

# FEEDING, CLEANING, AND SWIMMING BEHAVIOR IN LARVAL STAGES OF PORCELLANID CRABS (CRUSTACEA: ANOMURA)<sup>1</sup>

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## ABSTRACT

*Pachycheles rudis*, *Pachycheles pubescens*, *Petrolisthes eriomerus*, and *Petrolisthes cinctipes* have a swimming prezoal stage of short duration. The prezoal form is probably related to escapement of the larvae from the confined adult habitat.

Both zoeal stages are strong swimmers, moving both forward and backward by means of the maxillipedal exopodites, aided by the telson. Zoeae have a well-defined cleaning behavioral sequence for removal with the mouth parts of particles from the telson and the maxillipedal endopodites. The two zoeal stages are carnivorous and capture live prey upon contact but do not appear to locate prey visually. Prey are caught with the maxillipedal endopodites and held with the flexed abdomen and telson.

At the molt to megalopa, the larva becomes a filter-feeding herbivore like the adult. Other adultlike behavior of the megalopa includes use of the fifth legs for cleaning and attempts by older megalopae at swimming by clapping the abdomen. Megalopae filter feed only when suspended algal food is present; water movement enhances feeding but is insufficient alone to induce feeding. At first, using their abdominal pleopods, megalopae swim continuously, later swim intermittently, and finally settle permanently if a substrate suitable for clinging is available.

A large amount of information is available about the comparative larval morphology of most groups of decapod Crustacea. Further understanding of the adaptive significance of larval morphology and its changes during larval life requires comparable information, now largely lacking, about larval behavior and ecology. The present state of knowledge on the larvae of porcellanid crabs is typical in this respect, with a growing descriptive literature available but little known about other aspects of larval biology. A few observations on various features of porcellanid larval behavior have been given by Russell (1925), Spooner (1933), Foxon (1934), Gurney (1942), Lebour (1943), Greenwood (1965), and Knight (1966). None of these studies present a complete account of any behavior pattern

throughout development. Information on food and feeding is incomplete and somewhat inconsistent. The detailed studies on feeding and respiration of adults by Nicol (1932) and Knudsen (1964) indicate that adult porcellanids are specialized filter feeders. The available information indicates that zoeae are carnivorous or possibly also detrital feeders. Since it is now known that decapod zoeae are typically strict carnivores capturing live prey, a change in diet and mode of feeding during the development of porcellanids would be expected, but has not been clearly described.

Large numbers of live larvae of all developmental stages and ages were available in laboratory cultures during a study of the larval development of four species of porcellanid crabs (Gonor and Gonor, 1973). Several aspects of the behavior of the larvae being cultured were studied closely throughout development. Special attention was given to the ontogeny of normal respiratory, feeding, cleaning, and locomotory behavior patterns from hatching through development to the first juvenile crab stage. These

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observations are presented here to clarify some aspects of the ecology of both the larval and adult stages.

## METHODS

The species used were *Petrolisthes cinctipes* (Randall), *Petrolisthes eriomerus* Stimpson, *Pachycheles rudis* Stimpson, and *Pachycheles pubescens* Holmes. Adults of all of these species occur in the rocky intertidal or the shallow subtidal zone of the northeastern Pacific but their habitats differ (Haig, 1960). The *Petrolisthes* species occur in the upper intertidal beneath loosely bedded rocks and boulders, whereas the two *Pachycheles* species are crevice and burrow dwellers. *P. rudis* was collected from beneath root mats of the surf grass *Phyllospadix* in the lower intertidal zone and *P. pubescens* was collected from burrows and crevices in rocks. Both larvae captured alive in the plankton and larvae reared from eggs carried by females in the laboratory were available.

Gravid females were maintained in the laboratory at ambient sea temperatures until hatching occurred. Thereafter, larvae were cultured in filtered seawater kept at several constant temperatures and fed *Artemia* nauplii. Larvae captured in the plankton were similarly maintained in the laboratory. A detailed account of methods used in rearing and handling the larvae is given elsewhere (Gonor and Gonor, 1973).

## RESULTS

In laboratory cultures, larvae of each of the four species showed similar basic patterns of locomotion, feeding, respiration, and cleaning, as well as changes in these patterns through time. Consequently, separate accounts for each species will not be given. Basic body and appendage form is sufficiently similar in the first and second zoeae for Figures 2 and 3, of second zoeal appendages, to be referred to in the text for both stages. The descriptions given below are summarized from observations repeated throughout the rearing study as each of the cultures was examined daily. Table 1 gives the number of larvae of each stage kept in culture

for at least 2 days, and available for observations on behavior at some time during the 2-year period of the study.

## PREZOEAE

Females of all four species studied here release their larvae in the form of a prezoea (Figure 1).

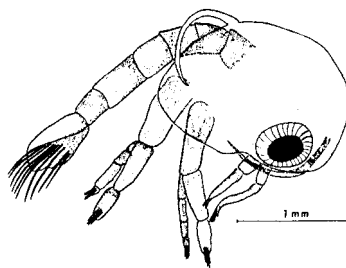


FIGURE 1.—Prezoea of *Pachycheles pubescens*, showing rounded form.

Gravid females were maintained in the laboratory for as long as 35 days, showing normal locomotion, feeding, and cleaning behavior before their eggs hatched. The following numbers of broods were hatched in the laboratory: *Pachycheles rudis*, 35; *P. pubescens*, 2; *Petrolisthes eriomerus*, 11; *P. cinctipes*, 10. In each case female behavior during hatching was of the normal type described elsewhere (Gonor and Gonor, 1973), and the larvae released were prezoeae which molted to viable first zoeae. The behavior patterns of the prezoea are simpler than those of later stages. Respiratory motions in the prezoea are effected by the fanlike scaphognathite of the second maxilla. The type of

TABLE 1.—Number and source of larvae of different stages available for behavioral observations.

Species	Zoea I	Zoea II	Megalopa
<i>Petrolisthes cinctipes</i> (reared)	727	19	1
<i>Petrolisthes eriomerus</i> (reared)	603	58	14
<i>Pachycheles rudis</i> (reared)	757	21	1
<i>Pachycheles rudis</i> (plankton)	76	58	28
<i>Pachycheles pubescens</i> (reared)	100	18	—
<i>Pachycheles pubescens</i> (plankton)	26	81	36
Total	2,289	255	80

cleaning behavior described below for the zoeal stages has not been observed in this stage. It probably is not present since the stage is short-lived and the major natatory and telson setae are confined beneath the larval cuticle.

Prezoeal locomotion consists of violent spasmodic flexions of the abdomen, and there is no feeding during this stage. The larva appears to be only slightly photopositive. The strong abdominal flexions finally split the cuticle longitudinally along the dorsal midline of the carapace just behind the point where the rostrum joins the carapace, and a first zoea emerges from the thin prezoeal cuticle.

### ZOEAL STAGES

The behavior patterns of the first true zoea are considerably more complex than those of the prezoeal stage. Respiratory currents are still produced by the beating of the maxillae and are aided by swimming, as was also noted by Foxon (1934). Detrital particles often become entangled in the plumose setae of the maxillipeds and telson. Cleaning behavior is simple but well defined in this stage. The telson and the plumose setae along its posterior margin are cleaned by curving the abdomen under the thorax and dragging the telson posteriorly across the functional mouth parts, thus loosening and scraping off clinging debris. This scraping also serves to remove large pieces of detritus from the peripheral setae on the mouth parts and from the setae of the endopodites on both sets of maxillipeds. The endopodites are used in feeding and require frequent cleaning. Direct cleaning of the exopodites and natatory setae and of the carapace spines was never observed, however. The cleaning observed was indirect and probably accidental, since it consisted simply of freeing the body surface of entangled debris by larval motion and reversal of swimming direction.

The first zoea swims primarily by beating the maxillipedal exopodites (Figure 2) which have long natatory setae, but this may be augmented by motions of the telson. The maxilliped endopodites are held extended ventrally and do not function in swimming. The zoea are strong swimmers and due to the configuration of the

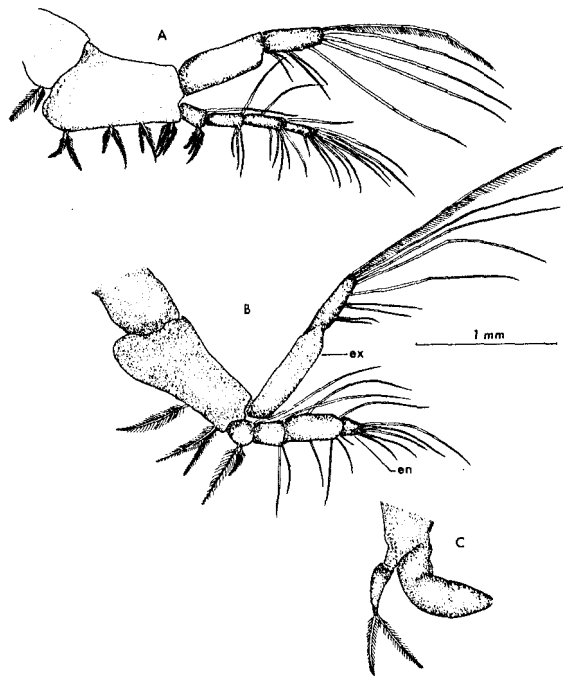


FIGURE 2.—Maxillipeds of Zoea II, *Pachycheles pubescens*, with setules omitted from most plumose setae. Ex - exopodite; en - endopodite; A - Maxilliped I; B - Maxilliped II; C - Maxilliped III.

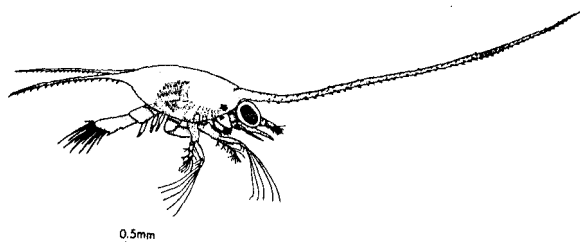


FIGURE 3.—Zoea II of *Pachycheles pubescens*, in forward swimming posture. Maxillipeds I and II rotated slightly for clarity.

carapace spines (Figure 3), swim predominantly backward and forward.

Forward motion is accomplished by synchronously beating both sets of exopodites downward and posteriorly, with the telson extended posteriorly. Reversal of direction can be achieved very quickly by a forward snap of the telson and a

simultaneous change in the pitch of the maxillipeds so that the exopodites beat downward and anteriorly. This rapid adjustment sends the larva on its way backward with its posterior spines leading. Unlike some larvae of the Galatheidae (Foxon, 1934), which swim only backward with the telson leading, the zoeae of porcelain crabs swim almost equally well in either direction. Normally, zoeae swim forward, reversing direction on contact with an object.

Zoea larva are voracious predators and are cannibalistic if not well supplied with other types of food. However, true hunting behavior of the kind reported for certain other predatory zoeae (Knudsen, 1960) was not observed. In fact, when a potential food organism touches any portion of the rostrum or posterior spines, or the top or sides of the carapace, the zoea immediately moves away from the point of contact, apparently in an act of avoidance. If, however, the prey approaches the thoracic region of a zoea closely enough to touch the setae of the ventrally extended maxillipedal endopodites (Figures 2, 3) or the ventral surface of the first two segments of the abdomen, the zoea reacts immediately. The prey is clutched between the endopodites, and the telson is used to force it forward and upward within reach of the functional mouth parts. This sequence has been observed many times, with no indication that sight is involved in locating and capturing the prey. The zoea also demonstrates what appears to be sensitivity to water movements. If a prey organism passes near the thoracic or abdominal region of the zoea but does not touch the sensitive setae, the zoea, without the stimulus of direct contact, will go through all the motions normally associated with the capture of prey. In these cases, the prey is usually out of reach, and the attempts to capture the passing animal fail.

The second zoeal stage is only slightly more complex morphologically than the first stage, and behavior patterns remain essentially the same throughout both zoeal stages. Metamorphosis to the megalopa (Figure 4), however, brings about immediate and drastic changes in structures and habits of the larva. Basic behavior patterns which were stable in the zoeal stages undergo progressive changes throughout the

megalopa stage, gradually becoming more adult-like in nature.

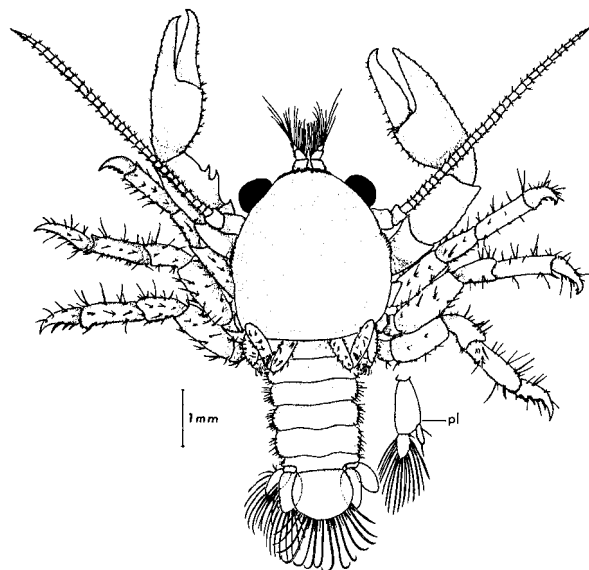


FIGURE 4.—Megalopa of *Pachycheles pubescens*, in forward pleopodal swimming posture, except antennae not extended posteriad. Pl, detail view of pleopod.

#### MEGALOPA

In the megalopa respiratory currents are produced primarily by fanning motions of the maxillary scaphognathites (Figure 5C) and are aided by the outward flicking of the setose exopodite of maxilliped II (Figure 5B). The outward flicking causes an exhalent current by "spooning out" the branchial cavity. The exopodite of maxilliped III is nonfunctional at this stage. In addition, a newly settled larva elevates its body above the substrate and concurrently vibrates its pleopods (Figure 4), thus increasing circulation of the surrounding water.

Cleaning behavior becomes highly complex in the megalopa. The fifth pereopods (Figure 4), which are mobile, chelate, and armed with specialized hooked setae and dense clusters of short bristles, are carried folded along the sides of the carapace when not in use. These structures serve to clean all portions of the abdomen and telson, the three pairs of functional walking legs,

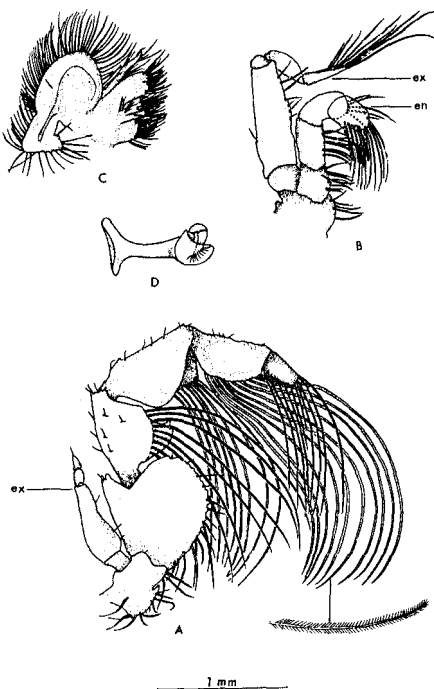


FIGURE 5.—Megalopa respiratory and feeding structures *Pachycheles pubescens*. Setules omitted from all plumose setae. Ex - Exopodite; en - endopodite; arrow - detail of a plumose seta. A - Maxilliped III; B - Maxilliped II; C - Maxilla II; D - mandible, anterior view, palp folded in place.

and the under side of the carapace in the branchial chamber. The foremost one-fourth of the carapace cannot be reached by these legs, and in dense algal suspensions, fine hairs on this portion of the megalopa may become entangled with algae and other detritus.

The chelipeds are freed of foreign matter by rubbing the dorsal surface of one on the ventral surface of the other in a simple lateral scraping motion. The antennules are cleaned singly or simultaneously in the following manner. An antennule is lowered to the level of a raised third maxilliped and inserted into a notch on the maxilliped formed by a long and a short group of dense setae. The setae and aesthetes of the antennule are then effectively combed free of particles as the maxilliped is drawn forward and down and the antennule passes between the setal brushes.

The grooming of the feeding mechanism is the most complex cleaning behavior. This behavior can be seen in actively feeding animals as well as in nonfeeding megalopae which have been placed in a dense suspension of algal cells. The long feeding setae of the third maxilliped (Figure 5A) are combed clean by the short dense setal brushes located on the two terminal segments of the second maxilliped (Figure 5B). The short setal brush is inserted at the bases of the feeding setae and rolled downward and inward toward the mouth following the long curve of the setae being combed. When the entire length of the filtering setae has been combed free of particles, the brushes of the second maxilliped are then combed out by the first maxilliped and inner mouth parts. Undesirable particles are rejected into the exhalent current and swept out by the flicking of the exopodite on maxilliped II.

The diet and feeding behavior of the megalopa are drastically different from those of the zoeal stages. Predatory habits are replaced immediately by filter-feeding habits when the molt is completed and the megalopal skeleton has become hard enough to permit motion. The megalopae of all four species rejected newly hatched *Artemia* nauplii as food and would feed only on suspended phytoplankton. Several monoalgal and diatom cultures (*Tetraselmis* sp., *Isochrysis* sp., and several unidentified diatoms) and nutrient culture medium inoculated with raw seawater were tried singly and in various combinations as food. In each case the megalopae fed on the suspended organisms in the cultures in the same manner.

The behavioral change from prey capture to suspension feeding is reflected in changes in mandibular and maxilliped form. The natatory second maxilliped and the functionless third maxilliped of the zoea become highly specialized parts of a complex feeding mechanism in the megalopa. The feeding pattern most commonly observed in the laboratory is composed of the following sequence of events.

The endopodite of the highly setose third maxilliped is extended and a "setal net" spread open. After a moment, the maxilliped is lowered and swung in toward the body, where the setae are

combed out by the process described earlier. The terminal brushes of the second maxilliped are subsequently cleaned by the first maxilliped and so on, until the particles initially trapped in the extended net finally reach the mandibles. Somewhere in this chain of events particles are sorted, and undesirable portions of the catch are ejected in the exhalant respiratory stream. Particles which are acceptable as food are ground up between the curved bladeliike edges of the mandibles (Figure 5D) and passed into the mouth with the aid of the mandibular palp.

Most often the maxillipeds work rapidly and alternately, with one extended while the other is being combed. However, when a strong current of water runs steadily from a single direction, megalopae often extend only one maxilliped and leave it out for a time. When the setae have gathered a sufficient quantity of particles, the maxilliped is withdrawn and cleaned. At this point, the free maxilliped may be extended, or the same maxilliped may be extended again after it has been cleaned. The appearance of variable feeding behavior under varying conditions led to the question of the importance of water movement to megalopal feeding.

A 36-hr experiment was conducted in an effort to determine the effect of turbulence on feeding. Eighteen healthy megalopae, nine each of *Pachycheles rudis* and *P. pubescens*, were used. Each of the megalopae and a stone for it to cling to were placed in a flask of filtered seawater and starved for the first 13 hr of the experiment. A mixed algal suspension of *Isocrysis* sp. and *Tetraselmis* sp., previously found to be acceptable to megalopae as food, was supplied to the same 18 larvae for the remaining 24 hr of the experiment. At intervals of 2 hr, throughout the 36-hr period, the number of animals showing feeding motions was recorded before and after stirring the water. The flasks with the megalopae were held at 12°C in a water bath. The experiment was started at 0100 on one day and continued to 1300 the next before food was introduced, so that observations were made for both starved and fed conditions at night and during daylight hours.

Figure 6 summarizes the observations on the number of animals feeding under each condition, before and after stirring the water. When no food was present and the water was still, virtually no feeding activity was observed.

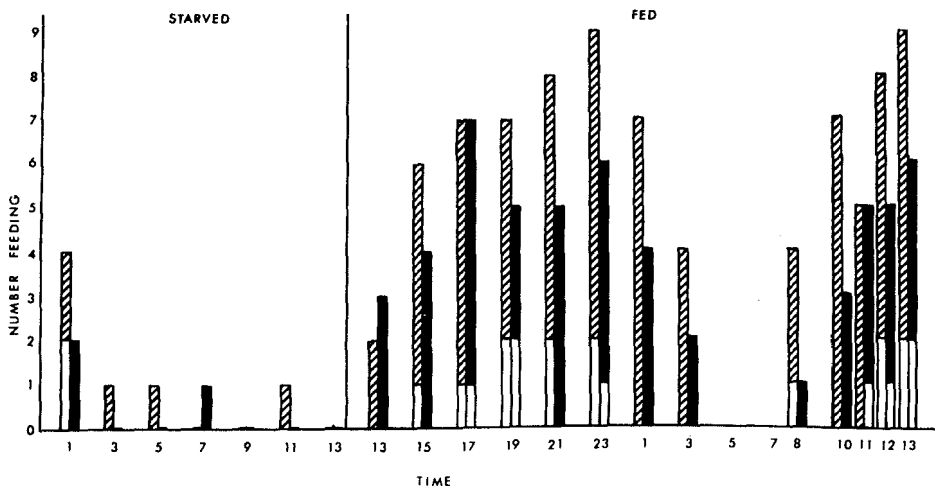


FIGURE 6.—Histogram showing effect of water movement on feeding behavior in megalopae of *Pachycheles pubescens* and *P. rudis* under starved and fed conditions. Left bars, *P. pubescens*; lower, open part of bar, number of larvae feeding in still water; cross-hatched part of bar, number feeding after agitation of water. Right bars, *P. rudis*; open part of bar, number of larvae feeding in still water; solid part of bar, number feeding after agitation of water.

Turbulence caused a few animals to undergo feeding behavior even when food was absent. When food was present, there usually was some feeding activity in still water. When the water was agitated and food was present, feeding behavior greatly increased. In the presence of food, water movement, although not essential for the initiation of feeding, favors both the initiation and maintenance of feeding activity, probably because turbulence suspends the particles so that they can readily be filtered. The results suggest that there is a periodicity to feeding activity, but the experiment was too brief to clearly demonstrate this. No effect of daylight or darkness on feeding behavior was observed.

Locomotory behavior gradually changed throughout the megalopa stage. The numbers of megalopae available for observation at different ages are indicated in Table 2, which gives the age of the megalopae in days since the molt from the second zoëal stage. Adultlike locomotory behavior slowly evolved as the megalopa grew older. Newly metamorphosed megalopae were strongly planktonic, swimming almost continuously by means of the pleopods, with the walking legs and chelipeds extended forward. After spending some time (1-4 days) as truly planktonic animals, the megalopae became more quiescent and began to demonstrate clinging tendencies. Small stones, to which the settling megalopae could cling, were introduced into the culture flasks at this point.

The megalopae which are just beginning to settle show no signs of recognizing a substrate suitable for settling. If a larva encounters a rock while swimming forward, it continues swimming motions, pushing against the obstacle with the extended chelipeds but not moving for-

ward. However, if megalopae of this age are artificially introduced to a rough surface, walking legs first, by means of turbulence or by direct placement, they cling readily and will usually remain on that surface unless disturbed. As the megalopae increase in age, they appear to develop the ability to recognize a suitable substratum. Larvae of 2 weeks or older were seen to collide head on with a rock, stop swimming, and put the walking legs down. They then turned around and backed onto the piece of gravel.

In the laboratory, recently settled megalopae can be induced to leave an apparently suitable substrate if the water is stirred vigorously or if the larvae are touched. In addition, when a settling megalopa encounters a stone that is already occupied, it will remain there only if it can do so without contacting the other occupant. If the stone is too small to allow this, the settling megalopa will usually cling only momentarily and then resume swimming. In a few cases, however, the settling megalopa forced the original occupant to leave its stone and begin swimming.

A specialized form of behavior was observed in advanced megalopae of *Petrolisthes eriomerus*. After locating a stone, a swimming megalopa will settle on it and then elevate and lower both chelipeds simultaneously several times. If the megalopa then moves a short distance over the rock, the cheliped elevation sequence is often repeated. This activity was observed only in individuals that had just arrived on a substrate and was exhibited whether or not another megalopa was present on the rock.

An advanced behavior was observed in still older animals (30-33 days in *Pachycheles pubescens*). These megalopae could not be induced to use their pleopods when swimming, even when they were so disturbed that they would finally leave their rocks. Instead, a disturbed animal would bob up and down in the water, clumsily clapping the abdomen to the thorax. The presence of the four pairs of fully developed pleopods prevented effective swimming by this action. Adult porcelain crabs, whose pleopods are reduced in size and often in number, swim only by clapping the abdomen to the thorax. The

TABLE 2.—Number and age in days of megalopae available for behavioral observations.

Species	Age in days							
	5	10	15	20	30	40	45	50
<i>Pachycheles pubescens</i>	34	32	27	23	18	9	4	
<i>Pachycheles rudis</i>	21	19	17	17	11	4	3	1
<i>Petrolisthes eriomerus</i>	14	8	7	1				
<i>Petrolisthes cinctipes</i>	1							
Total	70	59	51	41	29	13	7	1

megalopae therefore show in this situation the behavior of adults.

Further development along the lines already established by the megalopa is shown by the succeeding juvenile stages. Respiratory currents become much stronger and well defined and are now aided by the tandem motion of the two sets of maxillipedal exopodites. Feeding movements are the same as those described here for the megalopa and for the adult by Nicol (1932). In adults, food preferences vary according to species. Knudsen (1964) reports that pelagic diatoms are the preferred food for *Petrolisthes eriomerus* but does not state the preferences of *Pachycheles rudis*. In the laboratory, adults of all species readily fed in unfiltered seawater, but only *Petrolisthes* females accept and ingest fragments of mantle and adductor muscle of *Mytilus*. The preferred adult locomotion is pereipodal walking, but swimming by abdominal clapping is also used, especially in *Petrolisthes*.

## DISCUSSION

### PREZOEAE

Adults of both *Petrolisthes* species live where the larvae are released into turbulence caused by waves and currents. These conditions favor the presence of a short-lived, rounded initial larva with few body projections, that would more readily escape entangling algae and debris in the intertidal zone.

The habitats of the two *Pachycheles* species (Haig, 1960) more strongly favor a compact, rounded, initially spineless larval form. In many cases adults become so large that they are unable to pass out through the openings of the burrows or crevices they inhabit. Larvae are released within the adult burrow and must escape this confinement to survive. The prezoal cuticle covering the telson in *P. pubescens* larvae is well modified for swimming. This was described by Gurney (1942) for other decapods and by Lebour (1943), Wear (1965), and Greenwood (1965) for other porcellanids.

These observations suggest that in the four species considered here, and probably in the family as a whole, the prezoa is a short-lived natural stage and is not a laboratory artifact

as has often been suggested. Its existence as a transport stage is ecologically consistent with the natural habitat of the adults. Similar arguments have been put forth by Gore (1968) in defense of the interpretation of the prezoa as a natural stage in the commensal porcellanid *Polyonyx gibbesi*, which releases larvae from inside the tube of the polychaete *Chaetopterus*. Another observation supporting this argument is that, under laboratory conditions, true zoeae, with their long spines, respond very unfavorably to collisions, spine breakage, and collection of detrital material on the spines, all of which would be likely to occur in nature if full zoeae emerged from the eggs and were released into the adult environment. Photopositive swimming behavior would also prove useful to prezoae released in burrows and crevices, and the larvae studied showed a photopositive response. This response was, however, weak under laboratory conditions.

### ZOEAE

With the passage of the larva through the prezoal molt, the first true zoea emerges and becomes an actively swimming planktonic carnivore. Despite the good swimming ability and well-developed eyes of the zoea, no evidence of true hunting behavior was found. Instead, the larvae appear to rely entirely on chance encounters with prey, with capture behavior initiated by direct contact or by vibrations stimulating the maxillipedal endopodites and setae and the ventral surface of the abdomen. Similar stimulation of other parts of the body elicits an escape response by the zoea. Survival of these zoea in the plankton is probably highly dependent upon suitable prey density. The method of prey capture used by these larvae, involving the use of the telson to scoop up the prey and hold it from below, appears to be a feeding method used by zoea throughout the Decapoda. Knudsen (1960), for example, describes this method of feeding in xanthid Brachyura.

### MEGALOPA

Many of the adult behavioral features described by Nicol (1932) appear in the megalopa



when the structures used first resemble those of the adult, but before the adult mode of life is adopted. Attempted swimming by abdominal clapping is an example of the development of an adult behavior pattern before the adult structure is completed. Megalopae of these four species clean the body with the fifth legs in the adult manner, a feature also observed for other porcellanid megalopae by Lebour (1943) and Knight (1966).

At the molt to megalopa there is an abrupt change from carnivorous to a filter-feeding, herbivorous habit. As Nicol (1932) first noted, adult Porcellanidae are specialized for filter feeding on suspended material. Adults of the two *Petrolisthes* species studied here will also sometimes accept pieces of mussel as food, but the two *Pachycheles* species will not. The observations on the megalopae of these species and those of Lebour on *Porcellana* species, indicate that the acquisition of morphological and behavioral adaptations to filter feeding in the Porcellanidae involve both the adult and megalopa stages. Although many other anomuran adults feed on particulate material by some mode of filter feeding, it is not known whether this also involves the late larval stages. No information could be found in the literature on feeding by their post-zoeal stages. In hermit crabs, which are more generalized detrital-feeding Anomura, both zoea and postzoeal stages can be reared on *Artemia* nauplii, as found for example by Provenzano (1962).

Since population and species success depends upon the megalopae locating a suitable adult habitat, settling behavior is a critical part of later larval development. Settling behavior of barnacles, bryozoa, and some other forms has been studied; however, similar settling behavior in decapod Crustacea has not been studied, with the exception of shell selection by the glaucothoe stage of hermit crabs (Reese, 1962; Hazlett, 1971) and the coconut crab *Birgus latro* (Reese, 1968). For the megalopae studied here, the behavioral sequence of the true planktonic period, the settling and swimming period, and the period of final settlement seems to be highly specialized for substrate selection. Possession of this behavioral mechanism would permit, under na-

tural conditions of turbulent water movement, older megalopae to select or reject substrates encountered by random contact. No information is available on how settled megalopae reach the final adult habitat after initial settlement, but postsettling megalopae and very young juveniles have been found clinging to the base of surf grass and under stones with adults.

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