LARVAL GROWTH

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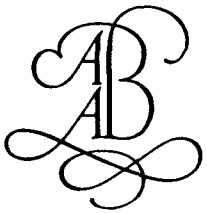
PATTERNS IN EARLY POSTLARVAL DEVELOPMENT OF DECAPODS

ABSTRACT

Early postlarval stages may differ from larval and adult phases of the life cycle in such characteristics as body size, morphology, molting frequency, growth rate, nutrient requirements, behavior, and habitat. Primarily by way of recent studies, information on these qualities in early postlarvae has begun to accrue, information which has not been previously summarized.

The change in form (metamorphosis) that occurs between larval and postlarval life is pronounced in some decapod groups but subtle in others. However, in almost all the Decapoda, some ontogenetic changes in locomotion, feeding, and habitat coincide with metamorphosis and early postlarval growth. The postmetamorphic (first postlarval) stage, herein termed the decapodid, is often a particularly modified transitional stage; terms such as glaucothöe, puerulus, and megalopa have been applied to it. The postlarval stages that follow the decapodid successively approach more closely the adult form. Morphogenesis of skeletal and other superficial features is particularly apparent at each molt, but histogenesis and organogenesis in early postlarvae is appreciable within intermolt periods. Except for the development of primary and secondary sexual organs, postmetamorphic change in internal anatomy is most pronounced in the first several postlarval instars, with the degree of anatomical reorganization and development decreasing in each of the later juvenile molts. Anatomical change during metamorphosis and the next few postlarval stages usually consists of degeneration of some anatomical features, redirection of some existent structures, and addition of some new structures. Examples of such processes can be seen in the early postlarval development of neurosecretory organs, musculature, muscle innervation, digestive organs, and even pigmentation patterns.

Comparative studies of early postlarvae may be of use in further resolving relationships between decapod taxa. To date, such relationships have been based primarily upon morphological comparisons of larvae or adults.

1 INTRODUCTION

In many instances, literature that compares growth phases of decapod crustaceans makes reference to characteristics of the larval life phase versus characteristics of the adult life phase. By inference, the non-specialist may be led to believe that decapod life histories are indeed partitioned cleanly between these two phases of growth and development, and

that structure and function within either of these phases may be subject to relatively little variation. Chapters 1 and 2 of this volume have provided a basis for rejection of such assumptions as they would apply to decapod larvae; those papers demonstrated that some pronounced ontogenetic changes in structure and function occur during the larval phase of growth for a number of decapod taxa. The present chapter documents that the early post-larval stages in the life history of decapod Crustacea may also be unique and varied in many respects; in particular, it documents the degree to which early postlarval stages may differ in structure and function from the adults with which they are frequently grouped.

Lately, a body of information on early postlarval stages has begun to accrue and there has been no previous attempt to review and evaluate specific information on the early post-larval life of decapods. From the late 1960's to the present, a number of papers added appreciably to knowledge of structure and function of these life stages; but, even at this writing, coverage of some subjects is rather limited. The reader may note, for instance, that coverage of certain topics is based upon a rather small set of examples which may not represent broadly all major subtaxa of the Decapoda. Often the coverage is biased toward species of commercial importance or those that are most readily available for laboratory studies. While it may be premature to draw broadly applicable conclusions on the basis of such limited examples, we incorporate them as the existing baseline data to which future findings may be compared. However, even for common commercially important species there remain conspicuous gaps in such fundamental subject areas as early postlarval mor-phology, behavior, and ecology. Authors who have contributed recently to knowledge of early postlarvae in these species have also pointed out subject areas that have not received adequate attention (e.g. Anderson & Linder 1971, Johnson 1975, Seaman & Aska 1974, Serfling & Ford 1975). Fundamental information, such as the number of early postlarval instars and diagnostic characters of these instars, has long remained unavailable for com-mon and well-studied species (Hogarth 1975). For example, morphological characters of postlarvae 10-25 mm in length were just recently described for several well-known *Penaeus* species (Mair 1981).

The paucity of such data perhaps reflects the difficulty of obtaining early postlarvae of known instar and parentage for most decapod species. Whereas larvae can be collected sometimes in large series from the plankton or reared from eggs of identifiable parental females in the laboratory, and whereas the larger adults are often readily collected and easily identified in large series, postlarval series are usually more difficult to obtain. If early postlarvae are collected in the field, they may be difficult to stage and to identify; if reared in the laboratory, they usually must be carried first through an entire larval series and, typically, a metamorphic molt during which there is often high mortality. Thus one can readily appreciate why much of the presently available information on early postlarval stages is biased toward either well-known species for which postlarval series have been thoroughly described or species that are the subject of aquacultural interests and therefore maintained routinely in culture.

In at least some well-studied examples, enough is known of the early postlarval life his-tory to suggest that it be recognized as a delimited phase in the overall life history. For example, a 20-30 day period following metamorphosis to the postlarva in *Penaeus* has been identified as a phase of considerable morphological change (Perez Perez & Ros 1975, Wickins 1976); the 'early period of juvenile development' from the puerulus stage to approximately 1.5 years of age has been termed 'another distinct phase in the life history' of a palinurid lobster (Phillips et al. 1977). However, we will also point out cases in which this early

period of development is not clearly demarcated, but rather exists as the earliest compo-
nent of a continuum toward the development of the mature adult body form. Regardless
of definition, the early postlarvae of decapods tend to share a number of biological charac-
teristics. In addition to their smaller body size, they may differ from later stages and ulti-
mately the adults in molting frequency, growth rates, metabolic demands, habitat require-
ments, behavior, morphology, susceptibility to predation, nutrient requirements, and a
host of other characteristics. These unique characteristics may furthermore confer differ-
ences in distributions and ecological roles from those of adult and larval stages. Even
characters that may clarify phylogenetic relationships can, in early postlarvae, differ from
those of both larvae and adults.

In the following treatment of decapod postlarval development, we specifically direct
our coverage to early postlarval stages. In general terms, we emphasize characteristics and
developmental trends of stages that 1) immediately follow the larval life stages, and 2) differ
appreciably in structure and function from mature or nearly mature adults. Thus, we do
not, except in making comparisons, address later specializations in secondary sex charac-
ters and development to sexual maturity. We also do not analyze the rates of change in
overall body size (absolute growth) and allometry (relative growth) of adult structures,
because both of these subjects recently have been covered in an excellent review by Hart-
noll (1982). Rather, we attempt to compile the presently diffuse and confusing literature
so as to gain insight into the diversity and ontogeny of structure and function during early
postlarval stages. We intend that this review serve as a current reference on the biology of
early decapod postlarvae and hope that it will stimulate further study of this relatively
neglected phase in decapod crustacean growth and development.

2 MORPHOLOGICAL TRANSITIONS IN POSTLARVAE

2.1 *Standardization of postlarval nomenclature*

Most crustaceans hatch at an early stage of development when they have relatively few
body segments and appendages. They are anamorphic in their postembryonic growth,
with the successive addition of new metameres and limbs in their progressive development
through a series of larval stages (Snodgrass 1956, Costlow 1968). There is, however, some
degree of metamorphosis superimposed on these anamorphic stages of development. Pas-
sano (1961) defined crustacean metamorphosis liberally as a change in form at a particular
point in the animal's life. If behavioral and physiological changes are included in this defi-
nition, metamorphosis may include 1) the gradual and successive changes leading up to
the transition, 2) the influence of environmental factors on these changes, 3) the internal
reorganization accompanying the more obvious morphological modifications, and 4) the
changes in mechanisms controlling and regulating this period of development (Costlow
1968). In the decapod infraorders Anomura, Palinura and Brachyura, where the larval
stages are typically pelagic and the adults benthic, change occurs in a well-defined meta-
morphosis. The larvae in such groups differ more strikingly from adults than in other
decapod infraorders, where all stages lead a similar life. However, in almost all the Decapoda,
some ontogenetic changes in locomotion, feeding, and habitat coincide with early post-
larval growth.

Early carcinologists were reluctant to accept the concept of complete metamorphosis

in the Decapoda (for a historical review see Gurney 1942), and the credit for the definite proof of crustacean metamorphosis belongs to Thompson (1828, 1829, 1831). In a number of cases developmental stages were given special names of generic significance, for example *Zoea* (Bosc 1802) and *Megalopa* (Leach 1814), both based on brachyuran forms. Gurney (1942) proposed a system for classifying decapod developmental phases based in part upon the method of locomotion; he recognized the nauplius and protozoea with antennal propulsion, zoea with thoracic propulsion, and post-larval form with abdominal propulsion. Williamson (1957, 1969, 1982a) modified this by including the penaeid protozoea with zoea and changing Gurney's 'post-larva' into megalopa. Gurney's use of the term post-larva is somewhat ambiguous. Any stage following the larval phase (zoea) can be termed a postlarva, including juveniles and adults. However, the first postzoeal stage in the Decapoda is often significantly different from subsequent juvenile stages and is sometimes considered a larval form (Williamson 1969).

Many names beside megalopa have been used by various workers to describe the post-zoeal stages of decapods, including puerulus, nisto, and pseudibacus for Palinuroidea; glaucothöe for Anomura; eryoneicus for Eryonoidea; mastigopus for Sergestoidea; parva for Caridea; and grimothea for Galatheidae. Except for Williamson's usage and that of a few other workers, the term megalopa has almost always signified the first postzoeal phase of a brachyuran crab. Williamson (1982a) was somewhat ambiguous with his usage of the term megalopa. While he states that the megalopa stage is confined to the Eumalacostraca, he uses the same term for Hoplocarida in his Table 1. Kaestner (1970) proposed the term decapodid for the first postzoeal phase of decapods having the full complement of metameres and appendages and the general characteristics of the order; we follow his usage in this paper and restrict megalopa to an equivalent name for a brachyuran decapodid. Throughout this paper, our usage of terms for larval and postlarval decapods will be defined as follows: nauplius = a larval stage with first three pairs of cephalic appendages setose and functional, other appendages absent or rudimentary (after Williamson 1969); zoea = a larval stage with setose natatory exopodites on some or all of the thoracic appendages and with the pleopods absent or rudimentary (after Williamson 1969); postlarva = any form that occurs after the zoeal stages inclusive of all developmental stages to the adult; decapodid = the first postlarval stage, the stage that occurs immediately after the molt from the last larval stage and that has setose natatory pleopods on some or all of the first five abdominal somites. Terms such as glaucothöe, puerulus, and megalopa will be considered synonyms for the decapodid stage of Anomura, Palinura, and Brachyura respectively. Since the decapodid is usually a transitional stage between the zoeal period of development and juvenile phase of growth, it is subject to considerable variation and special modification in some decapods, especially in those having abbreviated development (see Rabalais & Gore, this volume).

2.2 *Early postlarvae of the Dendrobranchiata*

2.2.1 *Penaeoidean decapodid and juvenile*
The Penaeoidea pass through a series of swimming nauplii, protozoeal stages, and a varying number of zoeal stages, before going through a final molt into the decapodid. At this molt, the mouthparts and maxillipeds assume their basic adult form, the fourth to eighth thoracic limbs become pereopods with enlarged endopodites and reduced exopodites and the first five pairs of abdominal appendages become functional pleopods. The swimming

function thus shifts during this molt from the thorax to the abdomen. The postzoeal change in structures is very gradual, and the morphological distinction between the decapodid and subsequent postlarvae is usually not very pronounced (Fig.1,i). Therefore, some workers have recognized more than one decapodid stage in penaeids (Heegaard 1953, Dobkin 1961, Kurata & Pusadee 1974). By our designation, the first postlarva is equivalent to a decapodid and subsequent postlarval stages may be considered early juveniles.

In *Penaeus duorarum*, Dobkin (1961) found that no conspicuous metamorphosis occurs from the last zoea to the first postlarva (decapodid), although the pereopods lose their exopodites and the exopodites of the maxillipeds are either lost or modified. The pleopods do not become biramous until seven or eight molts later. Kurata & Pusadee (1974) succeeded in rearing only the first two postlarval stages in *Metapenaeus burkenroadi;* the gills and epipods of the adult develop in these stages and a temporary degeneration of some of the mouthparts occurs. Later juvenile stages follow these early postlarval stages with further addition of appendages which fit a benthic existence. From laboratory-reared larvae of *Xiphopenaeus kroyeri*, Kurata (1970) described a decapodid that was very similar to the last zoea. That decapodid differs from the last zoea by having hepatic spines, flattened exopodites on the first maxilliped, and long setae on the pleopods. It differs from the subsequent postlarval stages in structure of mouthparts and rigidity of the legs.

2.2.2 *Sergestoidean decapodid and juvenile*
Sergestids pass through a nauplius and several zoeal stages before the molt to the decapodid. At this stage, sometimes termed the mastigopus, the spines of the carapace and abdomen are lost or reduced and the telson approaches the adult form. The fourth and fifth pereopods are lost or reduced to small stumps; these redevelop during subsequent postlarval molts. Relative sizes of adjacent gills also change during postlarval development (Burkenroad 1945, 1981).

Hansen (1922) and Gurney & Lebour (1940) described mastigopus stages for *Sergestes* from planktonic material. Other workers described the complete larval development of sergestids in the laboratory, as in studies by Rao (1968) and Kurata (1970) on *Acetes*, Omori (1971) on *Sergia*, and Knight & Omori (1982) on *Sergestes*. Kurata (1970) described six postlarval stages in *Acetes americanus carolinae*, in which development of the posterior pairs of pleopods and the pleopodal endopodites is gradual; the fourth pereopod redevelops after the sixth postlarval molt (Fig.1,ii). Omori (1971) reported on five postlarval stages in *Sergia lucens;* in the fifth postlarva, the first and second maxillipeds first become chewing and holding appendages. Knight & Omori (1982) described the first two postlarval stages in *Sergestes similis* and observed a progressive reduction of spines on the carapace, abdomen and telson over the course of development from the last zoeal stage to the second postlarva. After the second postlarva, the mouthparts approach the adult form, the pleopods are setose and functional and the endopodites become more setose at each molt.

2.3 *Early postlarvae of the Pleocyemata*

2.3.1 *Caridean decapodid and juvenile*
In the Caridea, the eggs are carried by the females on their pleopods and the larvae hatch as zoeae. Larval development within the Caridea involves a highly variable number of zoeal stages (Knowlton 1974). Carideans are like penaeids and sergestids in that postzoeal development is gradual and morphological distinctions between the decapodid and the
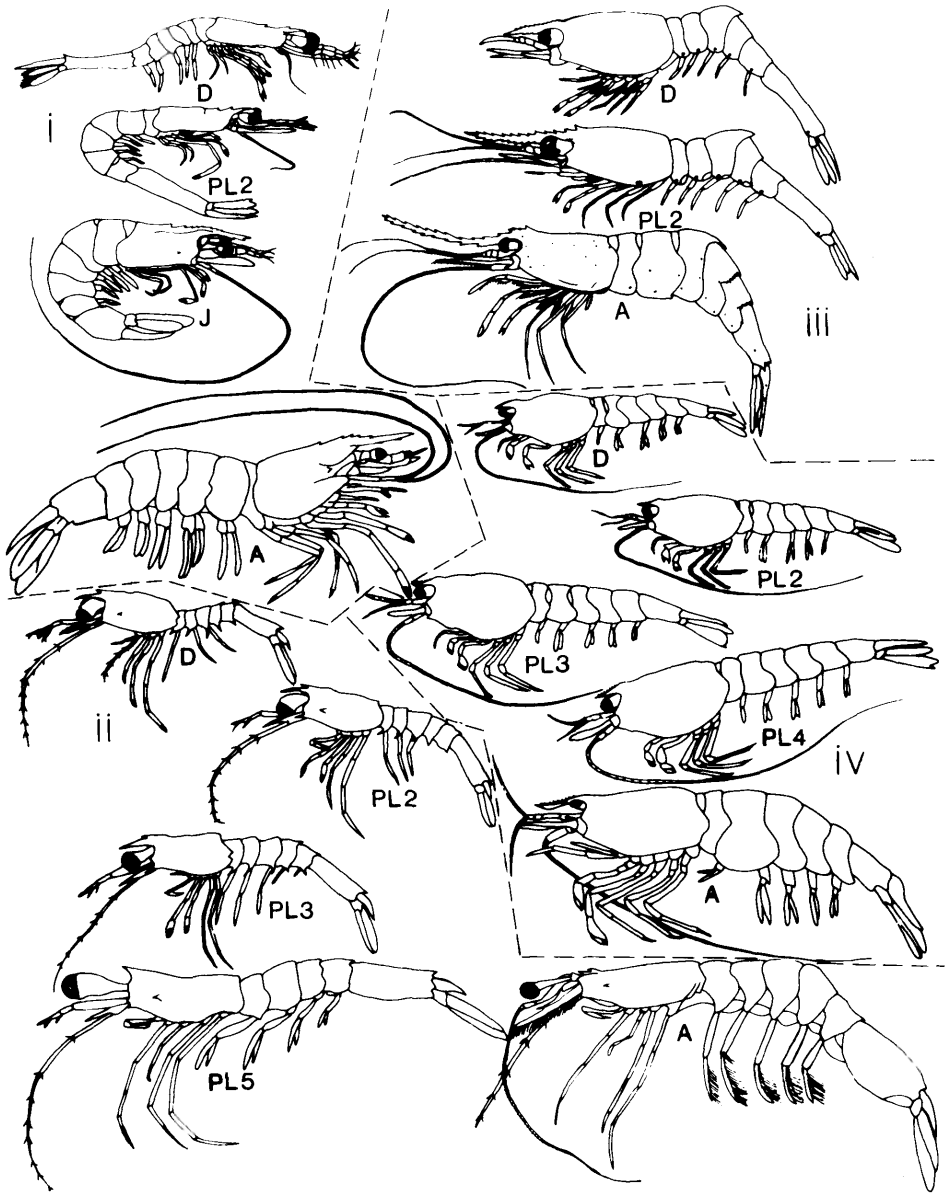
Figure 1. Early postlarval stages of representative decapods. Illustrations adapted from literature, see text. Abbreviations as follows: D – decapodid; PL – postlarva; J – juvenile; A – adult. (i) Family Penaeidae: *Penaeus setiferus*; (ii) Family Sergestidae: *Acetes americanus carolinae*; (iii) Family Oplophoridae: *Systellaspis debilis*; (iv) Family Atyidae: *Caridina denticulata*.

following postlarval stages are not pronounced. At present, there are over 20 recognized families of carideans; in six of these the larval stages are completely unknown. There are many families for which the early zoeal phases are known, but relatively few studies have addressed early postlarval stages. Our short summary of postzoeal caridean development will therefore be restricted to the few comprehensive studies on selected families.

In the Oplophoridae, the decapodid and subsequent postlarval stages have been described for a few species from planktonic material, as in studies by Kemp (1910) on *Systellaspis debilis,* Coutière (1906), Gurney & Lebour (1941) on *Acanthephyra purpurea* and Aizawa (1974) on *A.quadrispinosa.* Kemp (1910) examined a wide size range of *Systellaspis debilis* postlarvae taken from planktonic material collected off the Irish coast and documented changes of the mandibular palp, photophores, rostrum, eyes and branchiae with body size (Fig.1,iii). In *Acanthephyra quadrispinosa,* Aizawa (1974) considered a specimen of 12.9 mm body length to be the decapodid; its short rostrum bears four dorsal and a ventral tooth. In the next few instars eyestalks narrow, the rostrum is elongated, and thoracic exopodites are shortened. A specimen of about 30 mm total length (about half the adult size) resembles an adult, and has a long rostrum with 8-10 dorsal and 5-7 ventral teeth.

Most genera in the family Atyidae live as adults only in freshwater and have a suppressed larval development, but a few species have a complete series of larval stages. The first group is exemplified by *Caridina denticulata denticulata, C.brevirostris, C.denticulata ishigakiensis* and *C.singhalensis,* while examples of atyids with a normal series of larval stages are *Paratya compressa* and *C.pseudogracilirostris* (see Yokoya 1931, and Pillai 1975). In *C.denticulata denticulata* there are few differences between the decapodid, which is the second instar after hatching, and the adult shrimp (Mizue & Iwamoto 1961); the main differences are found in the spination of the rostrum and the shape of the telson and uropods (Fig.1,iv). An interesting aspect of this shrimp's life history is that it does not start to feed until the fourth postlarval stage, subsisting upon yolk reserves up to this point. Shokita (1973a, 1976) found that *C.brevirostris* and *C.denticulata ishigakiensis,* which are both restricted to freshwater, also reach the decapodid after the first post-hatch molt. These shrimps are near the adult form in the decapodid stage but do not start to feed until the next postlarval stage. Secondary sexual structures are developed by the fourth postlarva. *C.singhalensis* hatches in a form that is morphologically postlarval except for its spatulate larval telson lacking uropods and its rudimentary mouthparts (Benzie & de Silva 1983). Development of *Caridina mccullochi* is intermediate between the two basic atyid patterns (Benzie 1982).

‘ The family Pasiphaeidae is generally regarded as primitive because of the exopodites on all pereopods of adults (Fig.2, v). Most genera within the family have large eggs and abbreviated development, although *Leptochela* is an exception. The decapodid in *Leptochela* sp. has pleural armature and carapace spines that are absent in the adult, and exopods of its posterior pereopods not developed (Kurata 1965). Kurata felt that his adult specimens resembled *L.aculeocaudata,* but his figures are closer to *L.sydniensis,* with which the former species has been frequently confused.

In the family Palaemonidae, the molt to the decapodid is often not morphologically conspicuous, but it and subsequent postlarval stages generally take on a more bottom-living habit and progressively attain the characters of the adult shrimp, such as loss of pereopodal exopods. The work of Shokita (1973b, 1977, 1978) on the freshwater species *Macrobrachium shokitai* and *M.asperulum* shows these species exhibit 'abbreviated devel-
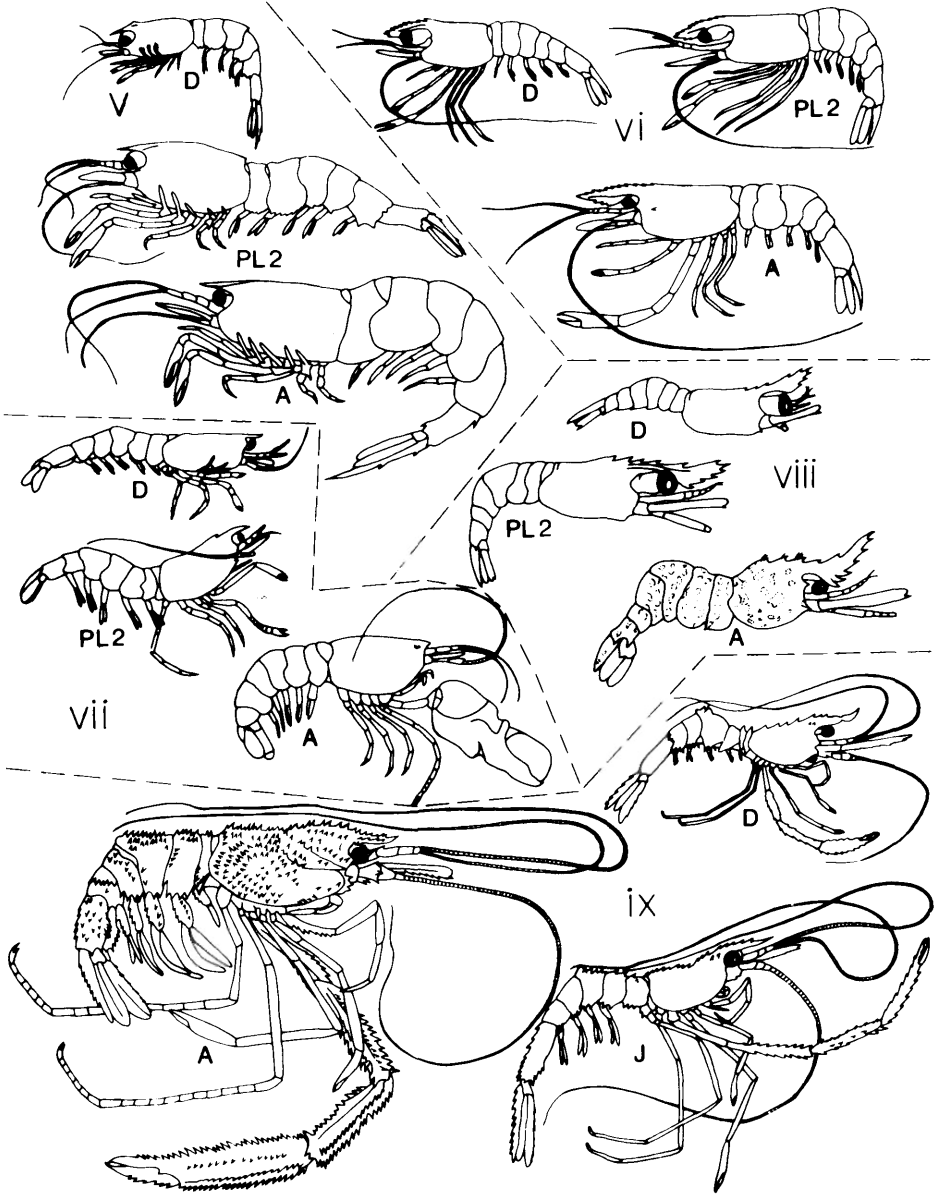
Figure 2. Early postlarval stages of representative decapods. Illustrations adapted from literature, see text. Abbreviations as follows: D – decapodid; PL – postlarva; J – juvenile; A – adult. (v) Family Pasiphaeidae: *Leptochela sydniensis*; (vi) Family Palaemonidae: *Macrobrachium asperulum*; (vii) Family Alpheidae: *Alpheus heterochaelis*; (viii) Family Hippolytidae: *Saron marmoratus*; (ix) Family Stenopodidae: *Stenopus hispidus*.

opment' (Fig.2,vi). By the second postlarval stage, both species are essentially adult in all respects but secondary sexual characters. An even more 'abbreviated' development is seen in *Macrobrachium hendersodayanum* and *Desmocaris trispinosa* that hatch essentially as decapodids (e.g., Jalihal & Sankolli 1975, Powell 1979). At the other extreme, the freshwater shrimp *Palaemon paucidens* has seven zoeal stages before the molt to the decapodid (Yokoya 1931). A characteristic change of the appendages to resemble the adult form and a considerable reduction in body size occur at the molt to decapodid.

In the estuarine and marine palaemonids, larval development is usually not 'abbreviated'. Gurney (1924) found that the postlarval stages of *Palaemon longirostris* (as *Leander longirostris*) and *Palaemon elegans* (as *L. squilla*) had the adult form in general structure in the decapodid, but with slight differences in the rostrum, antennae, and pereopods. Fincham (1977, 1979a, 1979b) reared these two species and *Palaemonetes varians* and found some variability among individuals, but his results were generally consistent with those that Gurney found using planktonic material. The brackish water shrimp *Leandrites celebensis* passes through seven zoeal stages before becoming a decapodid (Pillai 1974). Another estuarine palaemonid, *Palaemon semmelinkii* goes through 12 larval stages before the adult-like decapodid is reached (Jagardisha & Sankolli 1977).

A large subfamily of palaemonids, the Pontoniinae, is mostly marine, and many of its members are commensal with other invertebrates. Although some larval stages of a few pontoniine shrimp are known, none have to date been reared from eggs to postlarval stages. The majority of species within the subfamily have small eggs, so one would expect a normal sequence of larval stages. A possible exception to this generalization could be *Pontonia minuta* which has very large eggs and hatches as an advanced zoea (Bruce 1972).

The variety of developmental patterns within the snapping shrimp family Alpheidae makes it difficult to propose a generalized developmental scheme that would apply to early postlarvae. Species of *Alpheus* and *Athanas* with a normal sequence of five or more zoeal stages have not yet been reared in the laboratory to the decapodid stage. Therefore, what is known of alpheid postlarvae is based on planktonic material and a few species with abbreviated or direct development. Lebour (1932b) found that the last larval stages of *Alpheus glaber* (as *Alpheus ruber*) and *A. macrocheles* molted to decapodids which were not quite like the adults, although the carapace and chelate legs approached those of the adult. The molt to the second postlarva allows these species to be recognized by the adult characters. Development is direct in *Synalpheus brooksi* (Dobkin 1965), where the hatchling is a decapodid with the carapace covering the eyes as in the adult and with the adult form of appendages. Knowlton (1973) found that the first postlarval form of *Alpheus heterochaelis* assumes the adult form, though some larval characters, such as pereopodal exopods, are retained for another molt (Fig.2,vii). Characteristic asymmetry of the chelipeds occurs much later in postlarval development.

The family Bresiliidae contains the genera *Bresilia, Lucaya,* and *Discias.* Gurney & Lebour (1941) noted that the first postlarva of *Discias atlanticus* was very much like the adult. Bruce (1975) found two small males and a late larva in a sponge off Kenya. Interestingly, the late zoea had adult appendages and the second pleopod had an appendix masculina.

The monogeneric family Rhynchocinetidae exhibits larval characteristics of oplophorids, but certain adult characteristics of palaemonids. Gurney & Lebour (1941) found that *Rhynchocinetes rigens* from plankton material reached the tenth larval stage, with successive molts producing no great change except for the growth of the antennal flagellum. In

the decapodid some variation exists in the reduction of the pereopod exopods, and some of the mouthparts are not fully functional.

The larvae of Hippolytidae show such diversity in form that Gurney (1937b), from his studies on the larvae of *Lysmata, Tozeuma, Saron,* and *Latreutes,* suggested the family be divided into several subfamilies. Lebour (1931, 1932a) argued that, based on their larvae, the genera *Caridion* and *Spirontocaris* are closer to the Pandalidae and should be removed from the Hippolytidae. She later (1936, 1940) retracted that opinion after looking at the postlarvae of other *Spirontocaris* spp. and comparing them to species of *Thor.* Lebour (1931) found that after *Caridion gordoni* and *C. steveni* molted to decapodids in the laboratory, the postlarvae retained exopodites on the first four pairs of pereopods. In the second postlarva, both species lost exopodites on the pereopods, the second leg became fully developed, and there was a full adult complement of branchiae. Lebour (1932a, 1936) described the postlarvae of *Spirontocaris cranchii* reared from planktonic larvae. The decapodid was like the adult, with a sharp bend in the abdomen and a long antennal flagellum. The characteristic bifurcate rostrum develops in the fourth postlarva. Lebour (1936) also described the larval and early postlarval stages of *Spirontocaris occulta* and found its decapodid slightly more advanced than that of *S. cranchii.* She noted increases in carpal segments of the second pereopods for both species during early postlarval development. Pike & Williamson (1961) found some postlarval pleopodal characters developing in the last two zoeal stages of *Spirontocaris spinus.* In the decapodid, the pleopods become functional and exopodites are still present on the thoracic appendages. In the second postlarva the exopodites disappear and a supraorbital spine appears on the carapace. In the decapodid of *Thor floridanus* (see Lebour 1940, Broad 1957), there are remnants of exopodites on the first two pereopods and the carpus of the second pereopod is divided into three segments. The second postlarva has the outer antennular flagellum thick at the base, the exopodites have disappeared, and the second pereopod has four carpal segments. Sankolli & Kewalramani (1962) described the larval and early postlarval stages of *Saron marmoratus* reared in the laboratory (Fig.2,viii). Their protozoea is equivalent to the first zoea, while their first postlarva is actually the fifth and last zoeal stage (personal observation of cultured larvae from Hawaii, JWG). Their 'second' postlarva (= decapodid) has functional pleopods and a rudimentary exopodite on the third maxilliped; the exopodites on the pereopods are no longer present. The next postlarval stage has a rostrum characteristic of the adult. Kurata (1968a,b) reared the larval stages and several postlarval stages of *Eualus gracilirostris* and *Heptacarpus futilirostris.* In *Eualus gracilirostris,* the decapodid's rostrum appears as a short spine but it grows longer and develops teeth in successive molts. In *Heptacarpus futilirostris,* the decapodid has remnants of exopodites on the third maxilliped and on the first to fourth pereopods, but lacks epipods. By the second postlarva the exopods are mere rudiments and epipods are present on the third maxilliped and first three pereopods.

The family Pandalidae also shows a great variety of larval types and includes species with abbreviated and extended larval development. In the majority of other decapods, the development of functional pleopods, development of the pereopods, and changes in shape and body proportions provide a clear distinction between zoeae and postlarvae. In the Pandalidae, however, there is not always an abrupt metamorphosis in such characters (Haynes 1976, Rothlisberg 1980).

Kurata (1955) described the larval stages of *Pandalus kessleri* and found it difficult to designate a given stage as postlarval. He considered the fifth stage to be the first postlarva,

since it was essentially adult in character except for secondary sexual structures. The first pleopodal appendix interna appears at the sixth postlarva, and the second pleopods acquire appendices masculina at the eighth postlarva. Kurata proposed different appendages attain the postlarval condition at different stages. By his scheme, the postlarval phase begins in Stage IV (= last zoeal stage) in the right carpus of the second pereopod, stage V (= decapodid) in the left carpus of the second pereopod, stage VII (= third postlarva) in the rostrum, sixth somite, telson, antennal scale and third pleopod.

The larvae of *Heterocarpus ensifer* are considered to be among the largest decapod larvae known, with some reaching over 50 mm total length (Gurney & Lebour 1941, Gopala Menon 1972). This is a deep-sea species in which the change from larval to post-larval life involves no great change of habit and none of habitat (Gurney 1942). Therefore, stimulus for metamorphosis might be the onset of developments for sexual maturity. The development of carinae on the larval carapace is restricted to the genus *Heterocarpus,* and can be regarded as an adult character which develops precociously (Gopala Menon 1972). The larvae and early postlarvae of *Pandalus hypsinotus, P.goniurus* and *P.borealis* were described by Haynes (1976, 1978, 1979) from shrimp reared in the laboratory. He considered the molt after zoeal stage VI to be the decapodid for *P.hypsinotus* because at this stage the pleopods were functional and the appendix interna was distinct on all pleopods except the first pair. The second and third postlarvae differ only slightly from the decapodid with the major changes occurring in the gills. In *P.goniurus,* Haynes' stage VI is the decapodid, with a two-segmented mandibular palp, exopodites reduced on the third maxillipeds and pereopods, functional pleopods, and the telson showing the shape and spination of the adult. The second postlarva attains a typical adult rostrum and a three-segmented mandibular palp while it loses the exopodites. *Pandalus borealis* shows a similar developmental pattern to *P.goniurus* but the decapodid shows no trace of the mandibular palp, which appears in the next postlarval stage. Rothlisberg (1980) believed that *Pandalus jordani* did not have a decapodid stage. His first juvenile, though, is equivalent to a decapodid because the mandibular palp appears for the first time, the telson and rostrum have the adult shape, and the exopodites are present as rudiments and are no longer used for locomotion. By the next molt, the mandibular palp is three-segmented and the exopodites are lost. Because of heterochrony in the development of appendages in larval *Pandalus prensor,* Mikulich & Ivanov (1983) felt characters representative of zoeae, decapodids and even juveniles can be seen in a single instar. Natatory setae on the pleopods first appear in the fourth instar, which can be considered a decapodid.

2.3.2 *Stenopodidean decapodid and juvenile*
The Stenopodidea consists of only the Stenopodidae, which has a range of developmental patterns from abbreviated to extended larval development. Stenopodids are unique among the Decapoda in having four pairs of natatory limbs on hatching. Only *Microprosthema* sp. has been reared completely in the laboratory, so descriptions of larvae and postlarvae for other species are based on material from the plankton.

Cano (1892) described and figured the decapodid of *Stenopus spinosus.* He found that the adult characters were to a large extent present in the first postlarva, but the abdomen was still flexed at right angles at the third abdominal somite. Kemp (1910) described the newly hatched young of *Spongicoloides koehleri,* which is a deep water species commensal in sponges. This species shows direct development, and the hatchlings probably represent the decapodid which closely resembles the adult except for its pereopodal

exopods and sessile uropods. Gurney & Lebour (1941) described numerous stenopodid larvae and postlarvae of *Stenopus hispidus* (Fig.2,ix). They obtained a decapodid from a larva measuring 21 mm total length, yet they collected larvae of the same species as large as 31 mm in the plankton. The first postlarva, measuring 10 mm in length, had the adult form and coloration. The adult body and appendage spination is gradually acquired with successive molts and remnants of pereopodal exopods are lost. Gurney & Lebour (1941) also described postlarvae of two species they labelled 'Stenopid B' and 'Stenopid C'. From their description of the decapodid of 'Stenopid B' and their notation that it was the most common stenopodid larva encountered from the Bermuda plankton, this larval series probably represents *Microprosthema semilaeve.* Larvae and postlarvae reported as *M.semilaeve,* represent *M.validum* or a new species from the Indian Ocean. Developments beyond the decapodid include increases in rostral and body spination and setal numbers.

2.3.3 *Nephropidean decapodid and juvenile*
The known nephropid lobsters have only three larval stages after emerging from a prezoea of short duration. After molting into the fourth stage (= decapodid), they resemble the adult, yet continue to swim for several days before settling into a benthic habitat. The first pleopod is still absent in the first postlarva.

In the Norway lobster, *Nephrops norvegicus,* the first postlarval stage assumes the general characters of the adult (Farmer 1975) but uropodal exopods remain undivided as in the last larval stage. There are no first pleopods, but throughout the juvenile phase there is a gradual development of these and other external sexual characters. The juvenile stages are bottom dwellers, and construct burrows similar to those of the adults. Uchida & Dotsu (1973) described the larvae and early postlarvae of the tropical lobster *Metanephrops thomsoni.* At decapodid metamorphosis swimming function shifts from the thorax to the abdomen, and by the second postlarva the exopods are completely absent from the pereopods. Compared to *Nephrops norvegicus,* the larval development of *M.thomsoni* is of short duration, nine days as opposed to 2-3 weeks.

The American lobster, *Homarus americanus* (Fig.3,xi) and the European lobster, *H.gammarus,* have been the subject of research since the latter half of the last century. The fourth stage of development for both species is equivalent to the decapodid, because it loses the exopodites on the pereopods and the pleopods are used exclusively for swimming. After molting into the fourth stage, the first postlarva swims for a few days before settling to the bottom. The morphology of the juvenile stages, including the early postlarvae, is similar to that of the adult except for size. Carlsberg et al. (1978) have successfully hybridized these two species. The larvae of the hybrid bear the coloration and morphology of *H.gammarus,* while the early postlarvae are more like that of *H.americanus.* The early postlarvae of *H.americanus* have the claws very similar in morphology, musculature and innervation, but internal changes started in these stages will produce the differentiation into the cutter and crusher claws. The internal reorganization required to produce these specialized claws will be treated later in this chapter.

2.3.4 *Astacoidean decapodid and juvenile*
Freshwater crayfish of the families Astacidae and Cambaridae have a decapodid hatching with all of the appendages of the adult except the first pleopods and uropods. Gurney (1942) felt that, since the uropods do not appear until the second molt, the first three stages correspond to the first three stages of decapods with normal free larvae. The young
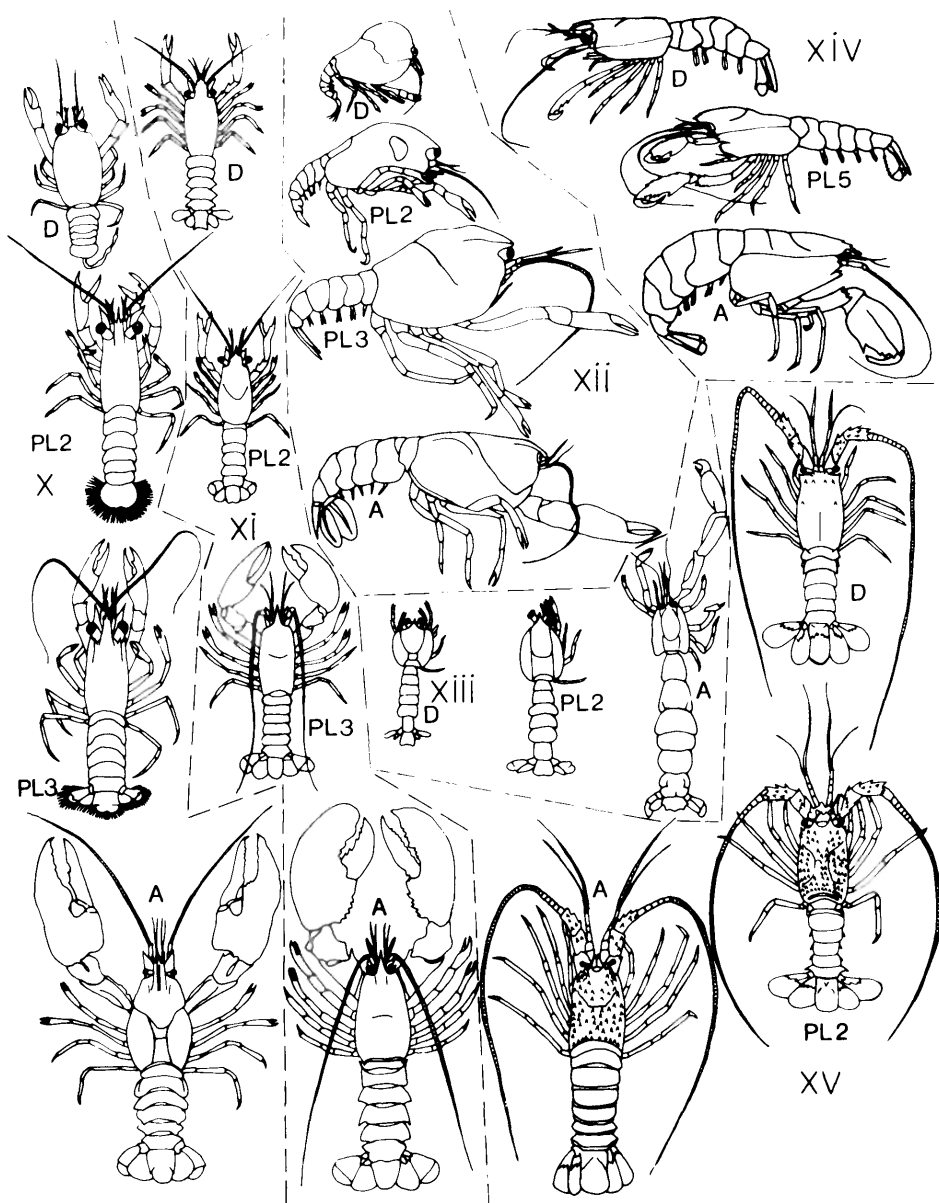
Figure 3. Early postlarval stages of representative decapods. Illustrations adapted from literature, see text. Abbreviations as follows: D – decapodid; PL – postlarva; J – juvenile; A – adult. (x) Family Astacidae: *Pacifastacus leniusculus*; (xi) Family Nephropidae: *Homarus americanus*; (xii) Family Parastacidae: *Engaeus cisternarius*; (xiii) Family Callianassidae: *Callianassa kewalramanii*; (xiv) Family Laomediidae: *Naushonia crangonoides*; (xv) Family Palinuridae: *Panulirus polyphagus*.

when first hatched remain attached for a short time to pleopods of the parent by a fila-
ment. This filament is the molted embryonic cuticle which attaches the telson to the
empty egg case. When this breaks the hatchlings cling to the pleopods of the adult by
means of the specially hooked first chelipeds. At the first molt, the chelipeds loose their
hooks and the body becomes more adult-like in shape.

Andrews (1907) conducted a thorough study of the early stages of *Pacifastacus lenius-
culus* (as *Astacus leniusculus*) and *Orconectes limosus* (as *Cambarus affinis*) (Fig.3,x). The
first three stages of these species are similar, but *P.leniusculus* is slightly more advanced in
development. In the second stage, *Pacifastacus leniusculus* will take short excursions from
the parental female, but *Orconectes limosus* remains firmly clinging onto the adult pleo-
pods. In the third stage, the uropods are free and the gills fully developed. Juveniles spend
a short time attached to the parental female and soon take up a free existence. The main
feature of the fourth stage is the development of the first pleopods.

2.3.5 *Parastacoidean decapodid and juvenile*
The family Parastacidae is also a freshwater group with an abbreviated developmental
sequence in which the hatchlings (= decapodid) remain attached to the adult pleopods for
the first three stages. The hatchlings differ from those of astacoid crayfish in that the
fourth and fifth legs are modified with recurved hooks for attachment, instead of these
hooks being on the first pereopods (Fig.3,xii).

The hatchlings of *Engaeus cisternarius* are soft and inactive, with reduced appendages
and sessile eyes (Suter 1977). After 2-3 days, they break the filaments that attached their
telsons to the adult's pleopods and grasp the pleopodal setae with small recurved hooks on
their fourth and fifth pereopods. However, they remain globular with a large cephalothorax
filled with yolk. The second stage, which remains attached to the pleopods by the pereopo-
dal hooks, has a longer rostrum and stalked eyes. The third stage attaches to the adult
pleopods by the chelipeds. They start to make short excursions from the parental female
and eventually become fully independent, with all appendages completely developed.
Suter also compared the similar development of *Engaeus fossor* to that of *E.cisternarius*.
The diagnostic characters of *E.fossor* were all well developed in the third stage.

2.3.6 *Thalassinidean decapodid and juvenile*
The thalassinideans are all burrowing forms, and larvae are known for all families. The
Thalassinidea do not seem to form a natural group on the basis of developmental stages.
The larvae of the Callianassidae and Axiidae are similar and somewhat resemble those of
the Nephropsidea. Larvae of the Upogebiidae and Laomediidae resemble more closely those
of the Anomura (Gurney 1938, 1942).

Forbes (1973) reported on the unusual abbreviated development of *Callianassa kraussi,*
but did not discuss changes in morphology. Sankolli & Shenoy (1975) described two post-
larval stages for *Callianassa (Callichirus) kewalramanii* (Fig.3,xiii). The decapodid resembles
the adult in general body structure, but has pereopodal exopod rudiments and some larval
characters in the telson and maxillipeds. The second postlarval stage approaches the adult
in details of appendages, gills, and carapace.

In *Upogebia savignyi,* a sponge commensal, the hatchlings are basically in the adult
form (Gurney 1937a). Shenoy (1967) described the first two postlarval stages of *Upogebia
kempi.* The decapodid has functional pleopods, reduced fifth pereopods, and exopodites
on the first three pereopods. In the second postlarva, the exopodites of the pereopods are

lost and a dense fringe of long setae develops on the maxillipeds and first two pairs of pereopods. Goy & Provenzano (1978, 1979) described the larval and early postlarval stages of the laomediid mud shrimp *Naushonia crangonoides* (Fig.3,xiv). The decapodid resembles the adult, but the mouthparts and appendages are not so setose as in the adult. In the first few molts after the decapodid, the morphology does not change conspicuously and there is a gradual development of adult characteristics. In the sixth postlarva, the cervical groove and linea thalassinica are well marked and the full complement of gills is reached.

2.3.7 *Palinuran decapodid and juvenile*
Nothing is known of the larvae or postlarvae in the family Glypheidae or the early larval stages of the family Polychelidae. The superfamily Palinuroidea is comprised of the families Palinuridae, Scyllaridae and Synaxidae and has a characteristic zoeal stage called a phyllosoma (see Phillips & Sastry 1980) and a characteristic decapodid variously called puerulus, nisto or pseudibacus. The last phyllosoma stage, which is usually about 35 mm in length, metamorphoses into the decapodid. Gurney (1942) stated that this metamorphosis is the most profound transformation at a single molt known among Decapoda. There is little pigment and an absence of calcium in the exoskeleton of the early puerulus which causes it to appear almost colorless and transparent. It has a generally smooth, rather than spinose exoskeleton, and relatively large pleopods bearing long setae.

The genus *Eryoneicus* has been established as the postlarval stage of the deep-water lobster family Polychelidae. Gurney (1942) felt that apart from the possession of exopodites on the first two legs these postlarvae have no special larval features. The great dilation of the carapace and thorax and the spination of the abdominal somites probably increase flotation by increasing surface area. The majority of workers feel these stages must settle to the bottom to metamorphose into the young adult. Bernard (1953) thought the adults of *Willemoesia* metamorphosed in the water column, because he found 'soft' small pelagic adult forms and 'hard' adult benthic forms.

Deshmukh (1966) described the puerulus and second postlarva of *Panulirus polyphagus* (Fig.3,xv). The decapodid is transparent, has very long and terminally spatulate antennae, and has the ability to swim upside down by using its large and heavily setose pleopods. After a short time, the decapodid (puerulus) sinks to the bottom, starts to acquire pigmentation, and molts within 3-4 days to a form much more like the adult (Silberbauer 1971).

Compared to the palinurid lobsters, the slipper lobsters or Scyllaridae have not been as thoroughly studied. Dotsu et al. (1966) gave a detailed description of the metamorphosis of *Ibacus ciliatus* and *I.novemdentatus*. They called the decapodid stages 'reptant larvae' and gave a brief description of this stage and young juvenile lobsters that they caught in traps. Lyons (1970) compared decapodids (pueruli) of *Scyllarides nodifer, S.aequinoctialis, Scyllarus depressus, S.americanus* and *S.chacei* (Fig.4,xvi). The transparent decapodids appear to be transitional stages that link planktonic phyllosomas with benthic juveniles and exhibit characters of both. A dramatic reduction in relative size of the pleopods at the molt from the decapodid to the second postlarva was noted in *Scyllarides nodifer, Scyllarus americanus, S.chacei* and *S.depressus*. Pleopods remain reduced in juveniles until after development of genital pores; they rapidly increase in size in successive molts and become fully developed by the time the lobsters reach maturity. More recently, Atkinson & Boustead (1982) described the complete larval development of *Ibacus alticrenatus* from New Zealand. The decapodid is nearly transparent and has vestigial exopodites on the
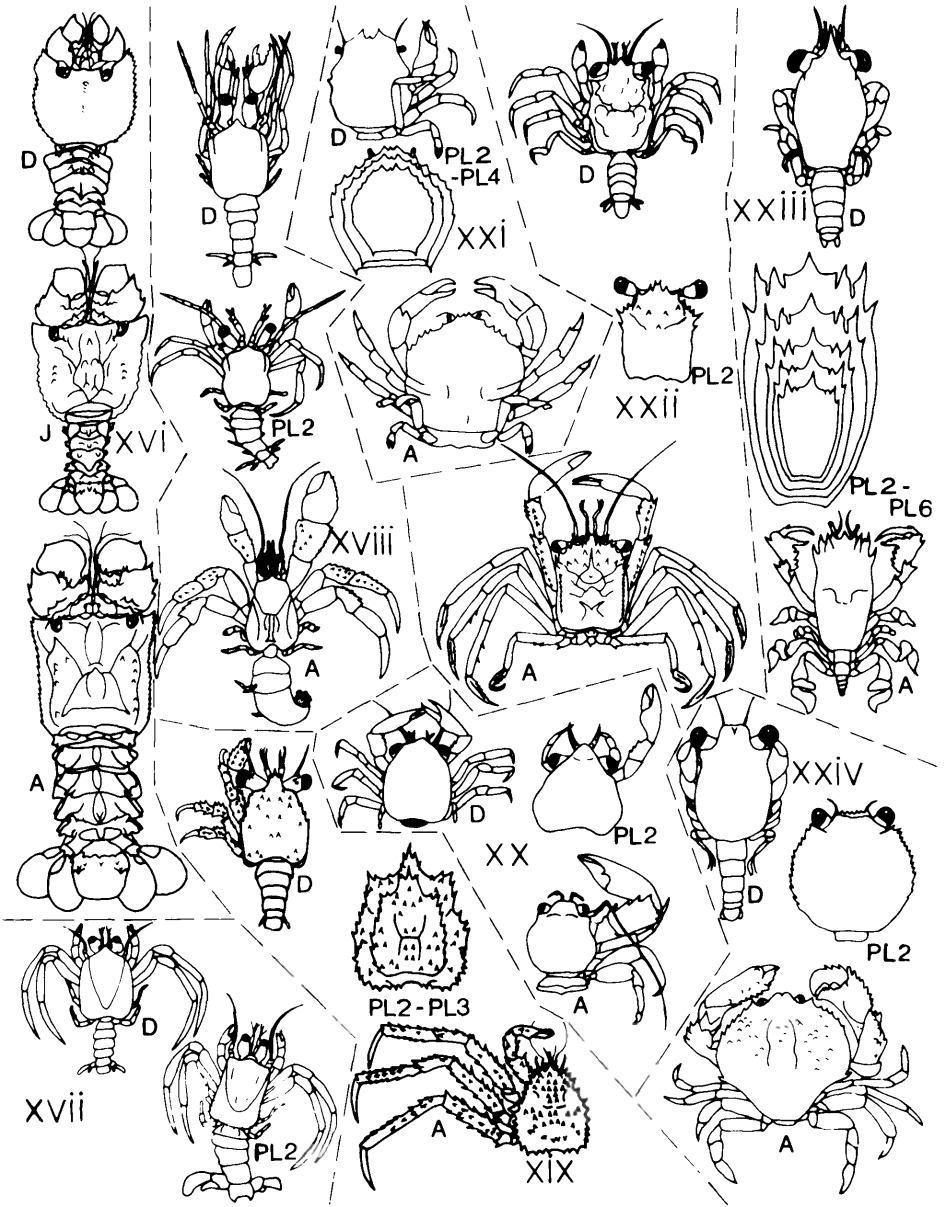
Figure 4. Early postlarval stages of representative decapods. Illustrations adapted from literature, see text. Abbreviations as follows: D – decapodid; PL – postlarva; J – juvenile; A – adult. (xvi) Family Scyllaridae: *Scyllarides nodifer*; (xvii) Family Diogenidae: *Diogenes planimanus*; (xviii) Family Paguridae: *Pagurus beringanus*; (xix) Family Lithodidae: *Paralithodes brevipes*; (xx) Family Porcellanidae: *Petrolisthes lamarckii*; (xxi) Family Dromiidae: *Cryptodromia octodentata*; (xxii) Family Homolidae: *Homola barbata*; (xxiii) Family Raninidae: *Raninoides benedicti*; (xxiv) Family Calappidae: *Cyclöes bairdii*.

pereopods. The pleopods are long, setose and apparently functional for swimming. In the second postlarval stage, the pleopods have become very reduced and the pereopodal exopodites are absent.

2.3.8 *Anomuran decapodid and juvenile*
The diversity of anomuran postlarval stages is even greater than that of some larval series, but very few studies have looked at early postlarval changes past the decapodid. In some families (Coenobitidae, Parapaguridae, Chirostylidae, Galatheidae, Albuneidae, Hippidae) only the early larval stages and decapodids are known, while no larvae have been described to date for the Lomisidae, Pomatochelidae, and Aeglidae.

The diogenid hermit crab, *Paguristes sericeus* was reared through its larval stages in the laboratory, and early postlarval stages were described by Provenzano & Rice (1966). They found that the first crab did not differ much from the decapodid (glaucothoe). Earlier works on the diogenid hermit crabs *Dardanus pectinatus* and *Clibanarius erythropus* by Forest (1954) and Dechancé (1958) showed these species lacked paired sexual appendages in early postlarval stages. In these hermit crabs, the first crab stage and sometimes other postlarvae have non-setose pleopods on the right side. By reduction at postlarval molts, these pleopods on the right side disappear rapidly. In the genus *Paguristes,* however, there are characteristic first pleopods in females and highly modified first and second pleopods in males. Provenzano & Rice (1966) found that the first crabs of *P.sericeus* have paired pleopods. At the second crab stage, the pleopods on the right side disappear along with the left pleopod of the second somite, leaving only single pleopods on the third to fifth somites. In males, this persists until the tenth crab stage when both pairs of sexual appendages appear anew. In the first crab of *Diogenes planimanus,* the uropods and abdomen are relatively symmetrical (Nayak 1981). At the next molt, the abdomen coils, the uropods are asymmetrical, and the pleopods of the right side are reduced to small buds on the second to fifth abdominal somites (Fig.4,xvii).

The metamorphoses of the pagurid hermit crabs *Pagurus annulipes* and *P.longicarpus* were described in the classic work of Thompson (1903), covering both external and internal changes in morphology and anatomy. The decapodid (glaucothöe) has a symmetrical abdomen, paired functional pleopods on the second to fifth abdominal somites, asymmetrical uropods, and thoracic appendages like those of the adult. The telson of the decapodid is rounded, there is an unsegmented mandibular palp, and a small ocular scale is present. The gills are present in the same number and arrangement as the adult. In the second postlarva the abdomen is coiled, the telson notched, the mandibular palp two-segmented, and the ocular scale much like the adult; there are no pleopods on the right side of the abdomen and the second pleopod on the left side is rudimentary. In the next few molts, the pleopod rudiment is lost, except in those crabs that will become females. In the young females, the rudiment of the second pleopod begins to grow to full size after about 30 days of development beyond the decapodid.

The larval development of the hermit crab *Pagurus samuelis* through early postlarval stages was described by Coffin (1960) and Kurata (1968d). There is a full set of functional pleopods on the second to fifth abdominal somites in the glaucothöe stage. The ocular scale is rudimentary, the uropods are slightly asymmetrical, and the mouthparts are not well developed, except for the third maxillipeds. At the molt to the first crab, the abdomen becomes coiled and the ocular scale is well developed. The pleopods are present on only the left side of the second to fifth abdominal somites (Fig.4,xviii).

All adult lithodid crabs are characterized by the lack of uropods and the presence of rudimentary fifth pereopods which are folded under the posterior margin of the carapace. Miller & Coffin (1961) described the developmental stages of *Hapalogaster mertensii.* In the decapodid, the pleopods are functional on the second through fifth abdominal somites, and the fifth pereopods are rudimentary and held beneath the carapace. In the first crab stage, the abdomen is flexed beneath the carapace and the fifth pereopods remain rudimentary. The pleopods are still present but are uniramous and lack setae.

Kurata (1956, 1960, 1964) described the development of *Paralithodes brevipes* (Fig.4, xix), *P.camtschatica, P.platypus* and *Dermaturus mandtii,* all from off Japan. The decapodids (glaucothöes) of these species usually have prominent and pointed rostrums, but no ocular scales. The uropods are symmetrical, and the right cheliped is usually larger than the left one. In the first crab stage, the mouthparts are more like the adult, the abdomen is folded underneath the cephalothorax, the uropods are absent, and the pleopods are rod-like remnants. Kurata (1960) also noticed that in *P.brevipes* and *P.camtschatica* there were occasionally intermediate zoeae in the last larval stage. The decapodids produced by molting of these intermediate zoeae were morphologically intermediate between normal decapodids and first crabs; furthermore, the first crabs produced by molting of the intermediate decapodids were intermediate in form between first and second crabs. In *Cryptolithodes typicus,* the carapace of the decapodid and first crab is triangular with a slightly undulate posterolateral margin, thus differing significantly from the adult (Hart 1965). Uropods do not occur in any stage, larval, postlarval or adult.

There have been numerous larval descriptions of the Porcellanidae (see Gore, Fig.5, this volume), in part because members of this group have only two zoeal stages; however, few descriptions have gone beyond the decapodid. In *Petrolisthes lamarckii,* Shenoy & Sankolli (1975) found that the decapodid resembles the adult in appearance; uropods are first developed at this stage and the statocyst is first implanted in the antennular base. In the second postlarval stage (= first crab), pleopods are reduced in size, the first maxilliped becomes more developed, and setae and spines of the carapace develop (Fig.4,xx).

2.3.9 *Brachyuran decapodid and juvenile*

In the Brachyura or true crabs, zoeal stages progress through a number of molts, at which time appendage setation becomes more complex, segmentation of the abdomen is completed, and abdominal appendages are added. The final zoeal molt gives rise to a decapodid (megalopa) in which the appendages are further modified, the thoracic appendages become functional, and the general morphology and behavior more closely resemble the juvenile crab. Almost all brachyuran megalopae have varying numbers of curved setae, 'brachyuran feelers', on the fifth pereopodal dactyls. The next molt produces the first crab stage. Passano (1961) called the megalopa a transitional form between the planktonic zoea and the bottom living adult, perhaps necessitated by the extreme morphological specialization of the crab form.

The megalopae known from dromiid species are rather homogeneous. They tend to retain the antennal exopod lost in decapodids of most higher crabs; also, the fifth pereopodal coxae are dorsal to the fourth, so the fifth pereopods are carried over the posterior carapace as in adults. Hale (1925) recorded abbreviated development in the two Australian dromiids *Paradromia lateralis* and *Cryptodromia octodentata* (Fig.4,xxi). In both these species, the hatchlings are in the decapodid stage and have well developed swimming pleopods, even though they do not leave the abdomen of the adult female.

There are very few descriptions of homoloid megalopae, but there is a great deal of variation in those described for the families Latreilliidae and Homolidae. Rice (1981b) summarized the main characters for decapodids of these two families. All known homoloid megalopae have well developed uropods with setose endopodites and exopodites. This feature confirms the primitive condition of homoloids shown by their zoeal stages, for setose endopodites of the uropods are found in decapodids of all anomuran groups and in some dromiid crabs. Rice (1964) described the last zoea, megalopa and first crab of *Homola barbata* (Fig.4,xxii). A wider carapace, bidentate rostrum, and gastric spines develop in the transition to first crab megalopae.

Knowledge of larval development of the primitive burrowing crabs within the family Raninidae is limited, so description of postlarval stages is also scanty. Raninid megalopae have the characteristic elongated sub-ovoid carapaces, simple triangular frontal regions, and deflected chelipeds so characteristic of the adults. Knight (1968) described development of *Raninoides benedicti* through the eighth crab stage (Fig.4,xxiii).

On the basis of a number of larval characters, Rice (1980) felt the families of the section Oxystomata are so distinct that members of this section are only united by shared convergent adaptations. There are at present no studies of early postlarval oxystomatous crabs which support this view. Lebour (1944) gave brief descriptions of the megalopae of *Calappa flammea* and *Cycloes bairdii* and provided rather crude illustrations of the first crab stages. The megalopae have somewhat narrowed carapaces that contain 12 or 14 large oil-like globules arranged symmetrically. At the molt to first crab, the carapace becomes more rounded and the chelae take on the shape characteristic of adults (Fig.4,xxiv).

As a result of their low number of larval stages many of the spider crabs have been described through the decapodid (megalopa) and some of the early crab stages. Lebour (1928), in her work on the larval stages of Brachyura around Plymouth, England, gave brief descriptions of the decapodids and early postlarvae for *Maja squinado* (as *Maia squinado*); *Eurynome aspera; Hyas coarctatus; Inachus dorsettensis; I.phalangium* (as *Stenorhynchus phalangium*); *I.leptochirus* (as *I.leptocheirus*); *Macropodia tenuirostris; M.rostrata* and *M.deflexa*. More recent studies of majid larval development have given more morphological details of megalopae and early crab stages. The complete larval development, megalopa and first crab stage of *Epialtus dilatatus* was described by Yang (1968). At molt to first crab, the entire surface of the crab becomes covered with capsules containing 'hooked hair' setae.

Kurata (1969) described larvae of 15 species of spider crabs belonging to 13 genera from Japanese waters. He also described the megalopae in the majority of these species, but he described the first crab stage only in *Achaeus tuberculatus, Pugettia quadridens* and *Acanthophrys longispinosus.* He also characterized the many spines, processes or protuberances that were on the megalopal carapaces. In *Hyas araneus* and *H.coarctatus* it is possible to separate the megalopa of each species by the differences in size of the rostral and dorsal carapace spines (Christiansen 1973).

Yang (1976) described the zoeae, megalopa and first crab stage of the arrow crab *Stenorhynchus seticornis.* This species lacks postlarval fusion of the basal antennal article with the carapace, as typically occurs in majids after metamorphosis. An interesting aspect of this study was that Yang obtained first zoeae from an ovigerous *Stenorhynchus* sp. from deep water. The adult was very similar in morphology to the shallow water *S.seticornis*, but the zoeae of the two *Stenorhynchus* species were readily distinguishable from one another. In contrast, the morphology of the adults of this genus is apparently similar enough to have caused considerable taxonomic confusion.
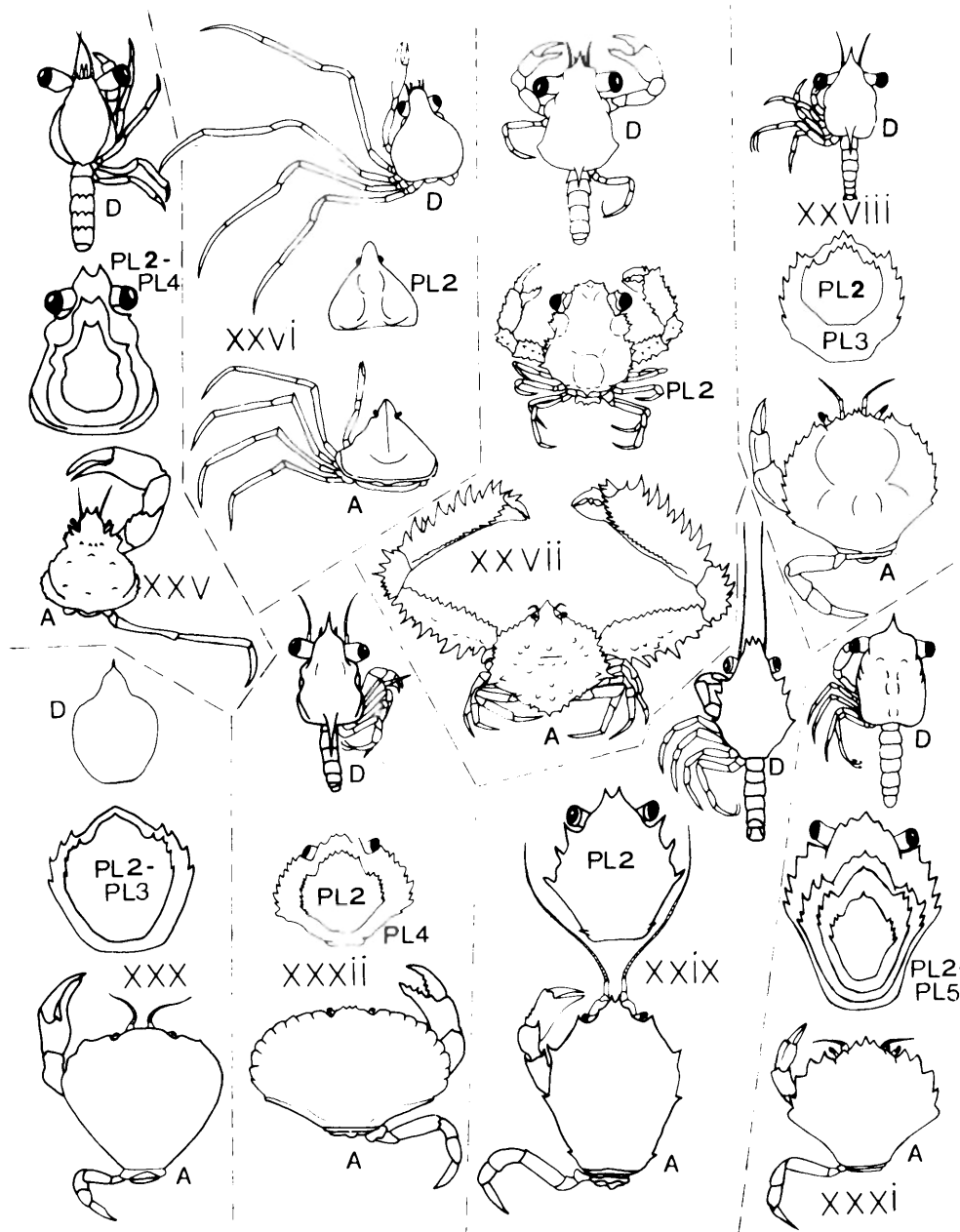
Figure 5. Early postlarval stages of representative decapods. Illustrations adapted from literature, see text. Abbreviations as follows: D — decapodid; PL — postlarva; J — juvenile; A — adult. (xxv) Family Majidae: *Inachus dorsettensis*; (xxvi) Family Hymenosomatidae: *Trigonoplax unquiformis*; (xxvii) Family Parthenopidae: *Parthenope serrata*; (xxviii) Family Atelecyclidae: *Atelecyclus septemdentatus*; (xxix) Family Corystidae: *Corystes cassivelaunus*; (xxx) Family Thiidae: *Thia scutellata*; (xxxi) Family Pirimelidae: *Pirimela denticulata*; (xxxii) Family Cancridae: *Cancer pagurus*.

The giant West Indian spider crab *Mithrax spinosissimus* has the typical two zoeal stages and megalopa of all majid crabs, but its development is abbreviated since it metamorphoses to the first crab stage in 5-6 days without feeding (Provenzano & Brownell 1977). The mouthparts of both the zoeae and megalopa are nonfunctional and the animal does not seem to take food until the juvenile stages. Ingle (1977) reared the scorpion spider crab, *Inachus dorsettensis* to ninth crab stage in the laboratory (Fig.5,xxv). Ingle concluded that at present the larval and early postlarval stages of *I.dorsettensis* cannot be distinguished from those of *I.phalangium* or *I.leptochirus,* but sexes could be distinguished by the third crab stage. Gill and epipodite development in the megalopal and early crab stages was examined in *Libinia erinacea* by Yang & McLaughlin (1979), who noted that five pairs of laminated gills in the megalopa are supplemented by four additional pairs developed anteriorly in subsequent crab stages. Rathbun (1914) presumed direct development in the majid *Paranaxia serpulifera* with young in the female brood chamber representing two stages by size class. Both had features of the adult, but were not termed megalopae since they did not leave the parent. Two more recent descriptions of majid larvae and postlarvae are those on *Pisa armata* by Ingle & Clark (1980) and *Macropodia rostrata* by Ingle (1982). Others will be discussed in section 4 of this chapter.

The section Oxyrhyncha, besides containing the Majidae, also contains the families Mimilambridae, Hymenosomatidae and Parthenopidae. Nothing is known of mimilambrid development. Numerous larvae of Hymenosomatidae have been described but the only mention of postlarval stages is in the work of Boschi et al. (1969) and Lucas (1971). For *Halicarcinus planatus* Boschi et al. (1969) described a megalopa that has rudimentary mouthparts, but no pleopods or uropods. Lucas (1971) however feels the hymenosomatids do not have a megalopal stage. We propose that his first juvenile crab is equivalent to a decapodid in the form of a benthic megalopa. This is supported by the recent work of Fukuda (1981) on the development of *Trigonoplax unguiformis* (Fig.5,xxvi). He recognized an atypical decapodid (megalopa) in this species, in which the abdomen shows an intermediate form between the last zoea and crab stages and the mouthparts have the characteristic form for a megalopa, even though natatory pleopods are absent. In one of the few developmental studies on parthenopid crabs, Yang (1971) described the megalopa and first crab of *Parthenope serrata* (Fig.5,xxvii). The first crab shows development in the carapace, antennular peduncle, and second maxillipedal podobranch.

The section Cancridea contains the families Atelecyclidae, Cancridae, Corystidae, Pirimelidae and Thiidae. There have been many larvae described for crabs of these families, but not much descriptive work is available on the postlarval stages. Lebour (1928) gave brief descriptions and illustrations of the early postlarval stages of the following cancridean crabs; *Pirimela denticulata, Cancer pagurus, Atelecyclus rotundatus (*as *A.septemdentatus)* (Fig.5,xxviii), *Corystes cassivelaunus* (Fig.5,xxix), and *Thia scutellata (*as *T.polita)* (Fig.5, xxx). In the family Pirimelidae, *Pirimela denticulata* has been reared through the fourth crab stage (Fig.5,xxxi) and *Sirpus zariqueyi* through the first crab stage (Bourdillon-Casanova 1960). In the family Atelecyclidae, the megalopa and the first crab of *Kraussia integra* have been described (Watabe 1971). In the Cancridae, the larval and postlarval development for *Cancer pagurus* has been described to the third crab stage (Ingle 1981) (Fig.5, xxxii). The most conspicuous early postlarval changes in the cancrids include an attenuated and/or subdivided rostrum, broad carapace, and carapace dentition.

The morphology of the larval stages among some representatives of the section Brachyrhyncha is so similar that the distinctions which can be made are rather inconspicuous.
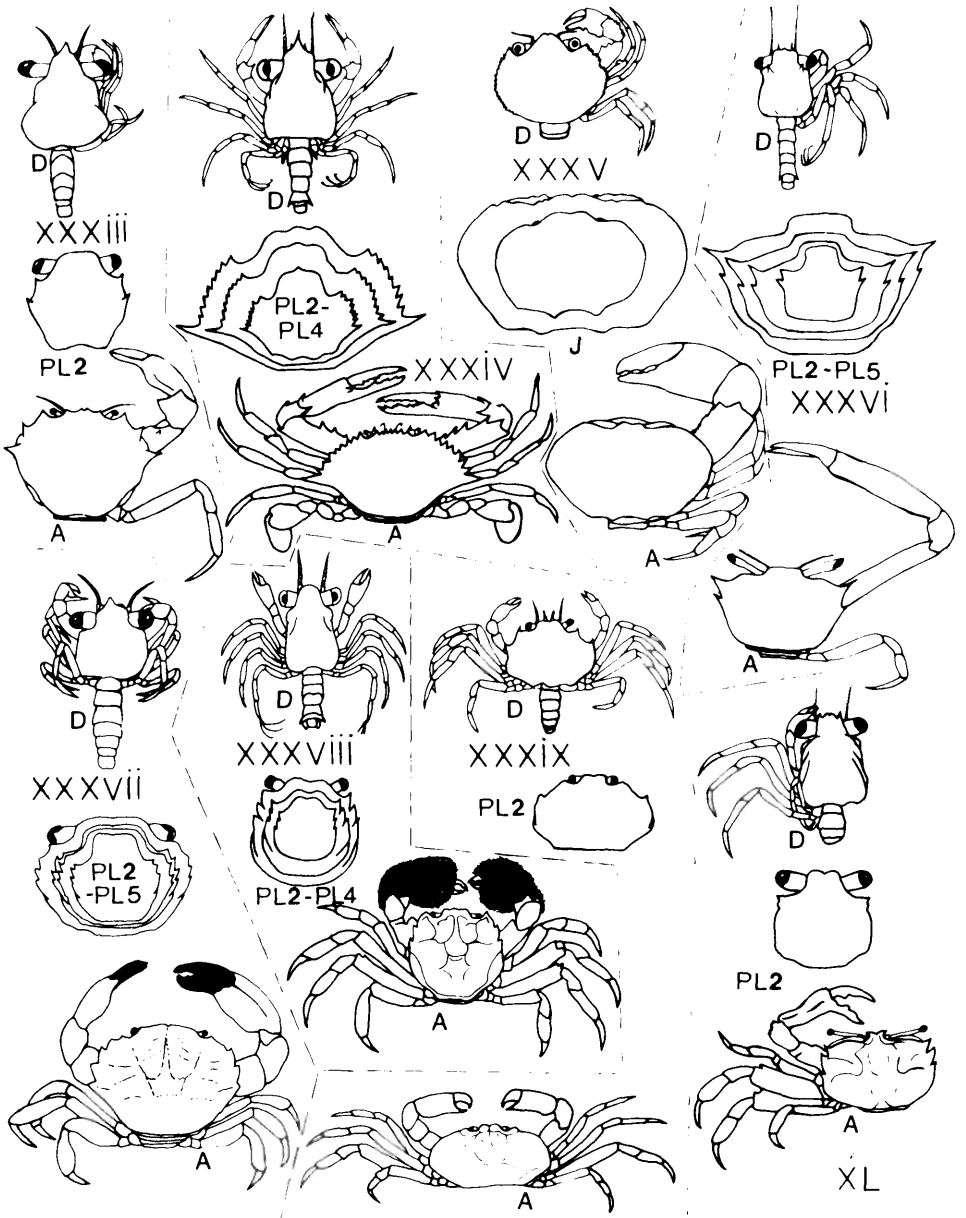
Figure 6. Early postlarval stages of representative decapods. Illustrations adapted from literature, see text. Abbreviations as follows: D – decapodid; PL – postlarva; J – juvenile; A – adult. (xxxiii) Family Geryonidae: *Geryon tridens*; (xxxiv) Family Portunidae: *Portunus pelagicus*; (xxxv) Family Bythograeidae: *Bythograea thermydron*; (xxxvi) Family Goneplacidae: *Goneplax rhomboides*; (xxxvii) Family Xanthidae: *Panopeus turgidus*; (xxxviii) Family Grapsidae: *Eriocheir japonica*; (xxxix) Family Pinnotheridae: *Pinnixa rathbuni*; (xl) Family Ocypodidae: *Macrophthalmus japonicus*.

However, Rice (1980, 1981a) recognized two groups of families based on zoeal characters: 1) a generally primitive group which broadly corresponds to the Cyclometopa or Guinot's (1978) Heterotremata, and 2) a more advanced group which corresponds to the Catometopa or Guinot's Thoracotremata. The decapodids (megalopae) of brachyrhynchan families are also similar, and it is sometimes only in the early crab stages that species begin to take on the characteristics of their respective families.

In the family Geryonidae, the megalopa of *Geryon tridens* has a longer than broad carapace with a ventrally deflected rostrum (Fig.6,xxxiii) (Ingle 1979). There develops in the first crab two strong teeth on each anterolateral margin and a median furrow on the frontal margin. Juveniles of *Geryon* spp. are not readily identifiable, but dactyl flattening (which distinguishes some species) is evident by the third crab stage in *G. tridens*.

In the Portunidae, megalopae and early crab stages have been briefly described for *Portunus pelagicus* (Fig.6,xxxiv) by Prasad & Tampi (1953), Chhapgar (1956), and Yatsuzuka & Sakai (1980), *Charybdis callianassa* by Chhapgar (1956), *Scylla serrata* by Ong (1966), *Charybdis acuta* by Kurata & Omi (1969), *Ovalipes punctatus* and *Thalamita sima* by Muraoka (1969), *Callinectes sapidus* by Kurata (1970), and *Carcinus maenas* and *C. estuarii* (as *C. mediterraneus*) by Rice & Ingle (1975). Aikawa (1937), in his description of the development of *Charybdis bimaculata,* illustrated two different megalopae that molted into two morphologically different first crabs. Since all his material was taken from the plankton, we suggest that he described two closely related portunids. Shen (1935) conducted a very thorough study on postlarval development through the first nine crab stages of *Carcinus maenas*. He examined morphological changes in the pleopods, abdomen and carapace, but also calculated molting frequency and rate of growth. Pleopods of the first pleomere develop only in the male and are present by the second crab stage. By the fifth crab stage sexes can be separated on the basis of abdomen shape.

The new superfamily Bythograeoidea and family Bythograeidae were described by Williams (1980) for a brachyuran crab from the vicinity of submarine thermal vents on the Galapagos Rift (Fig.6,xxxv). *Bythograea thermydron* has some characters of the families Portunidae and Xanthidae, with superficial resemblance to the family Potamidae. Williams also described megalopae and early juveniles of this new species. The megalopae differ from the adult in certain features, especially the well-developed eyes and fully formed normal orbits. Eyestalks degenerate at larger carapace sizes of postlarvae. Williams felt that failure of the interantennular septum to develop may be functionally related to loss of sight, along with heightened dependence on antennular chemoreception in a lightless environment. Both this and large size of the megalopa seem to be neotenic tendencies.

Among the few descriptions of developmental stages for the family Goneplacidae is Lebour's (1928) brief treatment of the megalopa, and several early crab stages of *Goneplax rhomboides* (Fig.6,xxxvi). Paired lateral teeth appear in the first crab stage, and thereafter, the carapace broadens anteriorly to take on the adult state. The adults of the crab *Asthenognathus atlanticus* have been placed with the Pinnotheridae by most workers, but not by Bocquet (1965), who placed them in the Goneplacidae on the basis of larval and postlarval stages since the megalopa has three sensory setae on the fifth pereopod dactyl (lacking in most pinnotherids and some ocypodid megalopae).

The family Xanthidae is one of the largest families in the Brachyura, and there are numerous studies on the larval development of these crabs (see Martin 1984). Most of these descriptions have included the decapodid, but few have gone beyond this stage of development. Postlarval development beyond the decapodid has been briefly described

in the following works: Lebour (1928) on *Xantho incisus* and *Pilumnus hirtellus;* Hart (1935) on *Lophopanopeus bellus bellus;* Chamberlain (1961) on *Neopanope sayi;* Kurata (1970) on *Menippe mercenaria, Rhithropanopeus harrisii, Neopanope sayi, Panopeus herbstii, Pilumnus sayi* and *Hexapanopeus angustifrons (*as *Panopeus occidentalis);* and Kurata et al. (1981) on *Eurytium limosum.* Two studies that provide details of postlarval development were on pilumnid crabs that undergo abbreviated development (Hale 1931, Wear 1967). In *Pilumnus vestitus,* the embryos emerge as soft, flaccid megalopae having a sedentary habit (Hale 1931). The first crab stage has pleopods modified for swimming, but these are lost at the molt to second crab. The adult pleopod buds appear in the third crab stage, and in succeeding stages the abdomen and pleopods progress rapidly toward the adult form. Wear (1967) found that *Pilumnus novaezealandiae* hatches as a megalopa, and *P.lumpinus* hatches as an advanced zoea that molts in 15-30 minutes into a megalopa. The megalopal pleopods in *P.novazealandiae* begin to atrophy in the first crab and continue through the third crab; thereafter, pleopods of the adult form develop. A comprehensive study of larval and early postlarval stages of *Panopeus bermudensis, P.herbstii, P.turgidus* and *Eurypanopeus depressus* was recently completed (Martin et al. 1984) (Fig.6,xxxvii).

For crabs of the family Grapsidae, larval development and subsequent early postlarval development is known for less than 20% of all species. Early postlarval development of grapsid crabs has been briefly described in works by Hyman (1924b) on *Pachygrapsus marmoratus;* Hart (1935) on *Hemigrapsus nudus* and *H.oregonensis;* Aikawa (1937) on *Plagusia dentipes;* Lebour (1944) on *Planes minutus;* Gamo (1958b) on *Varuna litterata* and *Eriocheir japonica;* Bourdillon-Casanova (1960) on *Brachynotus sexdentatus;* Muraoka (1965, 1967, 1971a,b) on *Plagusia depressa tuberculata, Percon planissimum, Hemigrapsus sanguineus, Gaetice depressus, Pachygrapsus crassipes, P.minutus* and *Grapsus strigosus;* Diaz & Ewald (1968) on *Sesarma ricordi* and *Metasesarma rubripes;* Kurata (1968c) on *Acmaeopleura parvula;* Baba & Miyata (1971) on *Sesarma dehaani;* Baba & Fukuda (1972) on *Chasmagnathus convexus;* Baba & Moriyama (1972) on *Helice tridens wuana;* and Fukuda & Baba (1976) on *Chiromantes bidens.* Both Hyman (1924b) and Aikawa (1937) described two megalopal stages for each of two species, *Pachygrapsus marmoratus* and *Plagusia dentipes.* Their descriptions were based on planktonic material; their second megalopa was apparently *C.bidens,* while their first megalopa probably belonged to a portunid crab. A more thorough study of development was given by Morita (1974) for *Eriocheir japonica,* which was reared through the fifth crab stage (Fig.6,xxxviii). Gill development was complete in the megalopa, and early crab stages were distinguishable by pleopod, maxilla, and carapace shape.

The freshwater grapsid crab *Metopaulias depressus* is confined to water that collects at the base of large tank bromeliads in Jamaica. It has an abbreviated development of two non-feeding zoeal stages and a predominantly benthic megalopa (Hartnoll 1964). The pleopods are rudimentary in the decapodid and completely lost by the first crab stage.

A similar case of abbreviated development occurs in *Geosesarma perracae* (Soh 1969). The non-feeding megalopal decapodid appears to be a juvenile crab but may be considered a modified megalopa since certain larval features remain in the telson, antennules, antennae, and mouthparts.

The Pinnotheridae contains about 26 genera and 220 species, most of which (as adults) are commensals of other invertebrate groups. Larval development is known in less than a quarter of the species, and early postlarval development is known in less than ten species. The Pinnotheridae differ greatly from most other brachyrhynchan larvae in their reduc-

tion of the antennae and tendency to lose one or more carapace spines. In these features they resemble the Leucosiidae and Hymenosomatidae. The megalopae tend to lack sensory setae on the fifth pereopod dactyl, though these are present in most other Brachyura. Early postlarval development has been examined briefly in works by Hart (1935) on *Pinnotheres taylori,* Irvine & Coffin (1960) on *Fabia subquadrata,* Roberts (1975) on *Pinnotheres chamae,* Muraoka (1979) on *Pinnixa rathbuni* (Fig.6,xxxix), Yatsuyuka & Iwasaki (1979) on *Pinnotheres* cf. *P.sinensis,* Konishi (1981) on *Sakaina japonica,* Pohle & Telford (1981) on *Dissodactylus crinitichelis,* and Pohle & Telford (1983) on *P.primitivus.* A pinnotherid with abbreviated development is *Pinnotheres moseri;* its megalopal stage is reached in 24-36 hours (Goodbody 1960). According to Faxon (1879) and Hyman (1924a), the last zoea of *Pinnixa sayana* molts directly to the first crab stage. Both authors, however, illustrated this stage with natatory pleopods on the abdomen, so this molt probably represents the decapodid stage.

All genera of the Potamoidea presumably have direct development, with the young hatching in the form of the adult and being carried for a time under the abdomen of the parental female (see Gurney 1942). The mode of development in these crabs indicates a secondary embryonization of the zoeal stages and megalopa. Ancestral larval phases of the Decapoda can still be recognized during this embryonization even with the presence of increased yolk. Pace et al. (1976) described in detail the embryonic development of the freshwater crab *Potamon edulis.* This species exemplifies an extreme form of secondary embryonization in that even the megalopa is imprisoned in the egg and the embryo hatches as a miniature adult.

The family Ocypodidae comprises some 20 genera and 230 species, of which the majority are semiterrestrial. Many of the early postlarval studies are based on megalopae captured in the plankton and the early crabs that were subsequently reared from them in the laboratory. Early postlarval development has been described for ocypodid crabs in works by Kemp (1915) on *Ocypode macrocera,* Rajabai Naidu (1954) on *O.cordimana* and *O. platytarsis,* Gamo (1958a) on *Scopimera globosa* and *Deiratonotus (as Paracleistostoma) cristatum,* Rajabai (1960) on *Dotilla blanfordi,* Kurata (1970) on *Uca pugnax,* Novak & Salmon (1974) on *U.panacea,* and Muraoka (1976) on *U.lactea* and *Macrophthalmus japonicus* (Fig. 6, xl). Some ocypodid megalopae are large in size and usually have special grooves alongside the carapace for folding their appendages tightly against the body. In the first crab, some species begin to burrow into sand and develop tufts of plumose setae between the walking legs. Abbreviated larval development in *Uca subcylindrica* is followed by an atypical *Uca* megalopa and first crab stages in which the carapace is more rounded than typical *Uca* (Rabalais & Cameron 1983).

3 ANATOMY AND FUNCTION IN EARLY POSTLARVAL LIFE

3.1 *Anatomical development*

3.1.1 *General overview*

The morphological changes that take place in transition from larval stages to the decapodid and in the transitions between postlarval stages that follow are often accompanied by considerable changes in behavioral and physiological patterns. These functional changes are related to marked ontogeny in anatomy of organs and tissues during metamorphosis and

early postlarval development (Bellon-Humbert et al. 1978). Unlike external morphogenesis of the exoskeleton, organogenesis and histogenesis need not be confined to changes at a given molt (Steele 1902, Thompson 1903). However, the new level of function can be dependent on endocrine changes associated with molting or exoskeletal modification expressed at the molt.

When a well-demarcated metamorphosis in external features occurs between larval and postlarval developmental phases in decapod crustaceans, it is often accompanied by some pronounced changes in internal anatomy. However, while the decapodid stage may represent a marked change in internal anatomy from the larval state, that internal anatomy often differs from adults. Except for the development of primary and secondary sexual organs, postmetamorphic changes in internal anatomy may be most pronounced in the first several postlarval instars, with the degree of anatomical reorganization and development decreasing in each of the later juvenile molts. Anatomical change during metamorphosis and the next few postlarval molts may in part consist of *degeneration* of some anatomical features, specifically of those that are legacies from larval behavior and physiology. Another facet of anatomical change may involve *redirection* of existent structure; in effect, this would require relatively minor modification of an anatomical feature or its controls in order to transform function from that operative during an earlier stage to that required by later postlarval stages. Finally, there can also be *addition* of anatomical structure; this can involve not only absolute increases or allometric increases in size with overall growth, but also, particularly in the early postlarvae, differentiation of new anatomical features.

The following sections on anatomical development will treat ontogeny of eyestalks and neurosecretory organs, musculature and innervation, the stomach, and a few other organs. Pigmentation will also be included, as it is usually the result of both anatomical structure and products of that structure. Limited reference will be made to gonadal development, a process largely restricted to later stages of development than early postlarvae; however, exceptions will be noted. The most thorough coverage of subjects is divided between references dating from near the turn of the century, which consist of a few meticulously illustrated anatomical monographs (for example, Thompson 1903, Waite 1899), and a contemporary set of papers that in combination provides an excellent coverage of several anatomical features in *Homarus* (reviewed in part by Govind 1982). Apparently, the early initiative in anatomical study of decapod postlarval development was abandoned well before there was representative coverage of the group. Recent efforts, while thorough and exemplary in modern technique, have barely touched upon the diversity of decapod taxa and the spectrum of anatomical structures subject to postlarval change.

3.1.2 *Eyestalks and neurosecretory organs*
The anatomy and function of eyestalks and neurosecretory organs has been relatively well studied in adult decapod crustaceans, but considerably less is known of this subject in early postlarval stages. The studies most applicable to postlarval ontogeny of these anatomical structures are restricted to a few species of the Palaemonidae, the anomuran *Pisidia longicornis,* and a few brachyurans (see LeRoux 1980, 1982 for a compilation of current literature). Observations on decapodid and postlarval histogenesis of these organs is provided for *Palaemon serratus* by Bellon-Humbert et al. (1978) and for several species of North American *Palaemonetes* by Hubschman (1963). Additionally, Hubschman (1971) noted the degeneration of suspected larval glands at metamorphosis to the decapodid in

Palaemonetes. Some assumptions of postlarval histogenesis in the sinus gland and X-organ can be made on the basis of Pyle's (1943) studies of egg anatomy, several larval stages, and adults of *Pinnotheres maculatus* and *Homarus americanus.* However, he did not specifically address histogenesis in early postlarvae. Likewise, our interpretation infers that postlarval stages undergo histogenesis that alters larval conditions to those found in adults (e.g. Orlamunder 1942, Dahl 1957, Matsumoto 1958, Elofsson 1969, Zielhorst & van Herp 1976). Among these, the studies by Matsumoto on *Potamon dehaani,* Pyle on *Homarus americanus,* and Zielhorst & van Herp on *Astacus leptodactylus salinus* are particularly valuable in that they document the appearance of some neurosecretory structures that occur much sooner after hatching in these species with abbreviated development than in those species with a more typical larval life (Bellon-Humbert et al. 1978).

The most pronounced rearrangement and development in anatomy of neurosecretory organs in *Palaemon serratus* and several species of *Palaemonetes* occurs during the transformation from an upside-down swimming larva to a dorsal-side-up postlarva (Bellon-Humbert et al. 1978, Hubschman 1963). Concurrent with this reversal of attitude, some eyestalk features rotate from the larval dorsal position (which would face downward in an upside-down swimming larva) to a ventral position in the dorsal-side-up postlarva; thus a structure that faced downward in the larva, such as the larval sensory pore (LSP; the pore of Hubschman's SPX), would also be directed downward in the postlarvae and adults (Fig.7). In his description of this phenomenon in *Palaemonetes,* Hubschman (1963) did not detail the rotational positioning of internal eyestalk structure during early development. He suggested repositioning occurred by a rotation of the eyestalk on its longitudinal
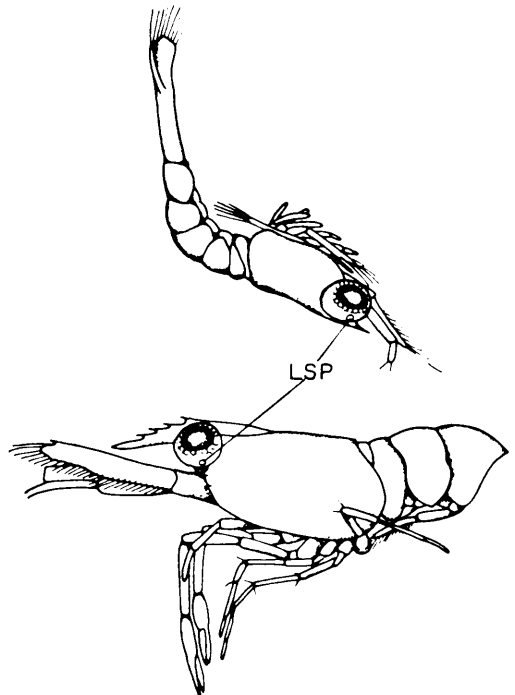

Figure 7. Diagram showing attitude of larval (above) compared to postlarval (below) *Palaemonetes,* with reference to relative position of larval sensory pore (LSP) (slightly modified from Hubschman 1963).
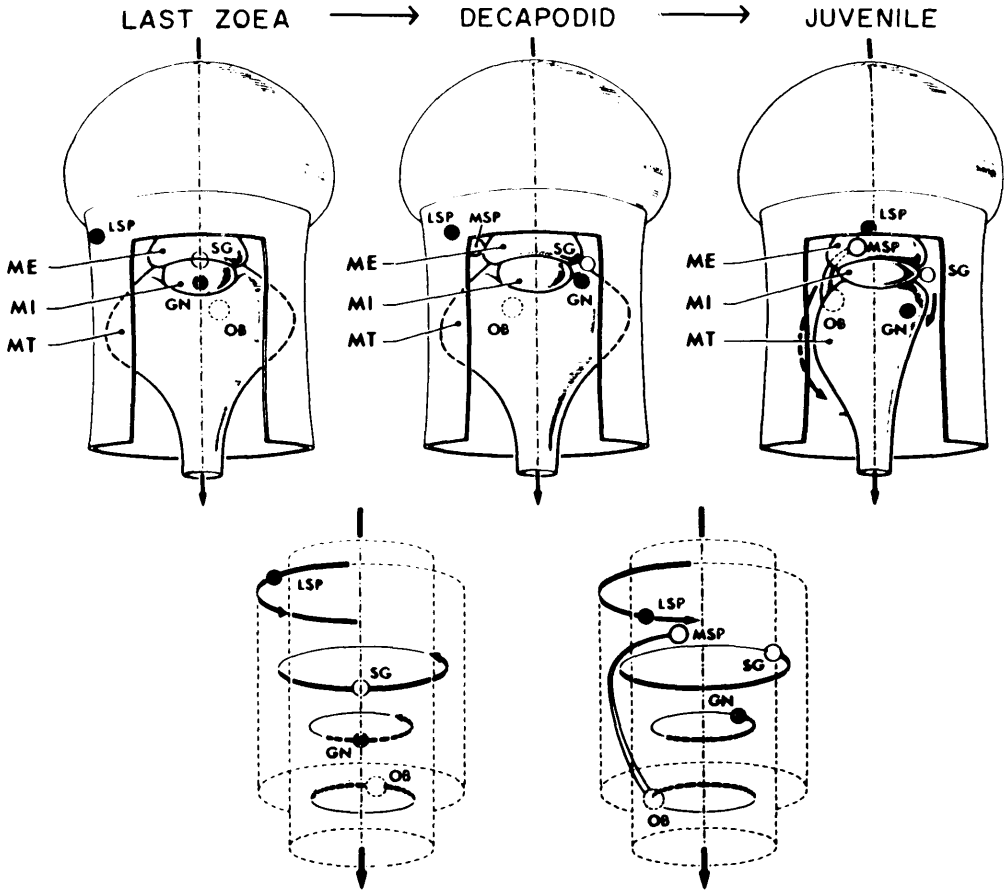
Figure 8. Schematic localization and hypothetical movement of sensory and neurosecretory structures in one right eyestalk (dorsal view) during last zoeal (last mysis), decapodid (postmetamorphic), and juvenile stages of *Palaemon serratus*. GN – giant neuron; LSP – larval sensory pore; ME – medulla externa; MI – medulla interna; MSP – main sensory pore; MT – medulla terminalis; OB – organ of Bellonci; SG – sinus gland (slightly modified from Bellon-Humbert et al. 1978).

axis. Bellon-Humbert et al. (1978) conducted a more thorough analysis of internal movements in eyestalk components during development of *Palaemon*. Their findings suggested that 'rotation of structures occurs around the longitudinal axis of the eyestalk' under the influence of relative growth and torsion in various of the eyestalk medullae (Fig.8). They also documented that the process begins in the larval molt preceding metamorphosis and continues into postlarval developmental stages.

In *Palaemon serratus*, the LSP undergoes its most pronounced movement from a dorsal to ventral position on the surface of the eyestalk (Bellon-Humbert et al. 1978) during the metamorphic molt from the last larva to the decapodid. The first unquestionable appearance of the main sensory pore (MSP) occurs at this stage. Also at this time, some cells begin to take on neurosecretory characteristics at the future locations of the medulla ex-

terna (ME) and medulla terminalis (MT) X-organs. The sinus gland (SG) and the giant neuron (GN) have moved to the external dorsolateral side of the eyestalk, but histological features of the SG and GN remain similar to those of the last larval stage. The organ of Bellonci (OB) remains inside the MT during the decapodid stage, and further developments in the OB, SG, X-organs, and medullae are reserved for following postlarval stages.

During these early postdecapodid stages, the eyestalk both grows and acquires the adult arrangement of its components. Medullae also individualize, the eyestalk completes its formation, and the eyestalk straightens on its longitudinal axis and becomes more parallel to the body. These movements, coupled with directional and allometric growth of some structures, bring components into their functional adult configuration (Bellon-Humbert et al. 1978). For example, it is during this phase of growth and development that the OB and the MSP first come into contact, and that the OB first contains stainable granules in vacuoles and extends partially out of the MT. The MSP also becomes more developed, the number of micropores increases, and a secretion product becomes evident at the micropore apertures. Neurosecretory cells become better differentiated into two distinct groups, one in the X-organ at the ventral region of the MT where the OB nerve tract makes its entry (this area termed $MTGX_2$ by Bellon-Humbert et al.) and the other forming the ME X-organ in front of the sinus gland.

Development of the sinus glands to a presumably active condition, with granules in three differently staining regions, becomes evident only after the decapodid stage, even though it is structurally distinguishable in the larval phase of development. Thus, the completion of an affiliation between the sensory pore complex and the distal part of the OB, the connection of the OB with the neurosecretory cells of the medulla terminalis via a nerve tract, the differentiation and development of neurosecretory cells in the MT and the ME X-organs, and the development of granulation in the OB and SG, mark major steps in activation of the sensory and secretory functions of eyestalk organs during early postdecapodid development.

The source of regulatory factors in early postlarvae is unclear. However, Hubschman (1963) demonstrated that in larval *Palaemonetes*, metamorphosis is not under eyestalk control, and he looked elsewhere for the site of regulatory factors that may be analogous to those of insects (Hubschman 1971). While Y-organs resemble prothoracic glands in some respects and are non-nervous secretory organs involved in the control of molting, none are known in larval *Palaemonetes*. Suspected larval glands were found at the base of the first maxilla in all larval stages of five species of *Palaemonetes*, and these deteriorated in the last phase of the terminal larval instar (Hubschman 1971). These glands were completely absent in the decapodid stage, so their activity, if any, could not have extended to postlarval stages. We are therefore left with no evidence of a source for regulatory factors governing early postlarval development in *Palaemonetes* or in *Palaemon*. Hubschman (1963) noted that the sinus gland, in particular that of *Palaemonetes*, does not appear to be functional until after the second or third postlarval molt. Likewise, there is anatomical evidence that the sinus gland in *Homarus americanus* does not function by the decapodid stage (Pyle 1943). When eyestalks were removed from larvae and/or decapodids of an anomuran (LeRoux 1980) and several brachyurans (Costlow 1963, 1966a,b), however, activation of the X-organ and sinus gland complex varied between taxa and sometimes occurred in the decapodid stage. Absence of both eyestalks in decapodids of *Pisidia longicornis, Callinectes sapidus,* and *Sesarma reticulatum* accelerated development, presumably by removing the source of molt inhibiting hormone. On the other hand, removal of eye-

stalks in larval *Rhithropanopeus harrisii* did not accelerate molting until the third post-larval molt, suggesting that the X-organ and sinus gland complex may not become activated until later in early postlarval development.

3.1.3 *Musculature and innervation*

Relatively little is known on just how embryonic nerves and muscles acquire their adult configurations (Govind 1982). That which is known for the period between embryonic life and the later juvenile stages is largely restricted to the larval stages and primarily represented by studies on the Astacidea. The review of crustacean nerve, muscle, and synapse development by Govind (1982) contains extensive coverage of embryological, larval, and later development of these structures. We confine our treatment solely to the period of early postlarval growth and expand upon coverage of decapod crustaceans.

The specialized asymmetric chelipeds of many species become adult-like during post-larval stages. Such chelipeds may be employed in sexual or agonistic behavior, as in the case of male fiddler crabs (Crane 1975) or crayfish (Stein 1976). Both pre- and postpubertal males of decapods may exhibit a positive allometric growth of chelae (Finney & Abele 1981). In other species, both sexes have asymmetric chelipeds and use them in defense or prey capture (Costello & Lang 1979), with mechanical advantage changing to fit feeding strategies that change with maturation (Warner & Jones 1976, Vermeij 1977). Where adult asymmetry exists, it may be fixed or plastic (Przibram 1931). In species having the fixed condition as adults, there may be a given developmental stage when the fate of either cheliped is fixed. For example, in *Homarus americanus,* the fate of chelipeds does not become fixed until the second postlarval stage (Emmel 1908, Lang et al. 1978). In species having a plastic dimorphism, the cheliped of either side can differentiate into either form of the dimorphic pair, regardless of the degree to which development has proceeded beyond early stages and regardless of how differentiated the cheliped pair has become. This was demonstrated in *Alpheus* by Mellon & Stephens (1979). Most commonly, this ability is evident in cases where the major cheliped has been lost and regenerated as a minor cheliped during subsequent molts, while the former minor cheliped has differentiated into the major form during those molts (see Govind & Lang 1978).

In early postlarval stages, decapods may have chelipeds that are indistinguishable from one side of the body to the other. Differentiation in shape, musculature and innervation occurs later. The most thorough studies of this process were conducted on the lobster, *Homarus americanus,* a species with the fixed form of cheliped asymmetry in adults (Costello et al. 1981, Costello & Lang 1979, Govind & Lang 1978, King & Govind 1980, Lang et al. 1977). In the decapodid and following stage, the chelipeds of the two sides are symmetrical both in external appearance and in fiber composition of the closer muscles. Both chelae contain closer muscles that consist of about 30 % short-sarcomere (fast) fibers and have the remainder composed of intermediate- to long-sarcomere (slower) fibers (Fig.9). Late in the second post larval stage, or at the molt to the third postlarval stage, the number of short-sarcomere fibers rapidly increases in one chela and slowly decreases in the other. This trend continues until about the 13th postlarval stage, when the closer muscles of both chelae have attained their adult distributions of fibers. Ultimately (Ogonowski et al. 1980), the 'crusher' chela loses all short-sarcomere fibers while the 'cutter' chela develops a high ratio of short- to long-sarcomere fibers. Concurrent with developmental changes in muscle fiber distributions, a disparity in fatigue resistance develops between the fast axon synapses of the crusher and cutter chelae, and facilitation values for slow axon
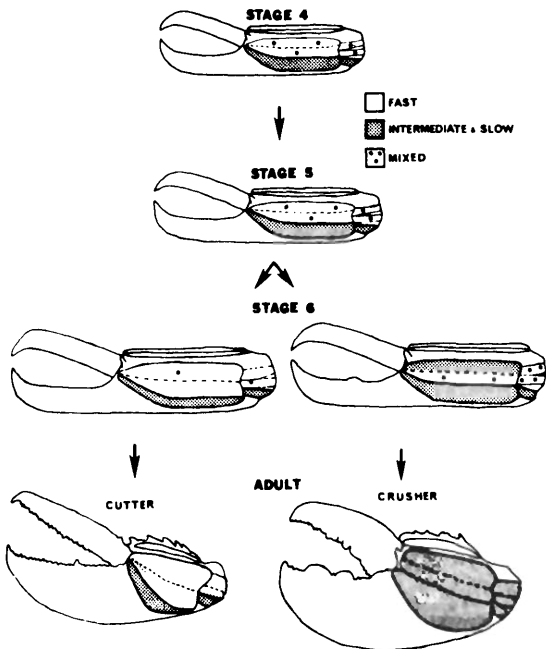
Figure 9. Mesial aspect of lobster (*Homarus americanus*) chelae closer muscles during postlarval development, with differentiation of cutter and crusher chelae (sizes not to scale); from Costello & Long 1979).

synapses in both chelae increases. As a net result, the dorsal bundle of the closer muscle of the crusher chela converts into a tonic motor unit, while the dorsal bundle of the cutter closer muscle retains an enhanced ratio of fast muscle units and becomes a specialized phasic unit (Costello et al. 1981).

Studies of excitatory innervation in chela closer muscles of *Homarus americanus* provided insight into proliferation of axonal tissues and enlargement of synpases in thoracic limbs, concurrent with postlarval growth (King & Govind 1980). Neither the extent of innervation nor the size of excitatory synapses in early postlarvae is as great as in adults, although both are greater in the decapodid stage than in the first larval stage. In the first larval stage, excitatory innervation is restricted to a few discrete muscle fibers. In the decapodid this innervation is more widespread, and in the adult all fibers receive excitatory innervation. Thus, increases in the percentage of innervated fibers coincide with growth of the muscle. The increase in the size of excitatory synapses during this period increases innervation during muscle growth. The size increase in such synapses between the decapodid stage and the adult is in excess of four-fold and is much greater than that which occurs between the first larval stage and the decapodid. King & Govind also noted that a larger proportion of adult synapses had two or more 'presynaptic dense bars' than did either larvae or decapodids. They suggested that adults may therefore also have a 'higher quantal content' for synpatic transmission.

The phenomenon of synaptic growth with development need not be characteristic of decapod species in general. Atwood & Kwan (1976) found that synapses in the limb opener muscle of crayfish remain constant throughout development, while growth of innervation occurs primarily by addition of new synapses. Govind (1982) reviewed the phenomenon of 'sprouting' from nerve terminals. New synapses so produced may be an additional means

by which innervation spreads to growing muscle fibers in lobsters.

Concurrent changes in muscular and neural growth occur during early postlarval development of lobsters (Lang et al. 1977). Such anatomical changes underlie allometric growth and the behavioral implications of such growth. In *Homarus americanus* larval and early postlarval stages, a tail-flip (abdominal extension and flexure) escape movement is the usual response to moving visual stimulus, while defensive posturing (display of open chelae) is favored over escape behavior in larger animals. Morphologically, this change in behavioral modes is then facilitated by allometric changes in both chelipeds and abdomen of developing lobsters.

In larval and several early postlarval stages of lobsters, the muscular abdomen comprises a substantial component of the total animal weight (Lang et al. 1977). The abdominal length is also great compared to carapace length (Fig.10). However, the chela weight and length are relatively small compared to the total weight and the carapace length. The ratio of abdominal weight to total animal weight remains nearly constant until an animal is 40-60 mm long. There is, however, strong positive allometric growth in the length and weight of the chela until the animal reaches a total length of about 50 mm and less so thereafter.

Negative allometric growth is characteristic of the abdomen once total length exceeds about 50 mm. Most of the growth in the medial and lateral giant axons has been achieved by the time the animal is 60 mm in carapace length (Lang et al. 1977). Thereafter, because of the relatively small further increase in diameter, and the relationship of velocity to diameter as a power function, the conduction velocity of the giant axons does not substan-
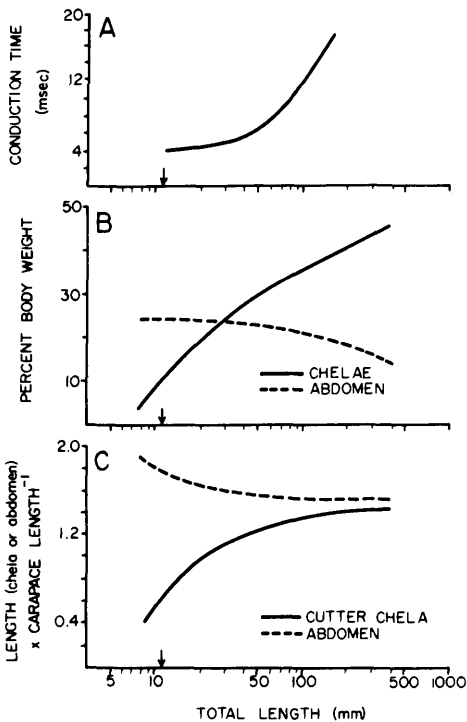

Figure 10. Curves approximating changes during growth of lobster, *Homarus americanus*; arrow indicates approximate size at metamorphosis to decapodid. (A) Conduction time in milliseconds for a spike in medial giant axon to travel from the brain to sixth abdominal ganglion. (B) Relative contribution of chelae and abdomen to total body weight; weight of chelae is combined weight of both claws, severed at autotomy plane; total body weight is weight of intact animal before chelae or abdomen are severed. (C) Cutter chela and abdomen length relative to carapace length; length of cutter chela is propodus length; carapace length measured from eye to posterior margin of thorax (curves are approximations from data points of Lang et al. 1977, originally published under 1977 copyright by the AAAS).

tially increase. In fact, the small increase in axon diameter is less than that needed to compensate for the increase in overall animal length, and there is a striking increase in conduction time. Thus, conduction time from the brain to the telson is 4-5 msec in early postlarval stages and remains relatively constant until the lobster reaches a length of 50 to 60 mm; conduction time then increases and response shifts from escape to defensive display of the chelae (Govind 1982).

There is some evidence that diminishment of tail-flip in adult lobsters has a counterpart in crayfish (Krasne & Wine 1975). However, as pointed out by Lang et al. (1977), crayfish may have relatively smaller chelae than lobsters as adults, and giant axons may differ in relative size between the two animals. Their preliminary experiments with *Procambarus acutus* suggested that at least this species differed from *Homarus* in its behavioral strategy.

The concurrence in changes in behavior and anatomy in astacideans suggests what kinds of anatomical changes should be expected in other decapods that alter behavior in early postlarval life, e.g., the transition from a brachyuran megalopa, with its extended abdomen, to the early crab stage, with a tightly flexed abdomen. It has been documented that relative sizes of abdominal flexor and extensor muscles can change during ontogeny from the megalopa to the adult brachyuran (Trask 1974). Such changes in a brachyuran would almost certainly differ from the ontogeny in shrimp abdomens that retain abdominal swimming as adults, but detailed studies at the neuromuscular level have not been made. Even early postlarval ontogenetic shifts between relative dependence upon the mandibles versus use of the cardiac stomach in mastication, as reported by Factor (1982) and discussed in the next section of this chapter, should be reflected in neural and muscular analogs.

Motor neurons also change during growth. Stephens & Govind (1981) have recently reported on the restriction of innervation fields in the common exciter and common inhibitor motoneurons of deep abdominal extensor muscles during early postlarval development of *Homarus americanus*. Fields that extend to three adjacent abdominal somites during the period from embryonic development through the second postlarva, become restricted to one somite in the third postlarval stage. This is accomplished by selective elimination of functional synapses from an initially widespread distribution. Another mechanism of neuromuscular development that may be operative is the redirection of oscillators, suggest as a possibility in the larval to decapodid stage transition of the lobster *Homarus gammarus* (Laverack et al. 1976). Muscles of thoracic endopodites are small and nonfunctional in the larval stages (Neil et al. 1976). They become well separated from those that cause swimming movements of the exopodites in larval stages and then degenerate in the decapodid (first postlarval) stage. In the decapodid, the exopodites of the pereopods become vestigial, while the endopodites develop as walking legs. Laverack et al. (1976) noted the similarities of patterning and other factors in larval swimming and adult walking of *Homarus*. They suggested that system was an 'oscillator that switches output from one set of muscles to another at the critical molt . . . (from the last larval stage to the decapodid)'. Alternatively, the change in modes of locomotion at metamorphosis could suggest that separate oscillators are present which either start or terminate their activity at the metamorphic molt.

3.1.4 *Stomach, antennal glands, and gonads*

Larval, early postlarval, and adult decapods typically masticate by the stomach and/or the mandibles. Factor (1982) recently compared the relative complexity of the stomach and mandibles in larvae and postlarvae of the xanthid crab *Menippe mercenaria* and reviewed

the limited literature that applies to this subject in other decapod species. Considerable change may be expected to occur between planktotrophic larval stages and adults that are dependent upon a wide variety of substantial food items in the benthic environment. However, there is not always a clear trend toward greater complexity with development. For example, the greatest complexity in the foregut of the shrimp *Crangon septemspinosa* occurs in the last larval stage (Regnault 1972), even though a true gastric mill is never developed in larvae or postlarvae of this species.

With the molt from the last larval stage to the decapodid stage in most decapods, the stomach becomes adult-like. However, further changes during early postlarval development may take place in such features as the strength of dentition and ridges, the length and density of setation, the relative sizes of chambers, and the distribution of fine denticles. The most pronounced changes in stomach morphology generally occur with the metamorphic molt. They are particularly pronounced in those species that have a gastric mill as adults, and this is the typical condition in the reptantious brachyurans, anomurans, and macrurans (Factor 1982. Patwardhan 1935). For example, in *Menippe mercenaria*, mastication of food shifts from mandibles to a rudimentary form of the gastric mill at the molt to the decapodid. Simultaneously, the molar process of the mandible becomes more simple (Factor 1982), a simplification largely completed in the early postlarval stages.

A developmental sequence similar to that of *Menippe* was described in *Pagurus annulipes* (as *Eupagurus longicarpus*) by Thompson 1903 (also see Roberts 1970). The full complement of gastric mill components appears at the metamorphic molt. Likewise in the lobster *Homarus americanus*, a full complement of gastric mill teeth first appears in the fourth developmental stage, the decapodid. However, unlike *Menippe* and *Pagurus*, neither the larval nor the postlarval stages of *Homarus* have a molar masticatory process on the mandibles, and it is unclear how food is masticated in the larval stages (Factor 1978, 1981). Thus, in the species that develop a true gastric mill, early postlarval developments are probably limited to further sclerotization and subtle elaboration of an apparatus that is prefigured at the metamorphic molt. From our own observations of stomachs in early postlarval stages in the thalassinidean *Callianassa major*, the processes of sclerotization, definition of setal fields, and chamber modification are completed in early postlarval development.

In the natantious species of the Penaeoidea, Caridea, and Stenopodidea, which typically lack a well-defined gastric mill and depend more fully upon the mandibles for mastication throughout the life history (Patwardhan 1935, Factor 1982), there may also be changes in the stomach during metamorphosis and postlarval development. LeRoux (1971a,b) noted that the pyloric and cardiac chambers of *Palaemonetes varians*, which freely communicate during the larval stages, become more separated after metamorphosis. Although there is no functional difference in these two chambers during the larval stages, after metamorphosis the cardiac chamber becomes specialized. It stores food and mixes that food with enzymes, and the pyloric chamber becomes a straining and (to a limited degree) a triturating apparatus. Heral & Saudray (1979) noted concurrent changes in the mandibles of this species.

As previously noted, metamorphosis of the caridean *Crangon septemspinosa* marks the loss of gastric armature that was progressively developed during the larval phase of growth. However, Regnault (1972) also noted that other structures of the stomach change toward maximal differentiation at the metamorphic molt. While Regnault did not specifically address early postlarval changes in the stomach of *C.septemspinosa*, a number of postlarval

elaborations, other than armature, are apparently added to the basic form of the stomach that is prefigured in the decapodid stage.

Much less is known of early postlarval development in the hepatopancreas and other digestive tract features. Thompson (1903) described a complicated metamorphosis in the hepatopancreas of *Pagurus* that takes place within the decapodid (glaucothöe) and the following postlarval stage. During the decapodid there is a reduction of lobes persisting from the zoeae, which gives rise to simple tubular hepatopancreatic masses. Adult-like diverticula develop in the second postlarva, and bilateral symmetry is obscured after the fourth postlarva. Such a developmental sequence may be typical of only those anomuran forms with highly asymmetrical abdomens. Trask (1974) noted, however, that *Cancer anthonyi* also has digestive glands of a simple tubular shape in the decapodid stage. Thompson (1903) observed development of chitinous portions of the gut, achitinous portions of the gut, folds of the gut wall and ceaca or diverticula that develop over the early postlarval stages, and LeRoux (1976a) reported on metamorphic development of the intestinal caecum in *Pisidia longicornis*.

Development of the green glands or antennal glands was treated by Thompson (1903) and Waite (1899) for *Pagurus* and *Homarus* respectively. Both authors pointed out the appearance and development of the nephrosac or vesicle during the decapodid stage, and noted that its growth relative to surrounding structures is a feature of further postlarval development, indicating osmoregulation may be further developed in the postlarval stages. However, the growth of the vesicle need not simply reflect an increased ability to maintain water balance with ontogeny; in fact, the opposite is often observed. For example, Davenport (1972) noted that juveniles of the hermit crab *Pagurus bernhardus* regulate volume in lower salinities than adults, and suggested that it is the size of the aperture of the nephropores in relation to body size that limits this ability in adults.

The reproductive system largely develops after early postlarval stages in decapod crustaceans. Small masses of sex cells may be distinguishable beneath the pericardial septum even in larval stages, and some increase in number apparently occurs during early postlarval development (see Thompson 1903). However, with few exceptions (see LeRoux 1976b), little is known of the earliest developments in internal organs, ducts, and orifices of the reproductive system for most decapods, and attention has usually been directed to noting the earliest morphological developments of externally evident secondary sex characters.

Shape of the abdomen and the form and number of abdominal appendages seem to be among the external characters that are most useful in distinguishing sex at an early postlarval stage (for example, see Forster 1951: Fig.2 and Morita 1974: Figs.20-2, 21-1, 21-2). Later development of the gonads can give rise to organs that are mature in most respects but lack mature sex cells (Knudsen 1960). Further growth of gonads with maturation of the sex cells can, especially in females (Finney & Abele 1981), relate to allometric changes in body form which often mark the attainment of maturity. The degree to which early postlarval stages show development in the gonads and secondary sex characters is probably a function of the number and duration of postlarval stages that occur between the decapodid and the mature adult. Thompson (1903) noted that sexual maturity is probably not reached until the second or third year in the life of *Pagurus*. However, gonads may become mature in crustaceans before secondary sex characters are fully developed (Charniaux-Cotton 1965).

In some small specialized decapod species, sexual maturity may be attained or closely approached shortly after metamorphosis from the larval phase. A particularly striking case

of this is represented by the male swarming stages of some commensal pinnotherid crabs. The male and female swarming stages consist of early crab stages. Males at this time may be sexually mature and may precociously inseminate females in which the ovaries are not yet fully developed (Kruczynski 1973, Pearce 1966).

3.1.5 *Pigmentation*

Both coloration and patterns formed of color pigments (chromatophoric and extrachromatophoric) or structural manifestations (scattering, diffraction, and interference of exoskeleton or setation) are usually subject to developmental changes during postlarval life of decapods. Even in the earliest postlarval stages, there is evidence that some color patterns, like many morphological features, are controlled by eyestalk neurosecretory structures. For example, eyestalkless postlarvae of *Pisidia longicornis* do not develop the characteristic color patterns of normal postlarvae (LeRoux 1980). In addition to the endogenous control of color and pattern, exogenous factors (such as decorating materials, epibiotic growths, and precipitates) may also alter apparent coloration, especially in later stages of postlarval development. Also in later stages, certain coloration changes may coincide with maturation, as in carapace whitening of some fiddler crabs (Crane 1975), molt to a 'white' stage in some palinurid lobsters (Sheard 1962), and certain transient patterns in *Ucides* and *Cardisoma*.

Coloration and patterning are unconservative qualities at taxonomic levels above that of species among the decapods. However, at the species level, it is often a useful taxonomic character and may be diagnostic of habitat or behavior. Both habitat and behavior may be altered at metamorphosis, and the degree to which they are altered is often greater over this phase of development than over any other in the life history of a decapod. Thus, striking changes in color and pattern may coincide with this early phase of postlarval development, but literature references are few and are restricted to isolated taxocenes. Occasionally coloration in postlarvae suggests restriction to a unique habitat. For example, Seréne (1961) reported a brachyuran decapodid with camouflage coloration exactly matched to the mantle coloration of a squid (*Loligo*) on which it lived.

Perhaps the most frequently noted case of ontogenetic color change in early postlarvae is that which occurs in the early postlarval development of palinurid and scyllarid lobsters of the genera *Panulirus, Jasus, Ibacus,* and *Scyllarides* (MacGinitie & MacGinitie 1949, Deshmukh 1966, Sorensen 1969, Lyons 1970, Silberbauer 1971, Ritz & Thomas 1973, Serfling & Ford 1975, Berrill 1975, Booth 1979 and Kanciruk 1980). In general, color development in these animals reflects the transition from a planktonic habitat to a benthic one. The decapodid stage, commonly called the puerulus, is the settling stage, transforming from a planktonic swimmer during its early period to a benthic form in its later period. The puerulus is rather transparent. Just prior to ecdysis to the postpuerulus stage, it gains pigment and a more opaque appearance, which may be concurrent with the fading of some isolated larval chromatophores. Both coloration and calcification become more pronounced during the first postpuerulus stage and several stages that follow, and the animal may become cryptically or disruptively patterned and match the benthic substrate and cover in which it has settled. The triggering of pigment deposition may be dependent upon the availability of appropriate substrates. Serfling & Ford (1975) noted that pueruli of *Panulirus interruptus* held without access to vegetation and epifauna typical of the postlarval environment remained transparent for 2-3 weeks and then died instead of molting to the postpuerulus. It also appears that the color and patterns of early postlarvae are not

simply developing adult patterns, but rather may serve as camouflage tailored to the juvenile habitat. The adults are often less protectively colored but may instead have an array of behavioral adaptations that are antipredatory (Kanciruk 1980).

Transparency is not the only color of larvae or settling postlarvae. At depth, in poorly lighted crevices, or under the darkness of night, even the apparent red coloration (in light) of some forms may conceal when incident red light is largely absent from the available light spectrum. Also, where seston or substrates may be brightly colored, brightly colored larvae or postlarvae may be effectively concealed.

In terms of ontogenetic color and pattern changes, few references (other than those for lobsters above) document postlarval schemes. Hart (1965) decribed the predominantly scarlet and reddish-orange coloration of zoeae and megalopae in the anomuran *Cryptolithodes typicus.* All postlarval stages seem to be well camouflaged for the rocky subtidal and intertidal habitats in which they live. Knudsen (1960) noted the plasticity of coloration that may occur in early crab stages of several xanthoid crabs. In *Paraxanthias taylori,* the early crab stages resemble the adults in color, while in *Cycloxanthops novemdentatus* and *Lophopanopeus leucomanus leucomanus* the young are of many different bright colors. While young of the latter two species generally occupy the adult habitat, they select the smallest crevices and spaces among coralline coverings and snail tubes atop rocks where bright colors would conceal them. In the case of *Menippe mercenaria,* early crabs and small juveniles may be much darker than adults (Hay & Shore 1918, Wass 1955, Manning 1961, DLF unpublished). These stages often inhabit deeper crevices of rubble and epifaunal interstices than do the lightly colored and less vulnerable adults.

Our own studies of western Atlantic reptantious decapods suggest that it is extremely difficult to generalize about early versus later postlarval colors and color patterns other than to note that early postlarvae may vary, often considerably, from later postlarvae or adults. We have encountered numerous cases in which early postlarval crabs are highly variable in color patterns while adults are somewhat more conservative (for example, in the xanthids *Panopeus, Hexapanopeus, Paractaea,* and *Micropanope*). In other cases, variations in coloration are pronounced in both the adults and the early crab stages (for example, in the xanthid *Xanthodius*). Among the Porcellanidae and the Majidae we have found cases where both adult stages and early postlarvae are not subject to great variation, but where the color of these two phases may be strikingly different (for example, in some *Petrolisthes* and *Mithrax*). These differences seem to be particularly common among shallow water majid crabs. In a few cases, it is uncertain whether color changes reflect an ontogenetic process or just a highly labile coloration response to food and substrates of habitats (for example, in *Acanthonyx* and *Mithrax*). Hines (1982) also noted the transition in color of the majid, *Pugettia producta.* Juveniles recruited onto red algae in the intertidal eelgrass zone were maroon in color, but changed to tan as they grew and migrated to the kelp forest.

Mimetic patterns may be confined to the earliest postlarval stages in some brachyuran species (for example, in *Calappa sulcata*), whereas in others, they may not appear until late during postlarval development. Commonly, crypsis is maintained with pattern change as body size increases and habitat and behavior change. Where adults and early juveniles share the same or a very similar substrate, the growth of the postlarval color markings may be negatively allometric and give adults a pattern of spots or venations that is as fine or finer than that of the early postlarvae. For example, this is characteristic of the portunid *Arenaeus cribrarius.*

3.2 *Behavioral and physiological adaptations to habitats*

Both migration and habitat selection in early postlarvae maximize growth rate, minimize population losses to predation, and facilitate recruitment to adult habitats. Relocation may relate to tolerances and capacities that differ between larvae and adults. Even postlarval metabolism may differ between early and late stages (Sastry & Ellington 1978).

Dietary requirements must be of major importance in inducing or limiting movements and distributions of early postlarvae, for these stages are usually characterized by rapid growth and high metabolic demand. Klein Breteler (1975b) noted the linear relationship between logarithms of oxygen consumption and weight in *Carcinus maenas* over postlarval development. In aquatic invertebrates requirements of food may be 3-4 times those needed for respiration (Jorgensen 1955). Thus, food requirements at early postlarval stages should substantially exceed those of later subadult or adult stages on a per gram organic body weight basis. Regnault (1971) indicated, for postlarval stages of *Crangon septemspinosa,* that the quantity of available food may determine both the molt frequency and final size attained, but optimal growth rate is also dependent upon quality of the diet available to young stages. Recent studies suggest the importance of diverse diets in penaeid postlarvae (Caillouet et al. 1976) and more specifically the benefits of dietary sterols (Teshima & Kanazawa 1971, Teshima 1972, Castell et al. 1975), linoleic acids and phosphatidylcholine (Castell & Covey 1976, Kanazawa et al. 1977, 1979, Conklin et al. 1980, D'Abramo et al. 1981), mineral content and ratios (Gallagher et al. 1978, Boghen & Castell 1981), and protein content or composition (Millikin et al. 1980, Boghen & Castell 1981), for optimal growth of young postlarval stages in a number of decapods. Even dissolved organic matter, such as D-glucose, has been demonstrated to improve nutritional state and growth rates in post-larval penaeid shrimp, albeit most probably by way of associated bacteria that may be used as a source of nutrition (Castille & Lawrence 1979).

Because larvae molt frequently and interrupt feeding to molt, nutritional reserves are more rapidly drained in these stages than in later ones (Bages & Sloane 1981). Specific food requirements appear to be essential during feeding periods, and these needs help determine larval migration routes and habitats. D'Abramo et al. (1981) have suggested, for example, that even small amounts of phosphatidylcholine in the diet may be especially important just prior to molting in juvenile homarid lobsters, before the animals enter pre-molt dependence upon reserves of the hepatopancreas. Even when physical parameters such as temperature, salinity, and substrate grain size vary along with quality and quantity of food, nutrition often appears to be the dominant factor in early postlarval growth (Chittleborough 1975, Klein Breteler 1975a, Caillouet et al. 1976, Labat 1977). Where habitat selection appears to be based upon substrate qualities, food organisms associated with those substrates may, in fact, be the basis for site selection by postlarvae (see Ruello 1973, Caillouet et al. 1976, Regnault 1976, Booth 1979, Aziz & Greenwood 1982). If migrations, as in the case of penaeid shrimp, route early postlarval stages over substrates that are not rich with nutritional organics, growth may be suspended to some degree until nursery areas are reached (Baxter & Renfro 1967). In some cases, metamorphosis itself appears to be stimulated by the presence of appropriate substrates or hosts (Hiro 1937, Serfling & Ford 1975, Castro 1978).

Substrate and cover cannot be completely separated from nutrients as factors in habitat selection. However, cover in nursery areas may diminish predation on penaeid postlarvae (Hackney & Burbanck 1976), and cover per se in part determines habitats selected (Giles

& Zamora 1973, Dall 1981). Both small size and frequency of molt renders postlarvae vulnerable to predation. *Homarus* decapodids construct burrows under obstacles at least two days before molting to second postlarvae, presumably as an antipredatory mechanism (Berrill 1974). Burrows of *Homarus* juveniles appear to serve the same purpose, and may be more complex than adult burrows (Howard & Bennett 1979). Cover is also important for young brachyurans, since their early postlarvae are preyed upon by small fish (Knudsen 1960, Felder & Chaney 1979).

Migration and habitat selection is often either facilitated or constrained by osmoregulatory capacities of specific age groups (Kalber & Costlow 1966, 1968, Kalber 1970, Foskett 1977, Young 1977a,b, Dall 1981). Capacities for postlarval osmoregulation tend to reflect salinity adaptation over the course of range distribution. The largest body of literature on this subject concerns penaeid shrimp. Postlarval penaeids generally migrate into estuaries following larval development in high salinity waters offshore. After a period of growth in inshore waters, mature adults return seaward and release eggs in high salinity water (Perez Farfante 1969, Allen 1972, Young & Carpenter 1977, Young 1978, Dall 1981). Temperature, currents, and local geography can influence salinity preference and periods of peak movement into estuaries (St Amant et al. 1963, Aldrich et al. 1968, Pullen & Trent 1969, Keiser & Aldrich 1976, Staples 1979). Tidal currents and behavioral (swimming) response to salinity appears to facilitate both inshore and offshore movements of *Penaeus duorarum* in Florida (Hughes 1969a,b), but the time of maximum movement may also depend on the coincidence of bright moonlight with nocturnal ebb tides (Beardsley 1970). Chemical factors, other than salinity, in inshore waters can influence movements of penaeid postlarvae (Mair 1980), and endogenous rhythms of feeding and activity may complicate their response to tidal cycles (Hughs 1968, 1969c, Allen 1972). In young penaeids, metabolic rates may not be altered significantly over a broad range of salinity (Gaudy & Sloane 1981) except at extremes (Kutty et al. 1971). The influence of salinity on postlarval growth is not dramatic (Zein-Eldin 1963, Zein-Eldin & Aldrich 1965) and appears to be much less than that of temperature (Zein-Eldin & Griffith 1966). However, movement of penaeid larvae to inshore waters low in salinity reflects a persistent pattern for most coastal species, and postlarvae of many tend to hyperosmoregulate to a greater extent than adults (Dall 1981, Castille & Lawrence 1981a,b).

Ontogenetic changes in osmoregulatory ability are known or suggested by migratory patterns in various representatives of the Caridea. Postlarvae of *Atya bisulcata* move through shallow areas between beach boulders and into the mouths of coastal streams in Hawaii, after metamorphosis from the marine larval phase. The movement coincides with loss of ability to survive in seawater (Ford & Kinzie 1982, Robert A.Kinzie, personal communication). *Macrobrachium rosenbergii,* after larval development and metamorphosis in brackish water, migrates up rivers in the postlarval stage toward adult freshwater habitats (John 1957, Raman 1967, George 1969, Ling 1969). High temperature inhibits this migration, possibly by impeding hyperegulation (Stephensen & Knight 1982). Ontogenetically, the postlarvae show a progressive development of hyperegulatory ability, as evidenced by a simultaneous decrease in the slope of regulation curves and in the isosmotic crossover concentration (Sandifer et al. 1975, Harrison et al. 1981). The hyporegulatory ability of early postlarvae is lost over the course of development to adulthood in *M.rosenbergii,* although it is present in adults of *M.ohione* to some degree (Castille & Lawrence 1981). Migration and osmoregulatory ability appear to be more complex in the genus *Crangon* (Haefner 1969, Labat 1977, Jansen & Kuipers 1980).

Among the Astacidea, adults of both the cambarid *Procambarus clarkii* and the parastacid *Cherax destructor* are more tolerant of salinity than earlier postlarvae (Loyacano 1967, Mills & Geddes 1980). For the thalassinidean *Callianassa islagrande,* preliminary evidence suggests that hyperosmotic and hyperionic regulation may occur in early juveniles while no such ability is evident in adults (Felder 1978). In the hermit crab *Pagurus bernhardus* juveniles regulate body water volume at lower salinities than do adults (Davenport 1972).

Among the brachyuran crabs, some species are known to have postlarvae that differ from adults in osmoregulatory capacities. However, a phenomenon more commonly reported is the difference in osmoregulatory capacities of larvae and adults, as related to their differential distributions (see Kalber & Costlow 1968, Foskett 1977). A number of species migrate, raft, or passively disperse as early postlarvae to nearshore areas or up estuaries (Knudsen 1960, Tagatz 1968, Dudley & Judy 1973, Williams 1971, Klein Breteler 1976, Saigusa 1978), and some stages experience marked salinity changes. Changes in the free amino acid pool may in part facilitate tolerance of salinity changes and estuary penetration (Costlow & Sastry 1966). In *Rhithropanopeus harrisii,* which is highly adapted to estuarine conditions, there is relative absence of salinity effects on molt duration in the postlarval stages (Costlow et al. 1966, Hartnoll 1978). In the semi-terrestrial ocypodid *Uca pugilator,* adults hyper- and hypoosmoregulate, but hypoosmoregulation does not become developed until the first crab (second postlarval) stage (Dietrich 1979). A similar pattern appears in *Uca subcylindrica,* which inhabits semi-arid areas and undergoes a strongly abbreviated larval development. Hypoosmotic regulation is evident at least by the megalopa (decapodid) stage and becomes stronger in the first crab stage (Rabalais 1983).

4   PHYLOGENETIC SIGNIFICANCE OF POSTLARVAL DEVELOPMENT

There is a view that a phylogeny derived from larval characters should coincide with adult phylogeny. This was basically the concept furthered by Gurney (1942), although he did acknowledge (p.30) that 'new characters special to the larva itself may arise and obscure to some extent the primitive form.' In decapods, the adults may be modified for their particular habitat requirements, while the larvae are almost all planktonic and therefore not subject to the same selection pressures as the adults (see Rice 1980, 1981a,b, Williamson 1976, 1982a,b). A second view on larval characters in phylogeny is that larvae and adults are modified independently, and larval groupings need not closely correspond to groupings of adults (Gordon 1955).

We suggest that an understanding of phylogenetic utility of developmental stages lies somewhere between these two viewpoints. There are undoubted examples of convergence among decapod larvae (Williamson 1982b), but there are many cases where larval morphology appears to accurately reflect phylogeny. Early postlarval phases in decapod ontogeny, the decapodid (= first postlarva, megalopa, glaucothöe, puerulus, etc.) and the early juveniles (= early postdecapodids), may sometimes provide more useful indications of phylogenetic origins than could be interpreted from larval or adult stages. Thus, an expanded theory on the phylogenetic significance of developmental stages would necessarily accommodate cases in which recently derived specializations, obscuring of ancestral

Figure 11. An example of convergence among brachyuran larvae. (A-D) family Majidae, subfamily Inachinae; (E) family Homolidae. (A) *Achaeus tuberculatus*; (B) *Macrocheira kaempferi*; (C) *Pleistacantha sanctijohannis* (all after Kurata 1969). (D) *Dorhynchus thomsoni* (after Williamson 1982b); (E) *Homola* cf. *barbata* (after Rice & von Levetzow 1967). Note the closer similarity between *Dorhynchus* and *Homola* than between *Dorhynchus* and other inachine majids.
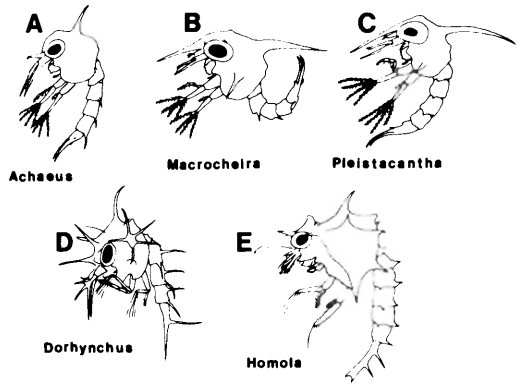
features, and potential for convergence may have been relatively 1) unidirectional, i.e. most pronounced either in the premetamorphic stages (larvae) or the late postlarval stages, 2) bidirectional, i.e. pronounced in both larval and adult stages, 3) non-directional, i.e. characteristic of all stages, or 4) punctuated, i.e. characteristic of isolated developmental stages or sets of stages.

The appeal of decapod larvae in systematics has been partially centered on the hypothesis that convergent evolution among adults may not be manifest extensively in the planktonic zoeae. However, the potential for convergence is probably common among planktonic larvae, as recently derived specializations appear to have extensively modified larval morphology. In the Decapoda many of the extremely spinous larvae such as the 'acanthosoma' stages of sergestoids, the greatly flattened phyllosomas of the Palinuroidea, and the inflated carapaces of the Eryonoidea, are all adaptations for a lengthy pelagic existence. Williamson (1982a) suggested that the flattened bodies of phyllosoma stages may be adaptations enabling them to cling onto scyphozoan hosts rather than as aids for flotation, although it should be noted that these larvae do not attach to the hosts immediately, nor do they remain on the host at all times.

Perhaps the most striking reported example of convergence among decapod larvae is the recent description of the larvae of *Doryhnchus thomsoni* by Williamson (1982b). The unusual larvae of this species (Fig.11) were first collected in 1959, and described by Williamson (1960) as a 'remarkable zoea' probably of the Majidae. The telson and appendages are similar to known majoid zoeas, but the carapace and abdomen bear a large number of spines, unlike any known larvae of the Majoidea. It was suggested, as alternatives, that these unusual larvae might belong to the Tymoloidea (Williamson 1965, Wear & Bathman 1975) or to an undiscovered family outside the Majoidea (Williamson 1976). The multi-spined zoeae are so similar to late zoeae of the Homoloidea that Williamson (1982b) coined the term 'homolomaja' to apply to zoeae which combine characters of the two groups. It is now known that these larvae belong to *D.thomsoni,* a member of the majoid subfamily Inachinae, and a species in which adults 'show no unconventional features' (Williamson 1982b:727). The zoeae and megalopa differ so dramatically from those of other inachine species that assignment even to superfamily level is not immediately obvious. Williamson concludes that the striking differences between the zoea of *D.thomsoni* and zoeae of other Inachinae are the result of recent evolution, but why these recent changes should have produced features resembling those of late homoloid zoeae remains a mystery.
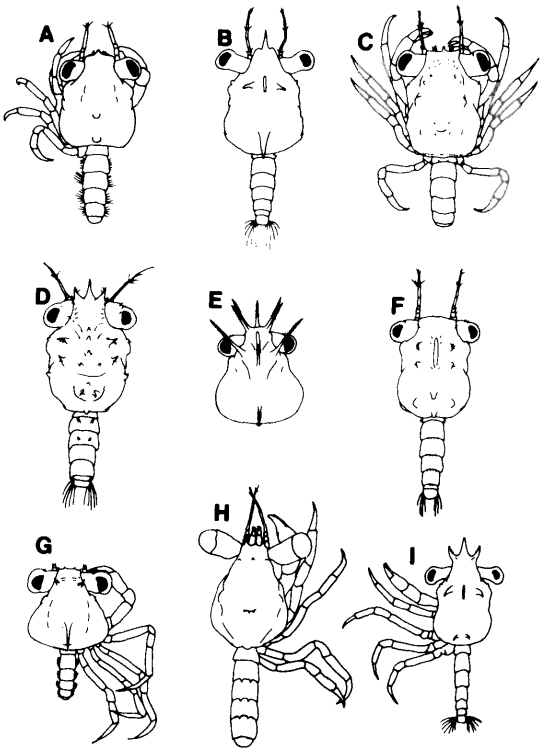
Figure 12. Diversity among megalopae in brachyuran family Majidae. (A) *Dehaanius limbatus* (after Kakati & Sankolli 1975); (B) *Macrocheira kaempferi* (after Kurata 1969); (C) *Libinia dubia* (after Sandifer & Van Engel 1971); (D) *Schizophrys aspera* (after Kurata 1969); (E) *Dorhynchus thomsoni* (after Williamson 1982b); (F) *Pisoides ortmanni* (after Kurata 1969); (G) *Anasimus latus* (after Sandifer & Van Engel 1972); (H) *Inachus dorsettensis* (after Ingle 1977); (I) *Chionoecetes opilio* (after Motoh 1973). Figures slightly modified and not to scale.

Consider now *Dorhynchus thomsoni.* The adults are clearly majids, subfamily Inachinae, but it is equally clear that the zoeae do not conform to the typical majoid zoeal form. Neither does the megalopa stage conform, for it is extremely spinose and unlike other known inachine or even majoid megalopae (Fig. 12). The final clue which established the relationship between zoea and adult was provided by neither zoea, megalopa, nor adult, but by the first crab stage which developed from a captive megalopa. Only by the subsequent examination of a series of juvenile crabs was the adult relationship of the first crab stage confirmed.

After consideration of the above and related evidence, we conclude that postlarval stages, either decapodid or early juvenile, deserve closer examination than has traditionally been paid them in studies of the Decapoda. These stages are to various degrees distinct from zoeae and adults in their morphology, physiology, ecology, and behavior. Phylogenetic information may be gleaned from these stages, as well as from larvae and adults.

A well-demarcated decapodid stage is not characteristic of all decapods. In the Penaeidea, Caridea and Stenopodidea there may be no abrupt transformation between zoeal (mysis) and decapodid stages, and the latter may acquire the adult body form by slight and gradual changes (see sections 2.2.1, 2.2.2, 2.3.1 and 2.3.2). Members of the brachyuran family Hymenosomatidae likewise lack a morphologically unique decapodid, as the zoeae metamorphose directly into a decapodid much like a young crab. In a large number of freshwater decapods and highly adapted semi-terrestrial forms with abbreviated development,
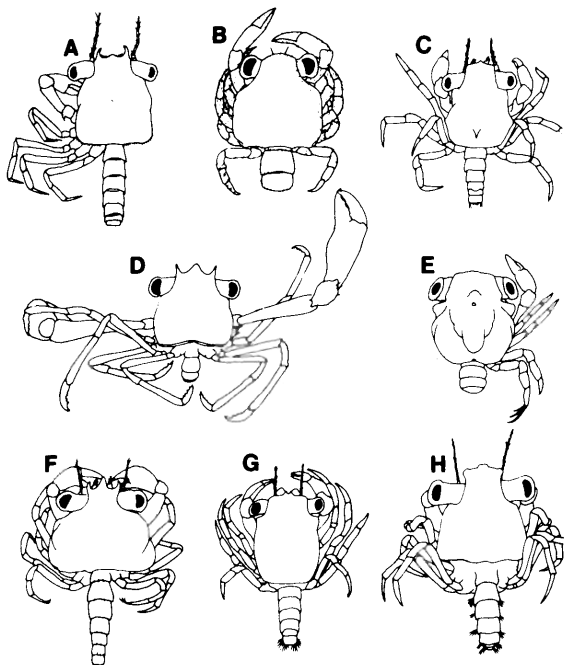
Figure 13. Diversity among megalopae in the brachyuran family Xanthidae. (A) *Hexapanopeus angustifrons* (after Costlow & Bookhout 1966); (B) *Heterozius rotundifrons* (after Wear 1968); (C) *Cycloxanthops truncatus* (after Hong 1977); (D) *Quadrella nitida* (after Garth 1961); (E) *Epixanthus dentatus* (after Saba et al. 1978); (F) *Panopeus herbstii* (after Costlow & Bookhout 1961); (G) *Platyxanthus crenulatus* (after Menu-Marque 1970); (H) *Lophopanopeus leucomanus leucomanus* (after Knudsen 1958). Figures slightly modified and not to scale.

stages are confined to the late developmental period of embryonated eggs, and the young emerge with a body form similar to the adult. However, the young are sometimes erroneously referred to as larvae.

In the remainder of the Decapoda, the decapodid stage is fairly distinct from zoeae and juveniles, although there are exceptions in some additional cases of abbreviated development (see Dobkin 1969, Rabalais & Gore, this volume) and in certain cases among the Caridea where the decapodid differs little from early juveniles. Within some Caridea the decapodid stage differs from most subsequent stages by retaining vestiges of the zoeal epipods on all pereopods, but the carapace appears intermediate between zoeal and juvenile stages. In the remaining decapod groups the decapodid stage (where known) is more clearly distinct from both zoeal and juvenile forms (Figs.1-6). However, among these groups the form of the decapodid varies greatly. Thus, we somewhat disagree with Williamson's (1982a: 84) statement that megalopae 'can usually be identified to an infraorder or superfamily on the basis of adult characters'. While this may hold true at the infraordinal level, it is often impossible to identify (for example) the superfamily of a given brachyuran megalopa, and especially not by strict application of adult characters. The variation of megalopal types in the superfamilies Xanthoidea and Majoidea (Figs.12, 13) illustrates that point.

Although several keys have been published for identification of decapodid stages (e.g. Cook 1965, Dutt & Ravindranath 1975, Mohamed et al. 1968, Williamson 1957), the phylogenetic significance of this stage has only recently been reviewed. Rice (1981b) lamented the incongruence of zoeal and adult classifications and noted (p.1003) that 'since both the adult and the zoeal phases of the Brachyura thus seem to have been affected by convergent evolution, any classificatory evidence from other sources is likely to be of value'; he there-

fore examined characters of the megalopa stage in representatives of the Podotremata of Guinot (1978). Unfortunately, examination of this stage added little to our knowledge of the evolution of the group. Rice (p.1010) concluded 'this review of podotrematous megalopas has therefore not assisted significantly in assessing either the interrelationships of the constituent groups or their overall relationship with the higher Brachyura'.

Rice's study represents, to our knowledge, the only attempt to employ decapodid characters at levels higher than that of family, although Williams (1980) used megalopal characters in establishing the superfamily Bythograeoidea. Many descriptive works include mention of similarities in this stage at the family level and below. For example, characters of the megalopa of *Pisa* have been used as the basis for hypothesized intergeneric relationships (Ingle & Clark 1980). In another approach, the absence of a unique megalopal morphology in decapodids of the Hymenosomatidae has been pointed out as a diagnostic character of that family (Muraoka 1977). References to identification of crustacean larvae listed by Williamson (1982a:90) provided a good starting point for review of other such papers.

Rice (1981b) noted that the megalopa stage possesses features found in both zoeal and juvenile phases, as well as some unique characters. Phylogenetic analyses of these characters have, in limited attempts to date, proven to be no less difficult than those based upon zoeae. Indeed, as the decapodid stage represents a transition from planktonic to benthic life in almost all decapods, it is likely that convergence has in at least some cases rendered this phase to be of limited use to systematists. However, it is also likely that certain megalopal characters, such as the paired sternal spines in many portunids and the recurved hook on the ischium of the cheliped in many xanthids, will prove to be of some phylogenetic significance. We have not attempted to examine all known decapodid stages in the same manner that Rice (1980) reviewed brachyuran zoeae. Rather, our intent is to encourage the study of this stage by pointing out the potential for useful characters for phylogenetic interpretation. Subsequent studies to Rice's (1981b) review of the pcdotremen megalopae and similar studies of decapodids in other groups should soon provide a better understanding of phylogenetic significance within this stage.

We contend that studies of the decapodid stages do not represent the only, nor necessarily the best, alternative technique to establish relationships on the basis of larval or adult morphologies. The earliest of postdecapodid stages, the early juveniles, may prove to be of equal (or in some cases, greater) phylogenetic significance. Zoeae and adults are variously modified according to their habitat. The postdecapodid juvenile is the first stage where all or almost all larval characters are lost, and the general adult body plan is apparent. However, the morphological attributes of the adult are not yet extensively superimposed on this basic plan.

Several pieces of evidence give credence to a hypothesis of plesiomorphy in early postlarval stages. In general these come from studies that demonstrate either 1) the restriction of presumed 'ancestral' characters to postlarval and sometimes earlier stages, or 2) the absence of presumed 'derived' specializations in early postlarval stages as compared to larvae or adults. Evidence to demonstrate either of these phenomena is limited in scope and has not been specifically used to build support for a theory of plesiomorphy in early postlarval stages.

The retention of ancesteral characters in early postlarval stages is, however, supported by our interpretations of papers concerning such subjects as the ontogeny of the decapod median eye (Elofsson 1963, Paterson 1970). The median eye is located dorsally or antero-

dorsally to the protocerebrum between a small pair of apical nerves. A mass of sensory cells here usually contains a band or scattered patches of dark pigment, in some respects comparable to the nauplier eye of those crustaceans that exhibit this structure as larvae and/or adults. Paterson (1970) noted that there is a tendency for ontogenetic degeneration of the median eye, especially during postlarval development. Furthermore, the degree of degeneration varies among higher decapod taxa. The median eye of adult palinurids is less degenerate than that of 'other Reptantia so far investigated', but the median eye of adult palinurids is more degenerate than in adult 'Natantia'. However, the median eye in the puerulus (decapodid) stage of palinurids is comparable to that of adult 'Natantia' (Paterson 1970). Thus, there is a strong suggestion that a potentially ancestral feature is, at least by degree, lost over the course of postlarval ontogeny and that the rate and degree of loss may reflect lineages at higher systematic levels.

At lower systematic levels, a number of examples indicate the ontogenetic diminishment of features that characterize probable ancestral stocks. For instance, Williams (1980) has described the gradual diminishment of eyes that takes place during postlarval ontogeny of *Bythograea thermydron.* The gradual degeneration of eyes and orbital features after the megalopal stage, in which eyes are of a typical size for the Brachyura, strongly suggests that this unusual deep-water species most resembles an ancestral form in its early postlarval stages. We have noted similar degeneration of eyes during postlarval development of fossorial forms, especially among the Thalassinidea. Even in behavior patterns, what appear to be ancestral characteristics are sometimes retained in restricted stages of early postlarval development. For example, the tendency for inhabiting gastropod shells in early postlarval stages of the semi-terrestrial coconut crab *Birgus latro* is postulated to be the retention of ancestral behavior from the hermit crab stock that gave rise to this species (Reese 1968).

Other examples of postlarval transitions from ancestral to derived character states may very well be represented among the numerous cases of postlarval character change noted in the earlier portions of this chapter. However, rather than documenting the degeneration or loss of ancestral characters during postlarval ontogeny, the majority of cases document the addition of specialized characters during this period of postlarval development. Gurney (1942:22-27) made a similar observation in his attempt to determine the degree to which ancestral characters 'lost in adults' may be preserved in larval stages. He expressed surprise at the few instances that could be cited and noted that it was much more common to find adult characters 'appearing directly' during postlarval development. It is precisely for this reason — that is, appearance of adult characters late in development — that limited systematic characters are available for use in the identification of early postlarval stages. For example, *Pasiphaea multidentata* and *P.tarda* do not become morphologically distinct until they reach a carapace length of 12 mm, 3 mm less than the size at maturity (Matthews & Pinnoi 1973). In *Paguristes,* even diagnostic characters of the genus may not be present in early postlarval stages (Provenzano & Rice 1966). The same is true of generic and higher level characters in many members of the Cambaridae (Hobbs 1962, 1981).

Similarly, characters traditionally used for justification of phylogenetic placement have been shown to change or develop progressively during postlarval ontogeny of the Brachyura (Morita 1974, Shen 1935, Yang & McLaughlin 1979). In at least one instance, a study of morphogenesis from juveniles to adults corrected a long standing misconception based upon adult features that were erroneously thought to be of major phylogenetic significance. Certain carapacial grooves of adult astacids, that were formerly thought to be remnants of somite boundaries, were found instead to be mechanically induced secondary features

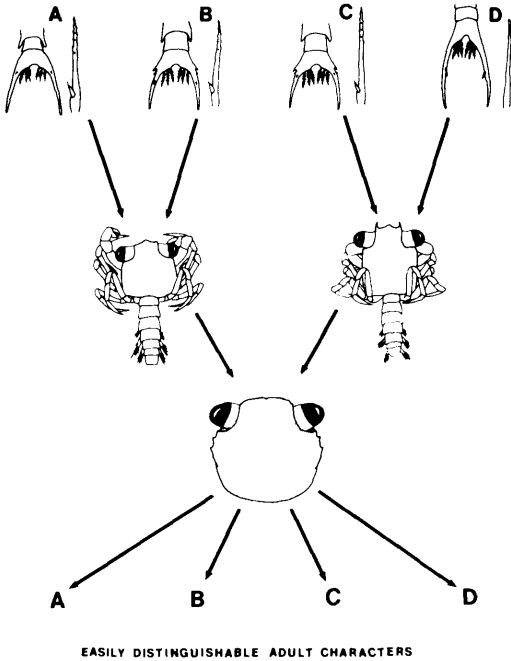EASILY DISTINGUISHABLE ADULT CHARACTERS

Figure 14. Diagram of ontogenetic transition from zoeal stages to adult stages in (A) *Eurypanopeus depressus*, (B) *Panopeus turgidus*, (C) *Panopeus herbstii* forma *simpsoni*, and (D) *Panopeus bermudensis*. Zoeal stages (above) characterized by armature of telson and antenna; development thereafter transcends one of two megalopal forms and common first crab form before adult characters become evident (after Martin et al. 1984).

which resulted from the attachment of muscles to the carapace. Thus, while these grooves can be used for diagnosis of certain systematic groups (presumably as artificial characters), they are not useful in studies of fundamental tagmatization as it applies to higher phylogeny (Albrecht 1981). The implication is that because the juveniles do not show this derived (albeit mechanically induced) character state to the extent of the adults, early post-larvae are less altered from architypal morphology than are later stages.

Also in favor of this opinion is a recent paper by Martin et al. (1984) in which four species of xanthoid crabs were reared from larvae to adult. Using selected characters of the first, third and fifth crab stages, Martin et al. found that phenotypic divergence increases with ontogeny. In addition, whereas all four species were readily identifiable at zoeal and adult stages, distinction was extremely difficult at the first crab stage (Fig.14). Thus, characters that applied to all four species in the first crab stage were considered plesiomorphic, and the later modifications of older crab stages were treated as derived conditions. If early juvenile stages are, in fact, representative of the more plesiomorphic character stages, then similarities detected in first juvenile morphology could unite natural groupings of the Decapoda and be relatively free of recently derived modifications. Present knowledge of this stage is far from complete. However, Martin et al. (1984) noticed similarities in the first crab stage of known ocypodids, in all known portunids, in known grapsids, and in most majids. Unfortunately, many of the characters employed in that study (e.g. mouthpart morphology) seem to be of limited taxonomic value at the first crab stage, and classificatory schemes based on this stage will have to await detailed descriptions of first juveniles in a larger number of decapod families. In particular, carapacial morphology appears to be a sound character for relating brachyurans to the superfamily level at the first crab stage.

The opposing view is that while larval characters are lost in the first juvenile stage, it is not true that recently derived specializations (and considerable potential for convergence) are absent. In the Pinnotheridae, for example, the widened carapace so typical in the adult is already distinguishable in the decapodid or first crab stage (Muraoka 1979, Kurata 1970). However, the highly specialized adaptations of some stages in commensal species might be expected to obscure plesiomorphy by *punctuated* or *non-directional* specialization which may give rise to such morphological forms as 'invasive stages' early in postlarval ontogeny.

It may also be argued that attainment of a crablike body by convergence in the Brachyura, some Paguroidea, and many Galatheoidea does not gradually develop as ontogeny proceeds but is readily apparent in an early juvenile stage. However, it can at least be noted that the first postlarva in each of these examples is less cancroid in form than are the later stages. A striking example is represented by the ontogeny of *Asthenognathus atlantica*, a goneplacid crab superficially similar to the pinnotherids as an adult. In this species the ratio of carapace width to carapace length changes gradually, from 1.14 in the first crab stage to 1.38 in the more pinnotherid-like (by convergence) fourth crab stage (Bocquet 1965).

Changes in carapace morphology from the first juvenile to later juvenile and adult stages are far more dramatic in other Brachyura. In some species these changes are gradual and subtle over the entire course of postlarval development, while in others the change is more dramatic as adult characters are more abruptly superimposed on an initial brachyurized form (Fig. 15). If the morphology of first juvenile stage decapods is going to be useful in systematics, it will probably be in those cases where changes are more dramatic, i.e. where conspicuous modifications greatly mask a more basic form of the first juvenile.
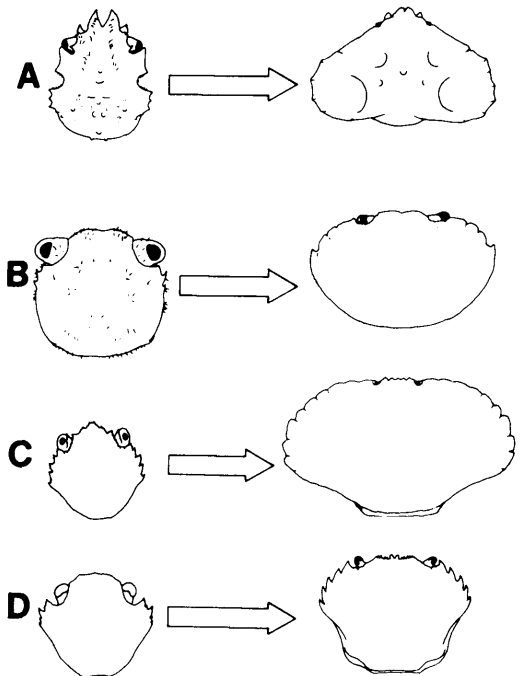
Figure 15. Examples of dramatic change in carapace morphology from juvenile (left) to adult (right) brachyuran crabs. (A) *Eurynolambrus australis* (Majidae) (after Krefft 1952); (B) *Eurytium limosum* (Xanthidae) (after Kurata et al. 1981, Heard 1982); (C) *Cancer pagurus* (Cancridae) (after Lebour 1928, Ingle 1980); *Liocarcinus puber* (Portunidae) (after Lebour 1928, Ingle 1980). Figures slightly modified and not to scale.

Several descriptive studies (e.g. Perez Farfante 1970, Mair 1979, 1981) have dealt with early juvenile stages of economically important species, but morphological comparisons of first stage juveniles have rarely been utilized in systematics. *Dorhynchus thomsoni* provided a good example of one application. For over 20 years both larvae and adults of *D.thomsoni* were known, but it was not known that they constituted life stages of one species until Williamson (1982b) observed a single first crab which died metamorphosing from the megalopa. The link between larvae and adult was realized, and further evidence came from a series of pelagic juveniles in which the characters were intermediate between first crab and adult. Krefft (1952) similarly clarified the systematic position of the majoid *Euryno-lambrus australis* only after observing the characters of the first crab stage. This species had originally been placed in the Pinnotheridae, then transferred to the 'cancerinae' by Miers (1879). Krefft (1952:574) noted that 'these postlarval stages are of the greatest value in the determination of the systematic position of this species'. The 'well-developed, divergent rostra; the incomplete orbit consisting of a supraocular eave' and other characters of the postlarvae positively placed *E.australis* in the Majidae; these and other characters are not readily apparent in the adult (Fig.15). Krefft stated (p.574) that 'the oxyrhynchous characteristics are minimised by this adoption of this cancroid form'.

The probability that decapodid and first juvenile stages are as subject to evolutionary adaptation as zoeae and adults cannot be denied. Indeed, cases may be discovered in which specialization over all life stages has been *non-directional* and pronounced. The extent to which convergence in early postlarval stages has altered basic morphology cannot yet be evaluated for the Decapoda in general. Yet we have shown that, in at least a few cases, examination of these stages has clarified systematic questions unanswerable from studies of larvae and adults. We feel justified, therefore, in pointing out the possible phylogenetic significance of these stages and hope that greater interest in their systematic utility will be forthcoming. Future study of these stages may be undertaken to determine characters for interspecific distinctions, to complete knowledge of life histories, to document ontogenetic changes in discrete organs and functions, to determine rates of growth and development, and to further define ecological roles of postlarvae. Regardless of the impetus for assembly of data, an eventual synthesis of this information could very well lead to a much improved understanding of phylogenetic relationships of the decapod Crustacea.

5 ACKNOWLEDGEMENTS

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