. Most probably, attached stages hang free and periodically bend to the surface of the fish to feed. The length of time spent in the first chalimus stage was approximately six and one half days, based on two specimens kept at 20°C. Prior to molting, the second chalimus stage is visible inside the first chalimus exoskeleton. This is most easily observed in the maxillipeds. Molting is similar to that of the copepodite. Several splits occur at the base of the filament and the second chalimus passes off the exoskeleton of the first chalimus posteriorly.

The first antennae (Figure 26) are attached ventrally near the lateral margins of the cephalothorax, about one fourth the length of the cephalothorax from the anterior end (Figure 25). The convex anterior margin of the first segment bears four naked setae. The proximal margin is nearly parallel to the longitudinal body axis and the posterior margin almost perpendicular to it. Continuous with the anterior margin of the first segment is the
The uniramous second antennae (Figure 27) attach posterior and medial to the first antennae, and are similar to the second antennae of the copepodite (Figure 18) except that they do not appear to be as well developed. The irregularly-shaped base segment lacks the thickened cuticle and the two posteriorly-directed knobs present on the second antenna of the copepodite. Distally, the irregular margin of the first segment joins the otherwise drumstick-shaped second segment which is twice as long as wide and bears the third prehensile segment. The third segment is identical to, but smaller than, the third segment of the second antenna of the copepodite. Again, this appendage is without setae.

The mandible of the first chalimus (Figure 28) is almost identical to that of the copepodite (Figure 19). It is now slightly larger, and the previously serrated medial margin of the fourth segment has become denticulated, bearing about 12 denticles. The mouth cone is unchanged except for several areas of slight sclerotization.

The post oral process (Figure 29) arises from an
irregular base which bears, in a medial direction, three naked setae. Otherwise it is similar in shape and location to the post oral process of the copepodite (Figure 20).

The uniramous maxillae of the first chalimus (Figure 30) are about twice as big as those of the copepodite (Figure 21). They attach posterio-laterally near the post oral processes. The length of the first segment is twice the width, the proximal margin rounded, the posterior margin flat, the anterior margin broadly convex, and the distal margin with two rounded projections on either side of a concave surface into which fits the ball-shaped proximal margin of the second segment. The anterior margin of the second segment is a straight line with a 20° outward bend at its midpoint. On the posterior margin, this bend occurs closer to the proximal margin. About seven times as long as wide, the second segment terminates in two processes like those of the copepodite maxilla, but without the serrated lateral margin on the lateral process.

The first segment of the uniramous maxilliped (Figure 31) is spindle-shaped with the greatest width about one third from the proximal end. From the widest region, the anterior and posterior margins taper proximally to a greater degree than they do distally. The distal end articulates with the two small projections of the second segment. The outer margin of the second segment is broadly convex, and the inner margin flat. Distally, this
segment bears a large medially curving claw with a stout seta-like process near its base on the inner margin. The second segment is almost five times as long as wide, and the terminal claw accounts for almost half this length. The first chalimus maxilliped is larger and more strongly developed than that of the copepodite (Figure 22).

The biramous first pair of thoracic legs (Figure 32) is attached ventrally at the posterior margin of the cephalothorax. The rounded protopodite bears a one-segmented endopodite and exopodite, and a naked, stout seta laterally at the junction with the exopodite. Proximal margins of the endopodite and exopodite are flat; distal margins are convex. The endopodite is one and one half times as long as wide, has flat medial and lateral margins, bears two naked setae of equal length from the distal margin, and is one third the size of the exopodite. The exopodite is almost three times as long as wide, has a flat medial margin, a wavy lateral margin bearing one naked seta near the midpoint, and distally bears seven naked, stout setae. Of these seven, the most lateral is equal in size to the seta of the mid-lateral margin; the second, third, fourth, sixth, and seventh are about two thirds the length of the fifth seta.

The biramous second pair of thoracic legs (Figure 33) is attached just posterior to the first pair on the ventral surface of the first free segment following the
cephalothorax. The protopodite is rounded with an irregular margin and bears two naked setae, one laterally at the exopodite articulation, and one medially opposite the first. Both proximal and distal margins of the endopodite and exopodite are convex, narrowed toward their protopodite articulation, and have rather straight medial and lateral margins. The exopodite is three times as long as wide, bears a naked seta on the lateral margin and seven naked setae on the distal margin. Of these eight exopodite setae, the middle two are slightly longer than the other six. The endopodite is twice as long as wide, bears a naked seta on the medial margin, and five naked setae on the distal margin. Moving medially, the second and third setae are slightly longer than the others.

The biramous third pair of thoracic legs (Figure 34) now appear as recognizable appendages on the ventro-lateral surface of the second free segment following the cephalothorax. The approximately kidney-shaped protopodite is twice as long as wide and bears one naked seta on its lateral margin. The rounded exopodite attaches next and posterior to the protopodite seta, and bears from the distal margin four naked setae of which one is twice the length of the remaining three. Immediately posterior to and slightly overlapping the exopodite is the rounded endopodite, half the size of the former, and with two minute knobs on the distal margin.
The fourth thoracic leg (Figure 35) first appears in the first chalimus stage on the ventro-lateral edges of the third free segment. It consists of one segment, flattened medially, broadly rounded laterally, and sharply rounded proximally and distally. The length is almost three times the width and a tiny naked seta arises from the distal margin.

Second Chalimus Stage

The cephalothorax of the second chalimus stage now includes the second pedigerous segment in addition to the first, otherwise it is quite similar to the first chalimus stage. The body of the second chalimus (Figure 36) is dorso-ventrally flattened and 1,083μm (986 to 1,216) long by 573μm (532 to 631) wide. Cephalothoracic length is 763μm (657 to 867); the three following segments total 321μm (250 to 375) long. The lateral margins of the cephalothorax are broadly convex and meet anteriorly at the base of the attaching filament which is 329μm (289 to 400) long. At the posterio-lateral corners, the cephalothoracic margin is sharply rounded, extends anteriorly a short distance, is then acutely rounded 180° and extends posteriorly, forming an inverted U-shaped indentation, the medial ends of which are connected by a curved line forming the concave posterio-medial margin of the cephalothorax. The status of the attaching filament, frontal
organ, eye, digestive tract, anus, and scattered pigment cells has changed little, if any, from that of the first chalimus stage. A very slight amount of purple pigment is present along the edges of the digestive tract of the second chalimus, and a short cephalothoracic groove extends anteriorly from the base of each of the U-shaped indentations.

The three free segments following the cephalothorax all have convex lateral margins, and the two junctions between them are straight lines. The first free segment has a convex anterior margin, is twice as wide as long, and ventrally bears the third pair of thoracic legs; the second free segment is three times as wide as long and ventrally bears the fourth pair of thoracic legs; the third free segment, anus, and caudal rami are identical to those of the first chalimus stage.

The activity, body movements, and molting of the second chalimus stage duplicate those of the first. Four specimens of the second chalimus stage lasted for about five days at 20°C.

The first antennae (Figure 37) have the same morphology and position as those of the first chalimus (Figure 26).

The base segments of the second antennae (Figure 38) attach posterior and medial to the first antennae. The base segment is elongate, three times as wide as long,
and distally has a concave margin into which fits the base of the second segment. Both the second and third segments are similar to those of the preceding stage (Figure 27), but the third segment appears to be slightly smaller.

The mandible (Figure 39) is identical to that of the preceding stage (Figure 28).

The three setae arising from the post oral process (Figure 40) are two to three times as long as those found on the post oral process of the first chalimus (Figure 29). Otherwise the post oral process remains unchanged.

The maxillae (Figure 41) have decreased slightly in size in the second chalimus. The anterio-medial edge of the first segment is now wavy and the lateral margins of the second segment are broadly convex. The articulation of the two segments and the two terminal processes are unchanged. The general shape of the maxillae remains unchanged from that of the previous stage (Figure 30).

The second chalimus maxilliped (Figure 42) has increased slightly in size, but its overall morphology is unchanged from Figure 31. Proximally, the first segment is more acutely pointed. On the inner margin of the terminal claw of the second segment is a smaller, stout seta-like process.

The second pedigerous segment is part of the cephalothorax in the second chalimus, and therefore the first pair of thoracic legs are ventrally located adjacent and
anterior to the second pair of thoracic legs which attach ventrally at the posterior margin of the cephalothorax. A small sternal plate separates members of each pair of thoracic legs. The protopodite of the first thoracic leg (Figure 43) is oblong, almost twice as wide as long, has broad wavy margins, and bears a naked seta on its posterio-medial edge in addition to the lateral naked seta at the protopodite-exopodite articulation. The armature and shape of the exopodite and endopodite of the second chalimus is unchanged except for an increase in length: the exopodite is three times as long as wide and the endopodite is over twice as long as wide. The first thoracic leg of the second chalimus is larger than that of the first chalimus (Figure 32).

The protopodite of the second thoracic leg (Figure 44) is smaller than that of the first chalimus (Figure 33) and lacks setae. Otherwise, the armature, shape, and size of the second thoracic leg is identical to that of the first chalimus (Figure 33).

The third pair of legs are ventro-laterally located on the first free segment following the cephalothorax. The protopodite (Figure 45) is similar to that of the first chalimus (Figure 34), but smaller and without seta. The rectangular exopodite attaches on the anterio-lateral margin of the protopodite, is twice as long as wide, and distally bears three naked setae of which the middle one
is twice the length of the other two. The endopodite is hemispherical and bears two short naked setae from the convex margin, one posterior and one lateral.

The two-segmented fourth thoracic leg (Figure 46) is located ventro-laterally on the second free segment following the cephalothorax. Each segment is roughly square-shaped with rounded corners. The distal margin of the second segment bears two small cuticular knobs.

Third Chalimus Stage

The first three pedigerous segments are now included in the cephalothorax of the third chalimus. Three new structures, the post antennal process, the fifth pair of legs, and the abdomen appear in this stage. The abdomen, however, is indistinctly separated from the genital segment. The oval body of the third chalimus (Figure 47) is dorso-ventrally flattened and 1,729μ (1,380 to 1,905) long by 1,054μ (926 to 1,170) wide. Cephalothorax accounts for 1,359μ (1,150 to 1,478) of this length; the segments total 370μ (230 to 486) in length. From a thickened portion of the anterior cephalothorax arises the attaching filament which is 433μ (394 to 486) long. The anterior margins of the cephalothorax are broadly curved from the base of the attaching filament and at the region of the first antennae curve sharply inward toward the eye for a distance equal to the base of the first antennae and then curve sharply
outward to form the broadly curved lateral cephalothoracic margins. This produces a slight indentation in the region of the first antennae. At the posterio-lateral corners, the margins curve medially, anteriorly, medially, and then connect in a broadly curved line which forms the posterio-medial convex cephalothoracic margin. From the lateral edges of the posterior indentations, cephalothoracic grooves extend toward the eye a short distance and then flare laterally and terminate just above the level of the eye. A horizontal groove at the narrowest point between the longitudinal grooves completes an overall groove pattern resembling a capital letter H. No purple pigment was observed along the edges of the digestive tract.

The free segments following the cephalothorax (Figure 47) all have convex lateral margins. The first segment has convex anterior and posterior margins, is three times as wide as long, and ventrally bears the fourth pair of legs. The second free segment, which is the genital segment, has a concave anterior margin, is indistinctly separated from the abdomen by a straight line, is almost three times as wide as long, and at the posterio-lateral corners bears the fifth pair of legs. Now a distinct segment, the abdomen is twice as wide as long, bears the oval caudal rami on posterio-lateral concave margins, and posterio-medially bears anal lamellae on either side of the anus. The six naked setae on the posterior margins of each of the caudal
rami are of approximately equal length. One, however, extends laterally at right angles to the other five.

The third chalimus is immobile, but is able to bend ventrally the portion of the cephalothorax anterior to the first antennae, so that the attaching filament is parallel with the longitudinal body axis. In this position, the filament can be held by the maxillipeds. Molting is similar to that of the preceding stages. At 20°C, seven specimens remained in the third chalimus stage about four and a half days.

The first segment of the first antennae (Figure 48) bears 11 naked setae from its anterio-distal margin. Aside from this, it is relatively unchanged from the preceding stage (Figure 37).

The second antennae (Figure 49) are more feeble and flaccid than those of the second chalimus (Figure 38). There is less sclerotization of the terminal segment and the divisions between segments do not appear as distinct. The base segment is diamond-shaped and twice as wide as long. Anterior and posterior margins of the second segment are broadly rounded, the proximal margin is concave, and the distal margin broadly convex. The triangular third segment tapers to an uncurved blunt point, and on the anterio-medial margin bears a limp seta-like projection.

The post antennal processes (Figure 50) are located
posterior and lateral to the bases of the second antennae. They arise from the ventral body surface, project posterior-laterally, bear a tiny posteriorly directed seta from the mid-posterior margin, and taper to a blunt point. The length is twice the width of the base, and the terminal half is heavily sclerotized.

The base segment of the mandible (Figure 51) appears to be more strongly developed than that of the second chalimus (Figure 39), and the fourth segment more curved.

The three setae of the post oral process (Figure 52) are half the length of those of the second chalimus (Figure 40). The form of this structure is otherwise unchanged, but it has almost doubled in size in the third chalimus.

The maxillae (Figure 53) are half again as large as those of the preceding stage (Figure 41). They now possess a fringe of hairs on the mid-proximal margin of the second segment, and the terminal, medial process is curved to a greater extent.

The maxillipede (Figure 54) is larger, but otherwise identical, to that of the second chalimus (Figure 42).

The first three pairs of thoracic legs are now incorporated into the cephalothorax, a situation found in the adult. The bases of the first thoracic legs in the third chalimus attach ventrally about one fourth the distance of the cephalothorax from its posterior margin. The ovoid
protopodite (Figure 55) has a wavy anterio-medial margin, rather flat posterio-lateral margins, and bears two plumose setae, one from the posterio-medial margin and one mid-laterally. Both exopodite segments are somewhat square and about two thirds the size of the protopodite. Laterally, the first exopodite segment bears one naked seta near its articulation with the second exopodite segment. From the distal surface of the second segment arise four robust naked setae all of which are about two thirds the length of three similar setae arising from the posterio-medial margin of this segment. The endopodite is reduced to a size only slightly larger than the smaller exopodite setae. It is tapered and bears one small naked seta terminally.

The two indistinctly divided protopodite segments of the second thoracic leg (Figure 56) together form a nearly perfect circle. The much smaller medial segment is crescent-shaped, bears a membrane-fringed stout seta posteriorly, and abuts medially a sternal plate. Mid-laterally, the larger protopodite segment bears a naked seta just anterior to the exopodite articulation. The first exopodite segment attaches to the protopodite mid-lateral margin, is half again as long as wide, has convex medial and lateral margins, rather flat distal and anterio-medial margins, and bears one seta posterio-laterally. The second exopodite segment is slightly smaller than the first and
bears nine setae from its irregularly rounded lateral and posterior margins; the medial margin is flat. The three lateral setae are one fourth to one fifth the length of the remaining six. Below and slightly overlapping the first exopodite segment is the triangular first endopodite segment attached to the protopodite. It is slightly smaller than the second exopodite segment and bears a lengthy seta from the posterior-medial edge. The second endopodite segment is a little longer than wide, flat medially, convex laterally, and bears seven setae of varying lengths from its convex distal margin. All exopodite and endopodite setae on this and the following appendage are stout and non-plumose.

In the third chalimus the exopodite and endopodite of the third thoracic legs (Figure 57) are both two-segmented. The protopodite is bullet-shaped, half again as long as wide, bears the exopodite and endopodite on the flat distal margin, and has a single naked seta laterally at the exopodite articulation. Elongate and small, the first exopodite segment bears a posteriorly directed seta on the posterio-lateral corner. From the posterior-medial margin, the rounded second exopodite segment bears seven setae of varying lengths. The oval first endopodite segment is about equal in size to the second exopodite segment and gives rise to a single seta on the medial edge. The rounded second endopodite segment is about equal in size to the
first exopodite segment and possesses four setae on the distal margin. The sternal plate at the posterior cephalo-thoracic margin bears a stout naked seta near the third thoracic leg.

The first segment of the fourth leg (Figure 58) is rounded and attaches ventro-laterally on the first free segment following the cephalothorax. The proximal margin of the second segment is concave, the distal margin flat, and the anterior and posterior margins convex. A single naked seta arises from the anterio-lateral margin near the articulation with the third segment. The first two segments are about equal in size and larger than the third. From the flat distal margin of the third segment arise four stout naked setae of unequal lengths. Opposite the flat medial margin is the roof-shaped lateral margin which bears a short stout naked seta at its peak.

The fifth pair of legs (Figure 59) extend posteriorly from the posterio-lateral corners of the genital segment and give rise to two posteriorly directed naked setae.

Fourth Chalimus Stage

The fourth chalimus has a new structure, the sternal furca, but is otherwise only a slightly larger replica of the preceding stage. The body length of the fourth chalimus (Figure 60) is 1,826μ (1,610 to 1,984). Of this length, cephalothorax accounts for 1,424μ (1,248 to 1,577)
and the free segments 408μ (348 to 486). The cephalothorax is 1,072μ (821 to 1,176) wide; the attaching filament 446μ (394 to 499) long.

The posterior margin of the fourth pedigerous segment, the first free segment (Figure 60), is concave due to the enlarged genital segment which follows it. All margins of the genital segment are convex and it is now only half again as wide as long. The abdominal segment is distinctly separated from the genital segment, but is otherwise the same as that of the third chalimus (Figure 47). There are six posteriorly directed naked setae on each posterior margin of the oval caudal rami of which the medial one and lateral two are half the length of the remaining three.

The activity and body movements of the fourth chalimus are identical to those of the third chalimus. Prior to molting the anterior margin of the fifth chalimus can be seen behind the anterior margin of the fourth chalimus exoskeleton and there is also a clear area at the base of the fourth chalimus attaching filament. The fifth chalimus emerges from the fourth chalimus exoskeleton in a manner similar to that of the preceding stages, but leaves behind the attaching filament. For eight specimens at 20°C, the fourth chalimus stage lasts approximately two and a half days.

The first antenna (Figure 61) bears 12 lightly plumose setae from the anterio-distal margin of the first segment,
but is otherwise unchanged from Figure 48.

The second antenna (Figure 62) is more rigid than that of the previous stage (Figure 49). The base segment has a convex proximal margin bearing a small posteriorly directed knob, a concave distal margin, and is twice as wide as long. The remaining two segments are unchanged.

The proximal attaching surface of the post antennal process (Figure 63) is better defined than that of its predecessor (Figure 50), but is otherwise similar.

The mandible (Figure 64) is like that of the third chalimus (Figure 51).

The base region of the post oral process (Figure 65) is not as well defined as that of Figure 52. The three medially directed setae are slightly longer.

The maxillae (Figure 66) lack the fringe of hairs present on the mid-proximal margin of the second segment in the third chalimus (Figure 53), but these appendages are otherwise alike.

The maxillipeds (Figure 67) is identical to that of Figure 54, but larger.

First present on the fourth chalimus, the sternal furca (Figure 68) is located ventrally along the longitudinal body axis midway between the maxillipeds and first thoracic legs. The oval base is twice as wide as long and has both horizontal and longitudinal grooves on it. From the posterior margin of the base arise two posteriorly
directed processes. Each process is tapered, bluntly pointed, and equal in length to the width of the oval base. The entire structure is rather flaccid.

The first thoracic leg (Figure 69) is larger than that of the third chalimus (Figure 55). The protopodite margins are more rounded laterally, medially, and anteriorly. The single endopodite segment is relatively smaller and bears two naked terminal setae. Otherwise, the armature and general shape of the protopodite, endopodite, and two exopodite segments remain the same.

The first protopodite segment of the second thoracic leg (Figure 70) is rectangular, four times as long as wide, and bears a stout naked seta from the posterior margin. The second protopodite segment is rounded anteriorly, laterally, and posteriorly, and is flat medially. The general shape of the two exopodite and two endopodite segments has not changed from that of Figure 56, but the first endopodite segment is more rectangular. One additional seta is now present on the fourth chalimus second thoracic leg: it arises from the mid-medial margin of the first exopodite segment. All setae are naked except for two on the mid-lateral margin of the second exopodite segment.

The armature of the third thoracic leg (Figure 71) is identical to that of the third chalimus (Figure 57). The protopodite is triangular with broadly rounded corners, a concave medial margin, and convex lateral and posterior
margins. The first endopodite and first exopodite segments are indistinctly fused to the protopodite and to each other. Also indistinct is the junction between the two exopodite segments.

The proximal margin of the first segment of the fourth leg (Figure 72) is flat. Aside from the flat margin and an increase in size, this appendage is like that of the previous stage (Figure 58).

The status of the fifth pair of legs (Figure 73) remains unchanged (Figure 59).

Fifth Chalimus Stage

The sexes are differentiated in the fifth chalimus stage: males possess the fifth and sixth pairs of legs, females only the fifth. Individuals of this stage are almost always unattached and free on the ventral surface of the flounder; rarely are they connected by a frontal filament. Most of the fifth chalimus setae are plumose, the frontal plates are distinct from the rest of the cephalothorax, and lateral cephalothoracic flanges are present.

In comparison to the fourth chalimus (Figure 60), the cephalothorax of the fifth chalimus (Figures 74, 75) is relatively wider: 1,515μ (1,330 to 1,631) in the male, and 1,810μ (1,730 to 1,900) for the female. The female is longer than the male: 2,893μ (2,260 to 3,302) long
compared to 2,441\(\mu\) (2,260 to 2,680). Of this length, cephalothorax amounts to 1,728\(\mu\) (1,540 to 1,900) in the male and 2,057\(\mu\) (1,919 to 2,300) in the female. The fourth pedigerous segment, genital segment, and abdomen are 718\(\mu\) (570 to 836) long in the male and 837\(\mu\) (646 to 1,007) in the female.

The U-shaped indentations at the posterior end of the cephalothorax (Figures 74, 75) are further expanded in the fifth chalimus. The elongate frontal plates are distinct from the anterior cephalothoracic margin and bear the first antennae on their concave lateral margins. Medially they meet at the edge of a tubule leading from the frontal organ. The convex distal margin of each frontal plate has a narrow transparent membrane-like flange. Below the flange is a narrow cross-striated band. The band and flange meet medially and form a circular structure. The anterio-medial cephalothoracic margin extends at right angles from the region of the frontal organ tubule for a short distance and then bends toward the base of the first antenna. Lateral transparent membrane-like flanges extend along the greater curves of the cephalothorax from the base of the first antennae to the lateral anterior curves of the U-shaped indentations. The eye is smaller, less developed, and more anteriorly situated than in the previous stages. Directly ventral to the eye is the mouth. The frontal plates, lateral flanges, eye, shape of the
cephalothorax, and the H-shaped cephalothoracic groove pattern do not change appreciably in the sixth chalimus (Figures 90, 91) and adult stages (Figures 106, 107).

The fourth pedigerous segment has flat anterior and posterior margins, and roof-shaped lateral margins. It is twice as wide as long in the male (Figure 74), half again as wide as long in the female (Figure 75), and bears the fourth pair of legs on the posterior-lateral edges. The genital segment of both sexes (Figures 74, 75) has flat anterior and posterior margins, and convex lateral margins. From the posterior-lateral corners, the male bears the fifth and sixth pairs of legs, the female only the fifth. Genital segment measurements can be found in Table I. The abdomen and caudal rami have not changed from the fourth chalimus (Figure 60), and do not change in the sixth chalimus (Figures 90, 91) and adult stages (Figures 106, 107). The setae of the caudal rami, however, are now plumose, and the medial one and one of the lateral setae extend in a more lateral direction than do the other four. This condition of the setae is unchanged in the stages which follow.

The fifth chalimus can scuttle rapidly over the surface of the host, but is usually still. The copepod can adhere tightly to the flounder using a suction cup action of the cephalothorax created with a downward pull by the anchored second antennae. Dislodged individuals dart
<table>
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about rapidly from place to place propelled by the second and third thoracic legs. The sixth chalimus escapes from the fifth chalimus exoskeleton through its anterior end. Nine individuals of the fifth chalimus remained in this stage for about two days at 20°C.

The first antenna (Figure 76) has a flat proximal surface, bears 15 plumose setae on the outer margins of the first segment, and a cuticular knob at the posteriolateral corner. The second segment has 11 naked setae on the distal margin and one near the mid-posterior margin.

The base segment of the second antenna (Figure 77) is ovoid, has a sclerotized posteriorly directed process arising from the mid-posterior margin, and articulates in an overlapping fashion with the larger second segment. Roughly circular, the second segment has a flat proximal surface; other margins are convex. The triangular prehensile third segment tapers distally and terminates in a well-developed, heavily sclerotized claw, the neck of which bends ventrally. A naked seta is present on the anterio-medial, ventral surface of this segment.

The ovoid base of the post antennal process (Figure 78) is more clearly distinguished from the lateral projecting process than it was previously (Figure 63). The distal half is more spine-like, narrower, and more heavily sclerotized.

The mandible (Figure 79) is like those of the
previous stages (Figures 64, 51).

The post oral process (Figure 80) now resembles a tooth with two roots which are about equal in length to the well-defined base portion. The lateral projection is curved laterally. The three medially directed, naked setae arise from an elevation separate, but near, the base articulation. This structure does not change in either the sixth chalimus (Figure 96) or in the adult (Figure 113).

The base of the maxilla (Figure 81) has a posteriorly directed articulating knob. The second segment is more slender, and the whole appendage larger, than that of the previous stage (Figure 66).

The maxilliped (Figure 82) is unchanged from Figure 67 except for a sclerotized region along the anterio-proximal margin of the base segment.

The sternal furca (Figure 83) is now a rigid structure with its base processes separated. The base lacks most of the grooves present on its predecessor (Figure 68) and the anterior base margin is irregularly wavy.

The endopodite of the first thoracic leg (Figure 84) is relatively smaller than in Figure 69. The oval first exopodite segment is narrowed near its base articulation and bears a fringe of hairs on the posterior margin. The armature of this appendage is identical to that of the fourth chalimus except the setae of the second exopodite segment are plumose, the four distal setae plumose
only medially.

The first protopodite segment of the second thoracic leg (Figure 85) is somewhat square. The rounded second protopodite segment has a membrane along the posterior margin. Both protopodite setae are plumose. The first exopodite and second endopodite segments are ovoid; the second exopodite and first endopodite segments are circular. A spine-like naked seta arises from the posterio-lateral corner of the first exopodite segment, and a plumose seta from near the mid-medial margin. The second exopodite segment laterally bears three short spine-like setae, posterio-laterally a stout seta that is plumose medially and has a membrane laterally, and five lengthy plumose setae from the curved posterio-medial margin. All endopodite setae are long and plumose. One arises from the medial surface of the first segment, and eight from the medial curvature of the second segment. The posterior margins of the first and second endopodite segments and the medial margin of the first exopodite segment are plumose.

The tabulate protopodite of the third thoracic leg (Figure 86) is cone-shaped with a broadly rounded anterior margin. On the mid-lateral margin is a plumose seta, above which is a membrane, and below which is the first exopodite segment. The posterio-medial margin of the protopodite abuts a sternal plate which bears a membrane, a plumose seta, and connects to the opposite protopodite. A stout
spine projects posteriorly from the oval base portion of the first exopodite segment. The rounded second segment has a hairy lateral margin, bears four short naked setae posterio-laterally, and five plumose setae posterio-medially. Slender and elongate, the first endopodite segment attaches posterior to the exopodite, also has a hairy lateral margin, and bears one long plumose seta medially. The circular second endopodite segment has a hairy lateral margin, and gives rise to five plumose setae from its distal margin.

The base segment of the fourth thoracic leg (Figure 87) is oval, almost twice as wide as long, and laterally bears a plumose seta. Posterio-laterally it articulates with the second segment which is three times as long as wide, has a convex lateral margin, a concave distal margin, and posteriorly a cuticular knob near the articulation with the third segment. Four very stout naked setae emerge from the irregular distal margin of the third segment. Twice as long as wide, this segment has flat anterior and posterior margins.

The fifth and sixth legs of the male (Figure 88) and the fifth leg of the female (Figure 89) are lobate projections on the posterio-lateral margins of the genital segments (Figures 74, 75). The fifth legs possess four lateral plumose setae; the sixth possesses only two.
Sixth Chalimus Stage

The sixth chalimus (Figures 90, 91) is similar to, but larger than, the fifth (Figures 74, 75) and was never found attached by a frontal filament. Males are 2,959μ (2,885 to 3,059) long by 1,904μ (1,881 to 1,919) wide; females are 3,842μ (3,740 to 3,998) long by 2,650μ (2,542 to 2,755) wide. Of the length, cephalothorax accounts for 1,949μ (1,881 to 2,014) in the male and the following segments 1,008μ (911 to 1,140); in the female these lengths are 2,680μ (2,561 to 2,850) and 1,159μ (950 to 1,330) respectively.

The fourth pedigerous segment and the genital segment of both sexes (Figures 90, 91) is unchanged (Figures 74, 75). Spermatophore rudiments are evident in the genital segment of the male (Figure 90).

The activity, movements, and molting of the sixth chalimus are similar to those of the fifth. The sixth chalimus male was most commonly found clasped onto either fifth or sixth chalimus females, fifth or sixth chalimus males, or adult females with or without previously attached spermatophores and/or egg strings. At 20°C, six specimens of the sixth chalimus remained in this stage about 24 hours.

Sixteen plumose setae arise from the latero-distal margins of the first segment of the first antenna (Figure
This appendage is otherwise the same as that of the fifth chalimus (Figure 76).

The proximal segments of the second antenna (Figure 93) are like those of Figure 77. The third prehensile segment is more elongate, most of the anterior margin concave, and the posterior margin convex. The flaccid non-plumose seta is present on the mid-anterior margin.

The post antennal process (Figure 94) is now directed almost posteriorly and the base has two setule-bearing nodules.

The mandible (Figure 95), maxilla (Figure 97), and maxilliped (Figure 98) remain unchanged from their counterparts of the previous stage (Figures 79, 81, 82).

Margins of the sternal furca base (Figure 99) are smooth and the edges of the two processes are sclerotized. This structure undergoes no further change in the adult (Figure 116).

The two exopodite and protopodite segments of the first thoracic leg (Figure 100) are relatively longer than those of the fifth chalimus (Figure 84). The ornamentation and the endopodite are unchanged except that the three lateral setae of the second exopodite segment are non-plumose.

The shape and armature of the protopodite segments of the second thoracic leg (Figure 101) are unchanged. Both exopodite and endopodite are now three-segmented. The
shape and armature of the first exopodite segment is like that of its predecessor (Figure 85). The ovoid second exopodite segment is equal in size to the circular third segment and bears posterio-medially a long plumose seta, and posterio-laterally a short non-plumose spine-like seta. The third segment laterally bears three stout setae of which one is naked, one with a lateral membrane, and one with a membrane laterally and plumose medially. Five long plumose setae arise from the convex posterio-medial margin. All endopodite setae are plumose. The circular first endopodite segment has one long seta from the medial margin and its opposite margin is haired. The second squarish segment bears two long setae medially and is laterally hairy. From the convex margin of the hemispherical third segment arise six setae, the lateral two being about two thirds the length of the other four.

The rigid membrane-like protopodite of the third thoracic leg (Figure 102) has expanded medially (Figure 86) and bears a membrane from the posterior margin. The status of the endopodite is unchanged, but the exopodite is now three-segmented. The first segment is similar to that of the fifth chalimus (Figure 86); the somewhat triangular second segment is haired both laterally and medially and bears three setae. One arises posterio-laterally and is naked, and the two plumose setae arise from the terminal corners of the medial margin. From the hairy
lateral margin of the hemispherical third segment arise
three stout naked setae, from the posterior margin four
plumose setae.

The terminal segment of the fourth leg of the fifth
chalimus (Figure 87) becomes two segments in the sixth
chalimus (Figure 103); the first two segments of both ap-
pendages are alike. The rhomboidal third segment bears a
very stout naked seta from the distal corner. The fourth
wedge-shaped segment gives rise from the flat distal margin
to three robust naked setae of which the medial is longest
and the lateral shortest.

The fifth and sixth legs of the male (Figure 104) and
the fifth leg of the female (Figure 105) are similar to
those of the previous stage (Figures 88, 89).

Adult

Adults (Figures 106, 107) are larger duplications of
the sixth chalimus (Figures 90, 91), except for the frontal
organ which was no longer discernible. Males are 3,448μ
(3,160 to 3,800) long by 2,155μ (1,957 to 2,375) wide;
females are 5,751μ (4,978 to 6,406) long by 3,369μ (2,945
to 3,710) wide. Cephalothoracic length in the male amounts
to 2,383μ (2,185 to 2,562) and the following segments
1,038μ (836 to 1,311); in the female these lengths are
3,509μ (3,228 to 3,899) and 2,221μ (1,520 to 2,759) respec-
tively. The size of the adult male increases very little
after the molt from the sixth chalimus, but the female may grow to nearly twice the size of the previous stage.

The male fourth pedigerous segment (Figure 106) is half again as wide as long, that of the female (Figure 107) similar to its counterpart of the previous two stages (Figures 91, 75). Two spermatophores were evident on the genital segment of all males (Figure 106). The female genital segment (Figure 107) swells with eggs to a rounded shape. All females had at least two attached spermatophores on the mid-posterior margin of the genital segment. One favored female was observed with so many attached spermatophores that they resembled a cluster of grapes. Egg strings, when present, attach on the posterior margin of the genital segment half way between the longitudinal body axis and the lateral margin.

Adults scuttle over the ventral surface of the flounder and can swim rapidly through the water if dislodged. All specimens released in the water table containing flounders always were able to locate a host. They feed primarily on flounder slime, but if an abrasion or cut is present on the fish, the digestive tract contents may be tinged with blood. Adult males were commonly coupled to sixth chalimus or small adult females, or were single. The length of adult life is not known, but is assumed to be at least two months and up to perhaps six or seven, based upon observed seasonal abundance.
The first segment of the first antenna (Figure 108) bears 20 plumose setae, 18 from the anterio-distal margin and two from the dorsal surface near the junction of the anterior and distal margins. The second segment gives rise to 14 naked setae distally and one from the mid-posterior margin.

The female second antenna (Figure 110) is like that of the sixth chalimus (Figure 93), but the second antenna of the male (Figure 109) has changed considerably. The elongate first segment has a flat proximal end, a tapered rounded medial end, is four times as long as wide, and much of the surface is reinforced by transverse cuticular ridges. The concave anterio-medial surface broadly articulates with the second segment which has diagonal, longitudinal, and transverse cuticular ridges. Drumstick-shaped with a flat distal margin, this second segment is half again as long as wide and has a swelling on the anterior and posterior margins near the distal end. The third segment is tapered distally, twice as long as wide, has a flaccid non-plumose seta near the mid-anterior margin and another one near the proximo-distal corner, and terminally bears three well-developed claws of which one is directed ventrally, one anterio-medially, and one posterio-laterally.

The denticulations of the mandible (Figure 112) are more pronounced and the proximal segment is relatively wider than in the sixth chalimus (Figure 95).
The post antennal process (Figure 111) is posteriorly directed in the adult and bears two setuliferous nodules on the base portion.

Both slender segments of the maxilla (Figure 114) are relatively longer than in Figure 97. The appendage is now rather flaccid and the junction between segments shows no special articulating projections.

The maxilliped (Figure 115) is like Figure 98, but relatively smaller and the first segment is not as stout.

The status of the first thoracic leg (Figure 117) is like that of the sixth chalimus (Figure 100), except that the endopodite is relatively smaller.

The second protopodite segment of the second thoracic leg (Figure 118) has irregular margins, but is somewhat circular. A continuous membrane is present on the lateral margin of the first and second exopodite segments, and the third exopodite segment bears an additional long plumose seta. Aside from the above mentioned differences, this appendage has changed little from the sixth chalimus (Figure 101).

The posterio-medial margin of the protopodite of the third thoracic leg (Figure 119) has expanded to the edge of the seta arising from the sternal plate, and the second exopodite segment now bears two short naked setae from the lateral margin. Otherwise, this appendage is like that of Figure 102.
The first segment of the fourth thoracic leg (Figure 120) is rectangular and three times as long as wide. The second and third rhomboidal segments each bear a seta and a tuft of hair at the distal end. Three claw-like setae arise from the flat distal margin of the triangular-shaped fourth segment. The margins of the four terminal setae bear very short setules; the most proximal is naked.

The fifth and sixth legs of the male (Figure 121) are unchanged. Due to lateral expansion of the genital segment, the fifth legs of the female (Figure 122) are in a medial-lateral position (Figure 107), and the most anterior seta is not visible. Occasionally the fifth leg is completely obliterated.

The changes which take place in the appendages and processes of the life history stages of *Lepeophtheirus hospitalis* are summarized in Table II.
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*N1 = First Nauplius; N2 = Second Nauplius; CO = Copepodite; Cl = First Chalimus; C2 = Second Chalimus; etc.; A = Adult. Figures after symbols indicate number of segments.
DISCUSSION

Seasonal Abundance

As far as could be determined, the only mention of caligid seasonal abundance concerns *Lepeophtheirus salmonis*. White (1940) found the numbers of these "lice" on Atlantic salmon entering the Moser River in Nova Scotia to increase through the summer to a peak in mid-August. He (White, 1941) stated that these parasites die and fall off when the fish return to fresh water. The starry flounder, *Platichthys stellatus*, also returns to fresh water for spawning in the spring months (Orcutt, 1950). In the present study, it was found that the flounders lost all specimens of *L. hospitalis* within 24 hours after being placed in fresh water, and therefore it is logical to assume the same thing occurs at spawning. The abundance of *L. hospitalis* on the population of Yaquina Bay flounders decreased through the winter months as the rainy season progressed. The copepod population probably increases, or is re-established, during the spring on the bay flounders when they mix with infected adult flounders passing through the bay to spawn upstream. Scott (1901) reported the presence of *Caligus* in tow-net collections and indicated that these copepods frequently leave the host. It seems that the amount of fresh water flowing through the bay regulates *L. hospitalis* abundance. Apparently a reservoir of
infected flounders exists along the coast.

Mating

The mechanical aspects of copulation among caligid species are similar. Males of all species studied apparently attach to the female primarily with their well-developed second antennae. Lewis (1963) observed the male maxillipeds of *L. dissimulatus* to be free during copulation and Scott (1901) stated that in the genus *Lepeophtheirus* the maxillipeds and fourth thoracic legs seize the posterior margin of the female genital segment. All accounts of the actual spermatophore transfer indicate a folding under of the posterior portion of the male body along the ventral surface of the female. The viscid caligid spermatophore (Scott, 1901; Wilson, 1905) is discharged and adheres to the genital segment of the female. Remating was not observed in *L. dissimulatus* by Lewis (1963) nor in *L. hospitalis*, but multiple spermatophores on the female indicate this is a common occurrence in the latter. Comparing the male and mature female, it is obvious (Scott, 1901) that fertilization cannot be accomplished when the female genital segment is fully developed. A single mating probably provides sufficient sperm for the entire egg production of the female (Wilson, 1905). Izawa (1969) claimed coupling takes place in *Caligus spinosus* during the first pre-adult stage, but spermatophores were not transferred.
His (Izawa) "first pre-adult" stage followed the third chalimus. He also saw males clasping first pre-adult females.

Egg String Formation

Eggs are fertilized as they are extruded (Wilson, 1905) into a thin chitinous tube which gradually lengthens as eggs are expelled (Scott and Scott, 1913). Each egg is wrapped in a cuticular material presumed (Lewis, 1963) to be secreted by a cement gland in the genital segment of the female. Wilson (1905) stated the egg tube is secreted only as there is a demand for more space and is extended by the pressure of the issuing eggs which also causes them to become flattened. The flattening of eggs Heegaard (1947) felt is due to absorbed water. Observations on L. hospitalis support the latter view.

Embryology

Details of caligid egg development are lacking, most probably due to the compressed disc arrangement the eggs assume in the egg string cases. Most records mention the occurrence of reddish pigment spots prior to hatching and provide an estimate of the time between ovulation and hatching, but fail to give a temperature on which their time estimates are based. Wilson (1905) claimed the incubation period for C. rapax is eight weeks, and for
L. pectoralis eight to ten weeks. Heegaard (1947) said this interval in all parasitic copepods "no doubt ranges over a period of from 14 days to one month." At 20°C, eggs of C. spinosus hatched out in "one or two days" (Izawa, 1969). For L. dissimulatus at "approximately 23°C," Lewis (1963) reported reddish pigment spots at 13 to 20 hours and from 30 to 40 hours movement was visible within the egg. All reports seem to agree that the reddish pigment is to be associated in some way with the eye. Izawa (1969) counted 10 to 20 eggs per egg string for C. spinosus, and Lewis (1963) said each L. dissimulatus female carried 20 to 60 eggs.

Hatching

Hatching in L. hospitalis is apparently typical for caligids in general. There is little variation in the given times for all individuals of an egg string to hatch. Izawa (1969) reported this time to be three to eight hours for C. spinosus at 20°C, and Lewis (1963) stated that two to ten minutes elapse between individual hatchings of L. dissimulatus eggs. Proper egg packing in the egg string seems to be necessary for successful hatching in L. hospitalis.
Naupliar Stages

Wilson (1905) mentioned a mouth opening being present in naupliar stages, but this has not been observed in L. hospitalis, L. dissimulatus (Lewis, 1963), nor in other nauplii (Heegaard, 1947). Light sensitive areas obviously exist in L. hospitalis, but a definite eye was not discernible. Wilson's (1905) figures of the naupliar stages of C. rapax and C. bonito also did not show a definite eye, but he mentioned "the eye" in the naupliar descriptions. The function of the relatively immobile naupliar balancers could not be definitely ascertained for either L. hospitalis nor L. dissimulatus (Lewis, 1963) although it has been suggested (Wilson, 1905) that they balance the nauplius when at rest.

At 20°C, the first nauplius of C. spinosus lasted four to six hours, the second 12 to 18 (Izwa, 1969). For L. dissimulatus at approximately 23°C, the above times were 4 to 13 hours and 9½ to 19 respectively (Lewis, 1963).

Copepodite

Copepodites of C. spinosus at 20°C die after five to seven days if a host is not found (Izawa, 1969). Finding a host is probably done by chemical means. Fasten (1913) stated this is accomplished using smell and/or taste; Wilson (1915) has reached the same conclusion. Wilkes
(1966) mentioned a unique flounder aroma, also noted in the present study, and suggested it functions as an attractant for the attaching stage of *Nectobrachia indivisa*. The actual attaching, filament formation, of the copepodite to the host fish is accomplished in the same manner in *L. dissimulatus* (Lewis, 1963) as it was in *L. hospitalis* and apparently varies little in other caligids.

Based on morphological differences, Wilson (1905), Russell (1925), and Heegaard (1947) decided *Caligus* has two copepodite stages. There is no direct statement in their publications that they observed a molt between these two. Gurney (1934) found "no evidence" of a second copepodite in *C. centrodonti* and *C. labracis*. No such stage was observed in *L. dissimulatus* (Lewis, 1963), *C. spinosus* (Izawa, 1969), nor in this study. Izawa (1969) further states, "the second copepodids, so named by the authors, seems to be equivalent to an advanced phase of one and the same copepodid stage."

Older copepodites rest ventral surface up, as if waiting for a host to pass over.

**Chalimus Stages**

Chalimus stages hang free from the host by the attaching filament and obtain nourishment at suitable intervals by folding the frontal region until they can grasp the fish (Wilson, 1905; Heegaard, 1947). White (1942)
found *L. salmonis* chalimus stages to "swing about" on their frontal filaments when not feeding.

The six chalimus stages of *L. dissimulatus* at approximately 23°C lasted about 40, 42, 33, 36, 24, and 24 to 30 hours respectively (Lewis, 1963). For *L. hospitalis* at 20°C these times are 6½, 5, 4½, 2½, 2, and 1 days. Lewis (1963) found most fifth chalimus stages to be attached and most sixth chalimus stages free on the host.

The attached chalimus stages of *C. curtus* produced a new attaching filament after each molt (Heegaard, 1947). For *L. dissimulatus* (Lewis, 1963) and *L. hospitalis*, an original filament was used by one individual through all its attached chalimus stages, and shed exoskeletons did not remain attached to the host, filament, nor copepod. Proximal annuli on the filaments of later chalimus stages indicate (Gurney, 1934) an increase in filament length at each molt. Filament length did increase in *L. hospitalis* (Table I) and *L. dissimulatus* (Lewis, 1963). Annuli were not observed.

A comparison of developmental stages of *Caligus* and *Lepeophtheirus* is in Table III. Heegaard's (1947) description and figures of a pupal stage clearly indicate to Izawa (1969) "that this ought to be called the first chalimus." No pupal stage was found in *C. spinosus* (Izawa, 1969), *L. dissimulatus* (Lewis, 1963), nor *L. hospitalis*. The changes occurring in the chalimus stages of
<table>
<thead>
<tr>
<th>Species Worker</th>
<th>Stages</th>
<th>naupliar</th>
<th>metanaupliar</th>
<th>copepodite</th>
<th>pupal</th>
<th>chalimus</th>
<th>pre-adult</th>
</tr>
</thead>
<tbody>
<tr>
<td>Caligus rapax Wilson (1905)</td>
<td></td>
<td>2</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td>at least 5</td>
</tr>
<tr>
<td>Caligus pageti Russell (1925)</td>
<td></td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td>at least 3</td>
</tr>
<tr>
<td>Caligus centrodonti Gurney (1934)</td>
<td></td>
<td>2</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td>4</td>
</tr>
<tr>
<td>Caligus curtus Heegaard (1947)</td>
<td></td>
<td>2</td>
<td>2</td>
<td>1</td>
<td></td>
<td></td>
<td>5</td>
</tr>
<tr>
<td>Caligus spinosus Izawa (1969)</td>
<td></td>
<td>2</td>
<td></td>
<td>1</td>
<td></td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Lepeophtheirus dissimulatus Lewis (1963)</td>
<td></td>
<td>2</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td>6</td>
</tr>
<tr>
<td>Lepeophtheirus hospitalis</td>
<td></td>
<td>2</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td>6</td>
</tr>
</tbody>
</table>
L. hospitalis agreed most closely with L. dissimulatus (Lewis, 1963) and agreed in general with those of other caligids, where known. Sexual dimorphism is the apparent reason for calling the last two stages of C. spinosus pre-adult (Izawa, 1969).

Adult

Parasitic copepods such as L. hospitalis which live on the ventral surface of bottom dwelling flat fish probably have their prehensile powers taxed to the utmost. The arched carapace of caligids acts as a large sucking disc, its margin being pressed close to the host surface and sealed with water and slime (Wilson, 1905). This adhesion in Lepeophtheirus holds them to such an extent that the free posterior segments can be torn from the anterior part without detaching it (Scott, 1901).

The damage to the fish host by caligids seems to depend on the number, the food, and the species involved. Scott (1901) claims Lepeophtheirus normally feeds on mucus, but can become cannibalistic. Wilson (1905) said caligids feed on blood. White (1942) found fish skin in the digestive tract of L. salmonis and further stated these copepods will even feed on the subcutaneous tissues. Light-colored abraded areas caused by L. salmonis became evident on salmon after the copepod falls off in fresh water (White, 1940). White (1940) felt the death of
salmon with abraded areas was caused in part by these parasites.

Appendages and Processes

The naupliar first antennae are used for swimming, but in the following stages are very fully innervated and evidently act as sensory organs (Wilson, 1905; Scott and Scott, 1913).

The biramous second antennae of the naupliar stages are swimming appendages, but become uniramous prehensile appendages in the following stages (Lewis, 1963), and are used as attachment organs. Wilson (1905) stated that the caligid copepodite second antenna is still biramous, but this was uniramous on *L. hospitalis* and *L. dissimulatus* (Lewis, 1963). Only after the molt to the sixth chalimus could the second antennae be used to distinguish the sexes in *L. dissimulatus* (Lewis, 1963) and *L. hospitalis*.

Heegaard (1947) claimed the post antennal process to be a true appendage, but Lewis (1963) felt that since it first appears in the third chalimus it is not, and that only further study will resolve the question. Wilson (1905) called the post antennal process the first maxilla and stated that they are of apparently no use, except possibly to irritate a wound and stimulate blood flow.

The naupliar mandibles are swimming organs, but change drastically in the copepodite to rod-like structures which
assist in the collecting of particles of food (Scott, 1901). The derivation of the mandible requires further work (Lewis, 1963).

Wilson (1905) called the post oral process the second maxilla, but Lewis (1963) preferred "post oral process" because its anlage is unknown. A possible function for this structure is that it serves to protect the mouth cone.

Following the terminology of Lewis (1963), the maxillae are the first pair of appendages immediately behind the mouth, but have been given a variety of names due to the terms applied to the post oral and post antennal processes. Wilson (1905) and Scott (1901) both agree that these appendages function to keep the mouth free from obstruction by a sort of combing action.

The maxillipeds are thought to be the first thoracic appendages in copepods and the maxillae the last cephalic appendages (Borradaile et al., 1958:347-348). Those who call the post antennal processes the first maxillae and the post oral processes the second maxillae must then call the first pair of appendages behind the mouth the first maxillipeds and the last pair of appendages before the thoracic legs the second maxillipeds. This does not follow the terminology set forth in the first statement. In this paper, maxillae are the first pair of appendages behind the mouth and maxillipeds the first pair of appendages anterior to the first thoracic legs. This is consistent
with Lewis (1963). The maxillipeds are organs of prehension (Wilson, 1905; Scott and Scott, 1913).

Lewis (1963) suggested that the sternal furca may be the remnant of the sternal plate which exists between the first three pairs of thoracic legs in many caligoids, including Lepeophttheirus, but Heegaard (1947) claimed it to be a cuticular spine. This structure acts powerfully to prevent slipping (Wilson, 1905).

The first three pairs of thoracic legs are adapted for swimming (Scott and Scott, 1913). The fourth pair of legs aids in grasping the female during copulation (Scott, 1901). The fifth and sixth pairs of legs are little developed (Fraser, 1920) and probably serve no function.
SUMMARY

The morphology and behavior of the ten life history stages of the parasitic copepod *Lepeophtheirus hospitalis* have been described. Measurements and figures for all stages were included.

Adults are motile ectoparasites on the ventral surface of the starry flounder, *Platichthys stellatus*. They adhere with prehensile second antennae, maxillipeds, and a suction cup action produced by the arched cephalothorax. The primary food was slime, but if an abrasion or cut was present, blood was sometimes ingested. Seasonal abundance of the parasite in Yaquina Bay, Oregon, seemed to be correlated with the amount of fresh water flowing through the bay.

Ovulation and egg string formation occurred simultaneously at night. At 20°C, 64 hours elapsed between ovulation and hatching. The major features of ovulation, egg string formation, embryology, and hatching have been described.

The two unsegmented naupliar stages were free-swimming, positively phototropic, and possessed three pairs of appendages: first antennae, second antennae, and mandibles all of which were used in swimming. The duration of the first naupliar stage at 20°C was seven and a half hours and at 15°C about 24 hours. For the second nauplius these times were 11 and 40 hours respectively. Mortality on the
molts following each of these two stages was less than five percent and five to ten percent.

The segmented body of the copepodite possessed those appendages present on the naupliar stages, and added the post oral processes, maxillae, maxillipeds, the first two pairs of thoracic legs, and the caudal rami. This stage was free-swimming, but died in three to eight days, at 20°C, if a host was not located. Copepodites held onto the flounder with their prehensile second antennae for four to six days, at 15°C, at which time they formed attaching filaments. This process began with a series of rapid jabs to the host substrate by the anterior cephalothorax. A droplet of frontal organ secretion appeared between copepodite and host and was pulled out into a filament which hardened immediately. At 15°C the molt to the first chalimus stage took place 36 to 48 hours after filament formation. Laboratory mortality from copepodite to first chalimus was over 95 percent.

The six chalimus stages at 20°C lasted 6½, 5, 4½, 2½, 2, and 1 days respectively. The first four stages were attached by a frontal filament, the fifth was usually unattached, and the sixth was always unattached. Sexual differentiation became evident in the fifth chalimus: males possessed a sixth pair of legs, females did not. Sixth chalimus males were usually found coupled to adult females or mobile chalimus stages of either sex. The
third and fourth pairs of legs appeared in the first chalimus stage. The post antennal processes and fifth pair of legs were new structures in the third chalimus, and the sternal furca was new to the fourth chalimus.

The above mentioned times, changes, and behavior were compared to that of other caligids. Possible functions for all appendages and processes previously proposed were given and it was herein suggested that the post oral process serves to protect the mouth cone.
BIBLIOGRAPHY


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LEGEND

N - Endopodite
X - Exopodite
P - Protopodite
Figure 1.  Egg case with eggs
Figure 2.  Egg case after hatching
Figure 3.  Side view of developing eggs
Figure 4.  End view of a developing egg
Figure 5.  Early pigment spots on developing eggs
Figure 6.  Later expanded pigment spots on eggs
Figure 7.  Hatching of first stage nauplii
First Stage Nauplius

Figure 8. Dorsal view
Figure 9. First antenna
Figure 10. Second antenna
Figure 11. Mandible
Second Stage Nauplius

Figure 12. Dorsal view
Figure 13. First antenna
Figure 14. Second antenna
Figure 15. Mandible
Copepodite

Figure 16. Dorsal view
Figure 17. First antenna
Figure 18. Second antenna
Figure 19. Mandible
Figure 20. Post oral process
Copepodite

Figure 21. Maxilla
Figure 22. Maxilliped
Figure 23. First thoracic leg
Figure 24. Second thoracic leg
First Chalimus Stage

Figure 25. Dorsal view

Figure 26. First antenna

Figure 27. Second antenna

Figure 28. Mandible

Figure 29. Post oral process
First Chalimus Stage

Figure 30. Maxilla

Figure 31. Maxilliped

Figure 32. First thoracic leg

Figure 33. Second thoracic leg

Figure 34. Third thoracic leg

Figure 35. Fourth thoracic leg
Second Chalimus Stage

Figure 36. Dorsal view
Figure 37. First antenna
Figure 38. Second antenna
Figure 39. Mandible
Figure 40. Post oral process
Second Chalimus Stage

Figure 41. Maxilla
Figure 42. Maxilliped
Figure 43. First thoracic leg
Figure 44. Second thoracic leg
Figure 45. Third thoracic leg
Figure 46. Fourth thoracic leg
Third Chalimus Stage

Figure 47. Dorsal view
Figure 48. First antenna
Figure 49. Second antenna
Figure 50. Post antennal process
Figure 51. Mandible
Figure 52. Post oral process
Third Chalimus Stage

Figure 53. Maxilla
Figure 54. Maxilliped
Figure 55. First thoracic leg
Third Chalimus Stage

Figure 56. Second thoracic leg
Figure 57. Third thoracic leg
Figure 58. Fourth thoracic leg
Figure 59. Fifth thoracic leg
Fourth Chalimus Stage

Figure 60. Dorsal view
Figure 61. First antenna
Figure 62. Second antenna
Figure 63. Post antennal process
Figure 64. Mandible
Figure 65. Post oral process
Fourth Chalimus Stage

Figure 66. Maxilla
Figure 67. Maxilliped
Figure 68. Sternal furca
Figure 69. First thoracic leg
Figure 70. Second thoracic leg
Figure 71. Third thoracic leg
Figure 72. Fourth thoracic leg
Figure 73. Fifth thoracic leg
Fifth Chalimus Stage

Figure 74. Dorsal view of male
Fifth Chalimus Stage

Figure 75. Dorsal view of female
Fifth Chalimus Stage

Figure 76. First antenna
Figure 77. Second antenna
Figure 78. Post antennal process
Figure 79. Mandible
Figure 80. Post oral process
Figure 81. Maxilla
Figure 82. Maxilliped
Figure 83. Sternal furca
Fifth Chalimus Stage

Figure 84. First thoracic leg
Figure 85. Second thoracic leg
Figure 86. Third thoracic leg
Figure 87. Fourth thoracic leg
Figure 88. Male fifth and sixth legs
Figure 89. Female fifth leg
Sixth Chalimus Stage

Figure 90. Dorsal view of male
Sixth Chalimus Stage

Figure 91. Dorsal view of female
Sixth Chalimus Stage

Figure 92. First antenna
Figure 93. Second antenna
Figure 94. Post antennal process
Figure 95. Mandible
Figure 96. Post oral process
Figure 97. Maxilla
Sixth Chalimus Stage

Figure 98. Maxilliped
Figure 99. Sternal furca
Figure 100. First thoracic leg
Figure 101. Second thoracic leg
Sixth Chalimus Stage

Figure 102. Third thoracic leg
Figure 103. Fourth thoracic leg
Figure 104. Male fifth and sixth legs
Figure 105. Female fifth leg
Adult

Figure 106. Dorsal view of male
Figure 107. Dorsal view of female
Adult

Figure 108. First antenna
Figure 109. Male second antenna
Figure 110. Female second antenna
Figure 111. Post antennal process
Figure 112. Mandible
Figure 113. Post oral process
Figure 114. Maxilla
Figure 115. Maxilliped
Adult

Figure 116. Sternal furca
Figure 117. First thoracic leg
Figure 118. Second thoracic leg
Adult

Figure 119. Third thoracic leg
Figure 120. Fourth thoracic leg
Figure 121. Male fifth and sixth legs
Figure 122. Female fifth leg