MORPHOLOGICAL DEVELOPMENT, IDENTIFICATION, AND BIOLOGY OF LARVAE OF PANDALIDAE, HIPPOLYTIDAE, AND CRANGONIDAE (CRUSTACEA, DECAPODA) OF THE NORTHERN NORTH PACIFIC OCEAN

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ABSTRACT

All published descriptions of pandalid, hippolytid, and crangonid larvae of the northern waters of the North Pacific Ocean are summarized. Included are recent changes in nomenclature, definitions of terms used in describing the larvae, and procedures for preparing larvae for examination. The general morphology of larvae of the three families is reviewed, and development of the morphological characters used for their identification is discussed. Principal morphological characters and number of larval stages of known larvae in each family are tabulated. Pandalid larvae are keyed to species and stage of development. A synopsis of the most important morphological characters used for identification is given for larvae of each family, genus, and species. Biology of the larvae is reviewed.

Larvae of the Pandalidae, Hippolytidae, and Crangonidae (order Decapoda, tribe Caridea) are common inhabitants of the neritic meroplankton of the northern (temperate and arctic) waters of the North Pacific Ocean. About 135 species of shrimps are found in these waters, and larvae have been described, at least in part, for 46 species. Many of these descriptions, especially of hippolytids and crangonids, are scattered in various foreign scientific journals.

This report summarizes the morphology of described larvae of the Pandalidae, Hippolytidae, and Crangonidae of the northern North Pacific Ocean and gives instructions for examining them. Development of the characters used for identification is discussed, and a generalized key to stage is given. Larvae of each family, genus, and species are characterized morphologically, and the principal morphological characters and the number of the larval stage are tabulated. Illustrated keys to species and stages are provided for 9 of the 13 pandalid species recorded from the northern North Pacific Ocean. Descriptions of larvae of the remaining four species of pandalids have not been published although their probable morphology has been discussed (Haynes 1980a). References to the published descriptions of larvae of each species and a review of the biology of the larvae are provided.

In the synopses of species, I have selected the most distinguishing larval characters; however, these characters may not always be repeated for similar species, and additional characters may be needed for a specific diagnosis. Other distinguishing characters for the larvae discussed here can often be found in the original published descriptions.

An annotated listing of published descriptions precedes the synopsis of each species. When two or more descriptions are listed, the most complete description is given first. Whenever a "?" appears after a species name or stage in the listings, the author of the original description was uncertain of the identification. In these cases, references to the corrected or verified identification are included in the listing. For a few species, descriptions of larvae are based on specimens from the Atlantic Ocean. It should be noted that morphological characters of larvae of the same species from different geographical areas may vary somewhat (Haynes 1978a).

Taxonomic Nomenclature

I used Rathbun's (1904) nomenclature of Pandalidae except for *Pandalus tridens*. After considering both the larval and adult morphology of *P. tridens* (see Rathbun 1902), I give this species full specific rank (Butler 1980; Haynes 1980a) rather than subspecific rank as *P. montagui tridens*, a Pacific subspecies of *P. montagui* Leach 1814.

Nomenclature of the Hippolytidae follows Holthuis' (1947) revision of the genus *Spirontocaris* sensu lato. Holthuis' revision, based on adult morphology, has been verified from larval morphology (Pike and Williamson 1961; Haynes 1981).

Nomenclature of the Crangonidae is based on the

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revision by Kuris and Carlton (1977), with one exception. I use only *Crangon*, rather than *Crangon* and *Neocrangon*, because I agree with Butler (1980) and consider Zarenkov's (1965) separation of the genus *Crangon* into two subgenera, *Crangon* s.s. and *Neocrangon*, to be invalid.

The synopsis of characters of *Crangon septemspinosa* larvae also applies to the characters of *C. affinis* larvae. Needler (1941), Kurata (1964b), and Tesmer and Broad (1964) have described these as two species, but according to Makarov (1967), the two species are synonymous. Descriptions of the lar-

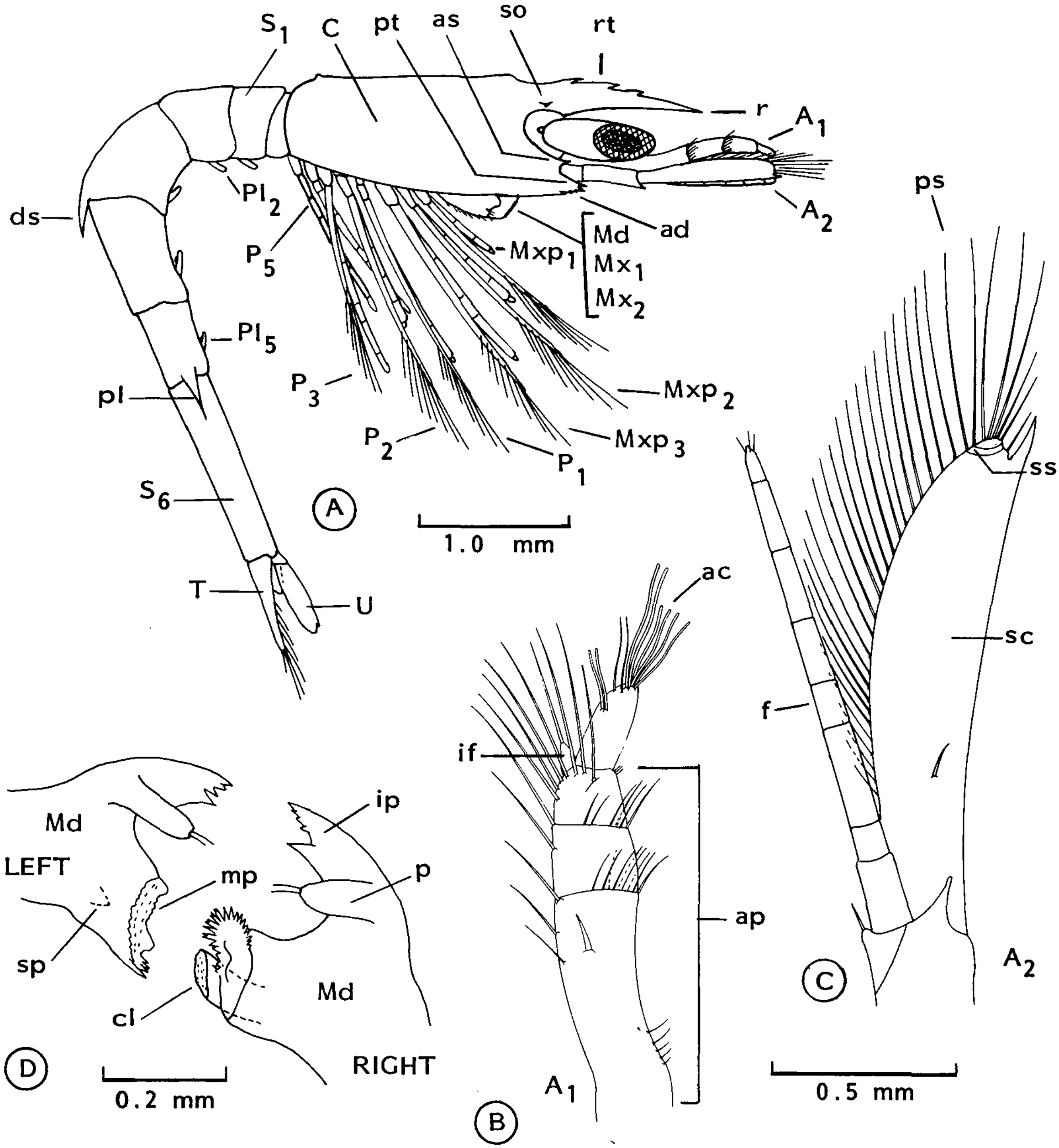

FIGURE 1.–Lateral view and body parts of a diagrammatic decapod shrimp larva. (A) A_1, antennule; A_2, antenna; C, carapace; Md, mandible; Mx_1, maxillule; Mx_2, maxilla; Mxp_1, maxilliped 1; Mxp_2, maxilliped 2; Mxp_3, maxilliped 3; P_1, pereopod 1; P_2, pereopod 2; P_3, pereopod 3; P_5, pereopod 5; Pl_2, pleopod 2; Pl_5, pleopod 5; S_1, somite 1; S_6, somite 6; T, telson; U, uropod; ad, anteroventral denticles; as, antennal spine;

vae of *C. affinis* and *C. septemspinosa* are very similar. More comments on nomenclature for certain species are given in the synopses.

Definition of Terms

I follow Williamson's (1969) terminology for decapod larvae and Haynes' (1979) terminology for larval appendages (Fig. 1). The terms are defined as follows:

abbreviated development – less than five zoeal stages.

carapace length – straight-line distance between the

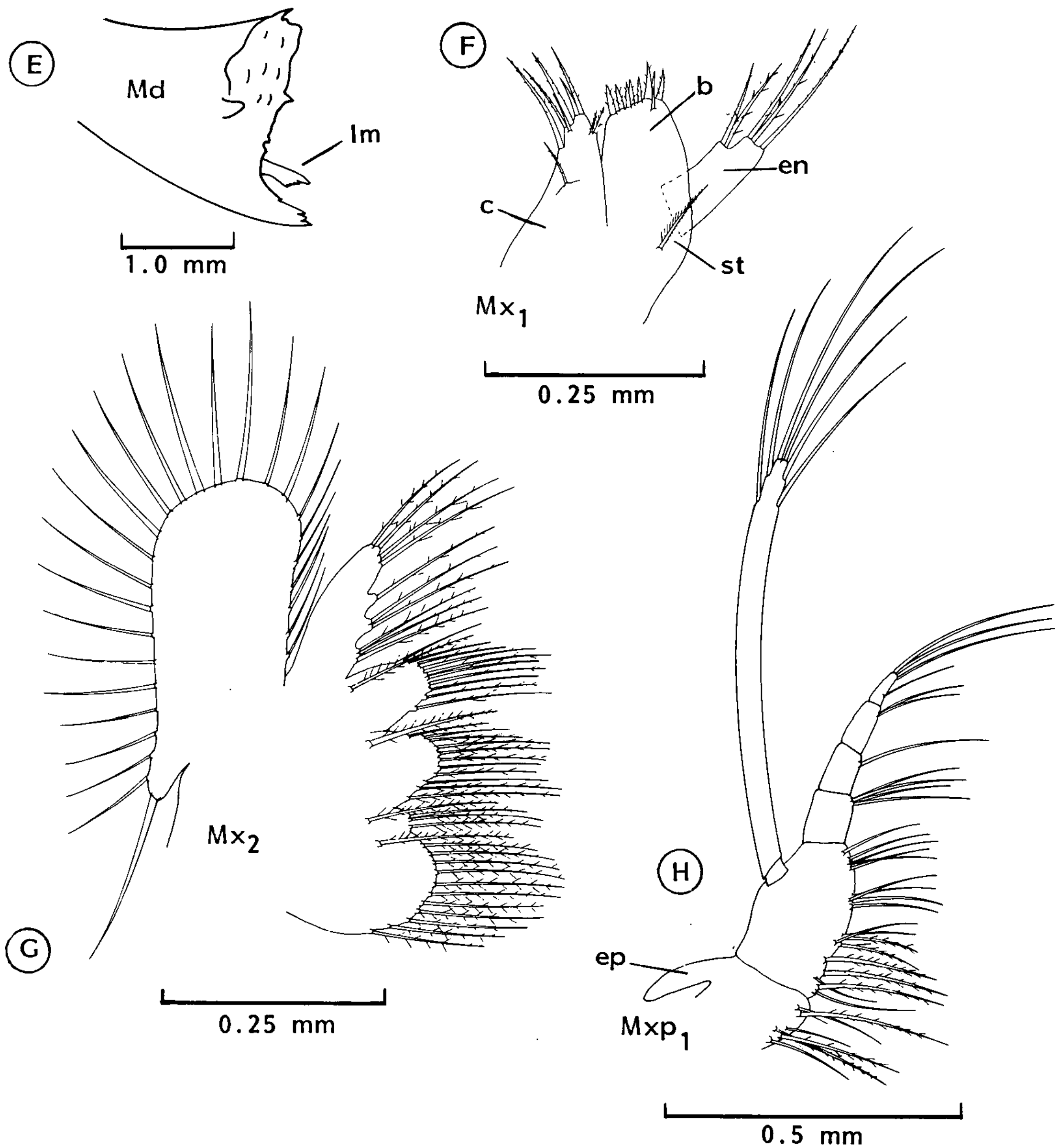

FIGURE 1. – *Continued* – ds, dorsal spine; pl, posterolateral spine; pt, pterygostomian spine; so, supraorbital spine; r, rostrum; rt, rostral teeth. (B) A_1, antennule; ac, aesthetascs; ap, antennule peduncle; if, inner flagellum. (C) A_2, antenna; f, flagellum; ps, plumose setae; sc, scale; ss, scale segments. (D) Md, mandible; cl, curved lip; ip, incisor process; mp, molar process; p, palp; sp, subterminal process. (E) Md, mandible; lm, lacinia mobilis. (F) Mx_1, maxillule; b, basipodite; c, coxopodite; en, endopodite; st, subterminal seta. (G) Mx_2, maxilla. (H) Mxp_1, maxilliped 1; ep, epipodite.

posterior margin of orbit and the middorsal posterior margin of the carapace.

denticles – toothlike projections on anteroventral margin of the carapace.

developed pereopods – segmented pereopods directed vertically under cephalothorax.

juvenile – young form, usually small, sexually immature, and generally resembling adult.

larva – a free-swimming phase in the life cycle of the individual whose morphology (such as body form, appendages, and spination) and habit are different from the adult. The term applies to both zoea and

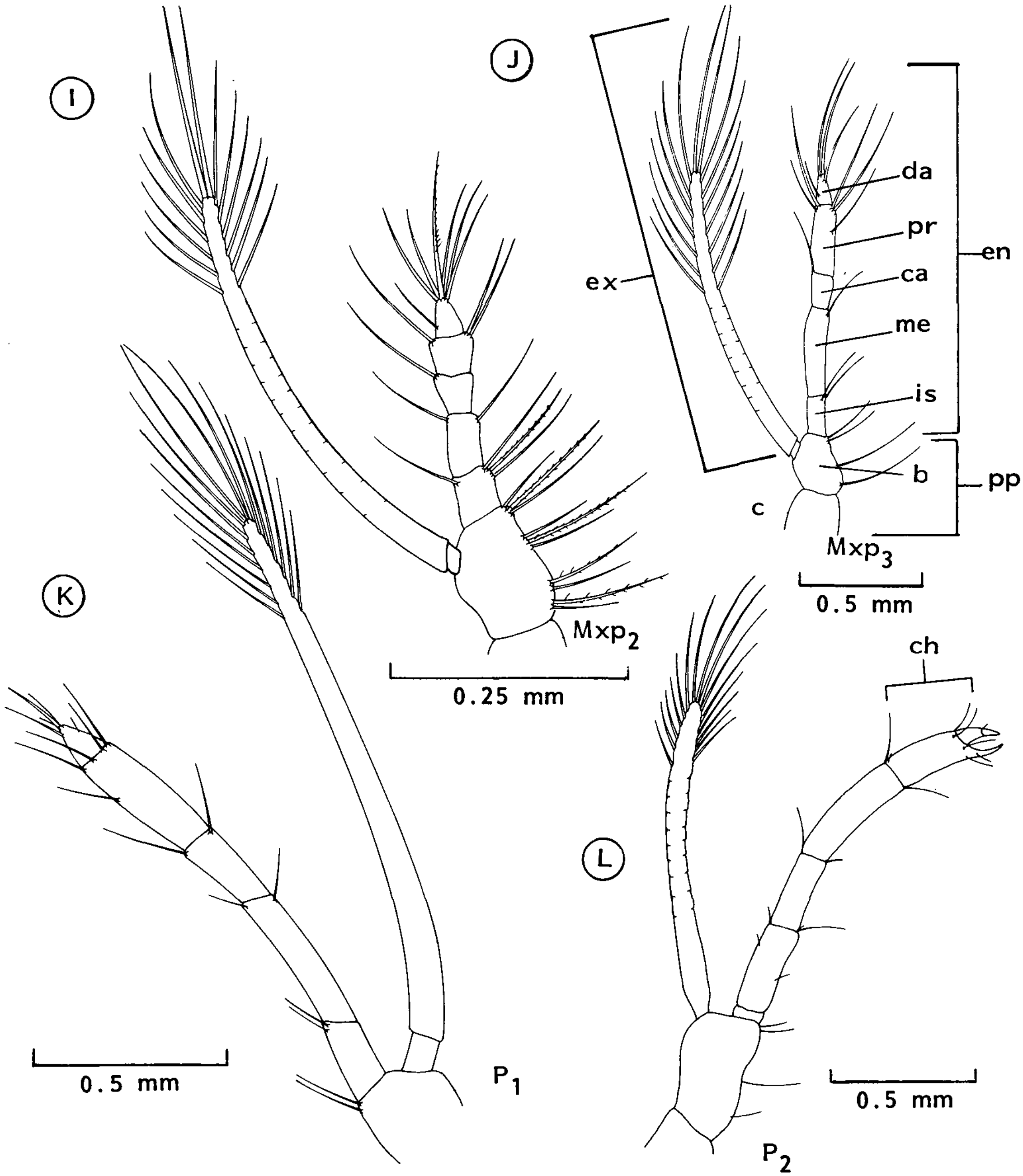

FIGURE 1. – *Continued* – (I) Mxp_2, maxilliped 2. (J) Mxp_3, maxilliped 3; b, basipodite; c, coxopodite; ca, carpopodite; da, dactylopodite; ex, exopodite; en, endopodite, is, ischiopodite; me, meropodite; pp, protopodite; pr, propodite. (K) P_1, pereopod 1. (L) P_2, pereopod 2; ch, chella.

megalopa. (For shrimp, the change from larva to adult is usually somewhat gradual and may include more than one molt.)

megalopa – larva with fully setose natatory pleopods[2] on some or all abdominal somites.

setation formula of telson – setae or spines along the terminal margin of the telson are numbered beginning at the middle of the telson. Thus, 7 + 7 means that the telson has seven pairs of setae along the terminal margin. The first pair is the medial pair.

setose – having setae (bristles).

spine – a sharp, pointed projection, usually long and narrow.

spinose – with many spines.

spiniform – shaped like a spine.

spinule – small spine.

spinulose – with small spines.

stage – intermolt.

subchelate – the dactylopodite (finger) folds against the preceding segment (propodite), as in the first pereopod of crangonid adults.

length – total body length: distance (mm) from the anterior tip of the rostrum to the posterior tip of

[2]In the Decapoda, the development of setose pleopods does not always provide a convenient and clear distinction between zoeal and postzoeal stages. Several species of Pandalidae metamorphose gradually into the postzoeal stage (see Haynes 1976). The term "megalopa", therefore, may include a single stage or several stages depending upon the species. In this paper, the number of larval stages includes all stages before the juvenile stage, regardless of whether the megalopa has one or more stages.

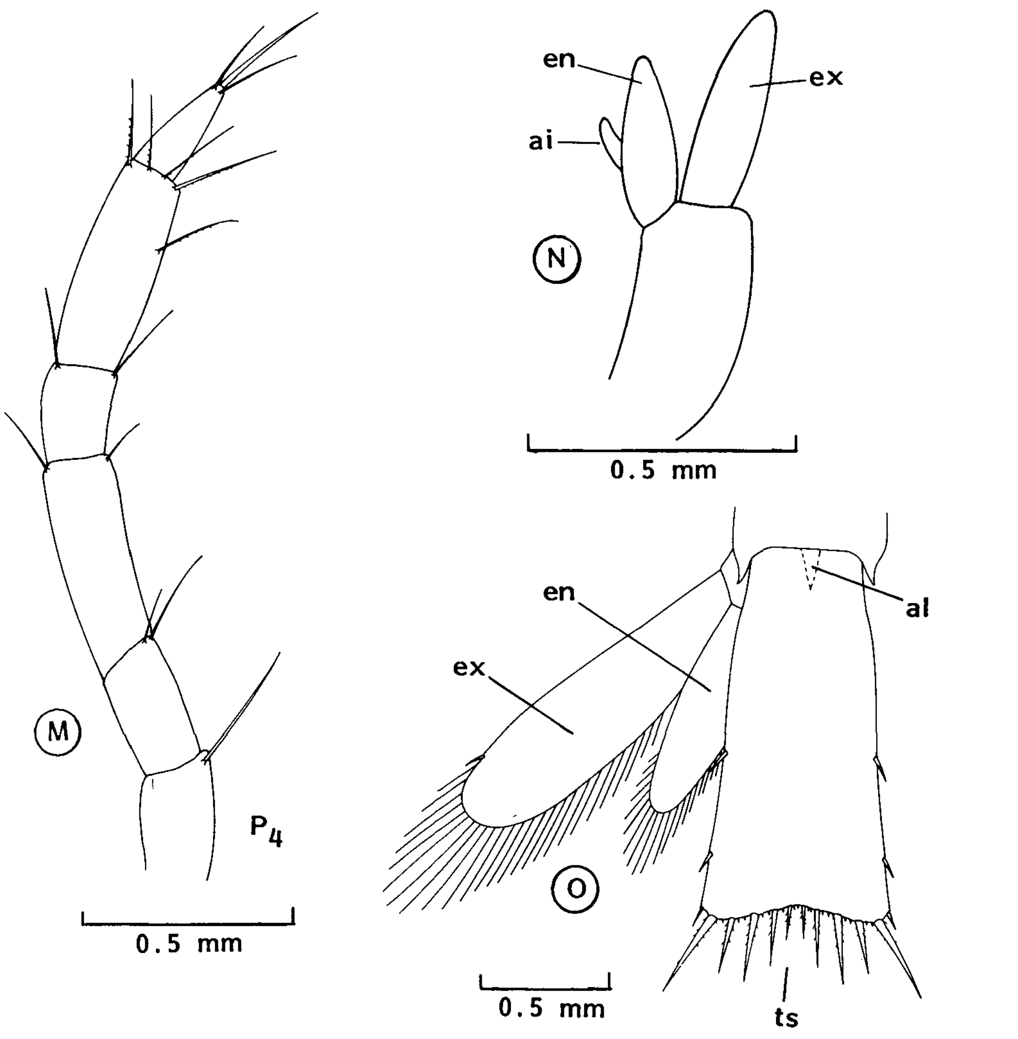

FIGURE 1. – *Continued* – (M) P_4, pereopod 4. (N) Pleopod; ai, appendix interna; en, endopodite; ex, exopodite. (O) Tail fan; al, anal spine; en, endopodite; ex, exopodite; ts, telsonic spines.

telson, excluding telsonic setae or spines.

unabbreviated development – five or more zoeal stages.

undeveloped pereopod – unsegmented pereopod directed anteriorly under cephalothorax.

zoea – larva with natatory setae on maxillipeds, without setose natatory pleopods on some or all abdominal somites 1-5.

Examination Procedure

It is usually necessary to dissect the animal and mount certain appendages on a slide before the identification characters can be used. Visibility of segmentation is often improved by clearing specimens for several days in 10% KOH or full-strength lactic acid. Larvae can be dissected with pins designed for mounting small insects. (The pins are available from most biological supply companies.) After dissecting the larva, place the appendage in a drop of mounting medium (I use Turtox[3] CMC red mounting medium) and cover with a cover glass. Gently press the cover glass to splay hairs and setae and make them easier to examine and count. After mounting the appendages, examine them using a dissecting microscope.

GENERAL MORPHOLOGY OF LARVAE

Pandalid, hippolytid, and crangonid larvae have three major body regions (Fig. 1): head, thorax, and abdomen. The head and thorax are coalesced and are dorsally covered by a common, unjointed cephalothoracic shield, the carapace. The body is divided into 19 true somites which, with their appendages (Fig. 1), are grouped as follows:

1) The head, five indistinguishable fused somites, is covered by the anterior portion of the carapace (C) and has the first five pairs of appendages: antennules (or first antennae) (A_1), antennae (A_2), mandibles (Md), maxillules (Mx_1), and maxillae (Mx_2).
2) The thorax is composed of eight somites that are dorsally fused with, and covered by, the carapace. Each somite has a pair of appendages: Somites 1-3 each have a pair of maxillipeds (Fig. 1A, Mxp_{1-3}); somites 4-8 each have a pair of pereopods (Fig. 1A, P_{1-5}).
3) The abdomen is composed of six somites (Fig. 1A, S_{1-6}) and a terminal segment, the telson (T). The first five somites each have a pair of pleopods (Fig. 1A, Pl_{2-5}). The sixth somite has uropods (U). The uropods, when present with the telson, comprise the tail fan.

[3]Reference to trade name does not imply endorsement by the National Marine Fisheries Service, NOAA.

CHARACTERS USEFUL FOR IDENTIFICATION OF LARVAE

Understanding the development of morphological characters is necessary for identifying genus, species, and stage of larval development. The following discussion emphasizes the characters most useful for identification. It should be noted, however, that these characters are based on relatively few species of a limited number of genera. For instance, in the family Hippolytidae, the subterminal seta is apparently absent in larvae of *Hippolyte clarki* from British Columbia (Needler 1934) but present in larvae of *H. inermis* and *H. varians* from European waters (Williamson 1957a). The seta may also be present in undescribed *Hippolyte* larvae from the northern North Pacific Ocean. Characterization of the family Pandalidae is based on only two genera, *Pandalopsis* and *Pandalus*. In the northern North Pacific Ocean, described larvae of these two genera develop exopodites only on pereopods 1-2 or 1-3, never on pereopods 1-4. Other genera of the family (e.g., *Plesionika*) may develop exopodites on pereopods 1-4 (Williamson 1957b). Additional descriptions of decapod larvae from the northern North Pacific Ocean will undoubtedly modify the morphological characterizations given here.

Rostrum

In pandalid larvae, the rostrum (Fig. 1A, r) is always long (at least one-third the carapace length). For most species of Pandalidae, the rostrum is styliform in Stage I and does not have teeth (Fig. 1A, rt) until about Stage III. The exceptions are *Pandalopsis coccinata*, *P. dispar*, and *Pandalus platyceros*. In these species, the rostrum is curved in Stage I and has teeth in all larval stages (Berkeley 1930; Kurata 1964a; Price and Chew 1972). In Stage I *Pandalus prensor*, the rostrum curves ventrally between the eyes (Mikulich and Ivanov 1983).

The rostrum of hippolytid larvae may be absent, or, if present, from minute to long. The rostrum is usually without dorsal or ventral teeth in all stages. European specimens of *Eualus gaimardii*, an exception, have two dorsal rostral teeth in the last zoeal stage (Stage V) (Pike and Williamson 1961). If the rostrum is short to long in Stage I, it is also styliform, except in Stage I *Lebbeus groenlandicus* (Fig.

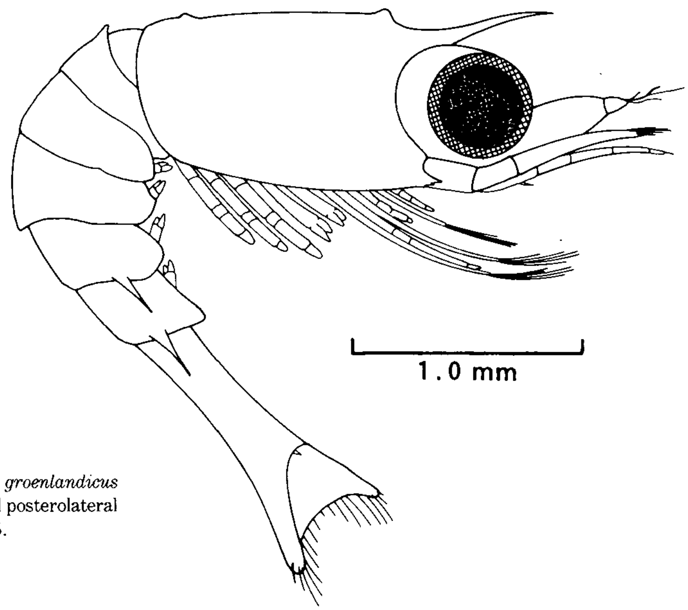

FIGURE 2. – Stage I zoeae of *Lebbeus groenlandicus* showing slightly sinuous rostrum and posterolateral spines on abdominal somites 4 and 5.

2) and *L. polaris*, which have a slightly curved rostrum (Haynes 1978b, 1981). In Stage I *Heptacarpus camtschaticus*, the rostrum is minute and curves slightly downward following the dorsal contour of the eyes (Haynes 1981).

In crangonid larvae, the rostrum is long, spiniform, and without teeth in all larval stages except for Stage I zoeae of *Sclerocrangon zenkevitchi* and *S. boreas*, which lack a rostrum, and Stage I zoeae of *Paracrangon echinata*, which have a spinulose rostrum (Birshteyn[4] and Vinogradov 1953; Kurata 1964b; Makarov 1968).

Spines on the Carapace

The presence or absence of certain spines on the carapace is useful for distinguishing between families and identifying one or more stages. The larval carapace (Fig. 1A, C) may have supraorbital spines (so), pterygostomian spines (pt), antennal spines (as), and anteroventral denticles (ad). Supraorbital spines are absent in all larval stages of the Crangonidae. For pandalid and hippolytid larvae, supraorbital spines are usually absent in Stage I and the megalopa, but present in the intermediate zoeal stages. However, there are some exceptions to these generalizations. Larvae of *Pandalus hypsinotus* have supraorbital spines only in Stages II and III, and larvae of *P. kessleri* have supraorbital spines only in Stage II (Kurata 1955; Haynes 1976). Larvae of *P. prensor* are without supraorbital spines in all larval stages (Mikulich and Ivanov 1983). In the Hippolytidae, *Spirontocaris spinus*, *S. lilljeborgii*, and probably *S. phippsii* have supraorbital spines in all larval stages (the spines are minute in Stage I). *Spirontocaris ochotensis* has minute supraorbital spines in Stage I; whether supraorbital spines develop later is unknown. *Lebbeus groenlandicus*, a species with abbreviated development, has supraorbital spines only in Stage II and the megalopa (Stage III) Pike and Williamson 1961; Haynes 1978b, 1981). In all three families, pterygostomian spines are usually present in all larval stages. Antennal spines are often absent in Stage I but usually develop in later stages. Anteroventral denticles are most prevalent in the early stages and usually, but not always, disappear during larval development. Branchiostegal and hepatic spines are rarely, if ever, present in the larval stages.

Eyes

Development of the eyes is the same for nearly all members of the three families. The eyes are compound and sessile in Stage I and are stalked in later stages. The exception, Stage I *Pandalopsis coccinata*, has compound eyes that are only partially attached to the carapace (Kurata 1964a).

Antennules

In the Pandalidae and nearly all hippolytid and

[4]Translator's spelling of "Birstein".

crangonid larvae, the peduncle of the antennule (Fig. 1B, ap) is unsegmented in Stage I and becomes three segmented later, usually in Stage II. The exceptions are Stage I *Sclerocrangon boreas*, which has a 3-segmented antennule; Stage II *Eualus suckleyi* and *E. fabricii*, which have 2-segmented peduncles; and both Stages I and II *Lebbeus polaris* and *L. groenlandicus*, which have unsegmented peduncles.

In Stage I pandalid and hippolytid larvae, the inner flagellum (Fig. 1B, if) of the antennule is usually a plumose seta, whereas in Stage I crangonid larvae, it is usually a setose spine. The only described exceptions are Stage I larvae of *Pandalus prensor*, *Sclerocrangon boreas*, *S. salebrosa*, and *S. zenkevitchi*. In Stage I *Pandalus prensor*, the inner flagellum is spine shaped and has a few simple setae medially. In Stage I *S. boreas*, *S. salebrosa*, and *S. zenkevitchi*, the inner flagellum is an oblong projection that is naked except for a few minute, simple setae terminally (Birshteyn and Vinogradov 1953; Makarov 1968; Haynes 1978b, 1981; Mikulich and Ivanov 1983).

Antennae

Segmentation of the tip of the antennal scale (Fig. 1C, sc, ss) is an important characteristic for distinguishing crangonid larvae from pandalid and hippolytid larvae. In crangolid larvae, the scale tip is unsegmented in all stages. In pandalid and hippolytid larvae, the scale tip is unsegmented in only four species: *Pandalopsis coccinata*, *Pandalus kessleri*, *P. prensor*, and possibly *Heptacarpus* (= *Spirontocaris*) *tridens* (Needler 1934; Kurata 1955, 1964a, b; Mikulich and Ivanov 1983). The absence of segmentation of the scale tip of *Pandalopsis coccinata*, *Pandalus kessleri*, and *P. prensor* is related to the extremely precocious development of these species. *Heptacarpus tridens*, however, has unabbreviated development (Needler 1934) and, presumably, a segmented tip. Needler (1934) may not have observed segmentation of the scale in *H. tridens* because she based her description on unstained larvae (staining emphasizes segmentation (Haynes 1976)).

Mandibles

Mandibles (Fig. 1D) are described for most pandalid larvae, but descriptions of mandibles for hippolytid and crangonid larvae in the northern North Pacific Ocean are usually limited to Stage I. I have supplemented these limited descriptions with information on larvae from other areas, particularly the North Sea. Descriptions of late stage larvae from the northern North Pacific Ocean are needed, however, to verify development of mandibles in hippolytid and crangonid larvae.

Zoeae of Pandalidae, Hippolytidae, and Crangonidae have similar mandibles in all stages, and both molar and incisor processes are present. In Stage I, the incisor processes of the left and right mandibles are typically biserrate or triserrate. The number of teeth increases in later stages. In some species, the left mandible also has a subterminal tooth and a lacinia mobilis (movable spine adjacent to incisor process; Fig. 1E). The subterminal tooth and lacinia mobilis are usually, if not always, absent on the right mandible. In the Crangonidae, the incisor process eventually becomes a molar process, usually at the megalopa.

The most distinctive character of the mandible is the absence of a palp in the zoeal stages. This palp first appears in the megalopa or first juvenile stage of Pandalidae and in the megalopa or later stages of the Hippolytidae. In one exception, *Pandalopsis coccinata*, the palp is present and segmented as early as Stage I (Kurata 1964a). The palp is absent in all stages of Crangonidae, including the adults.

The mandibular palp of the Hippolytidae may develop somewhat later than the mandibular palp of the Pandalidae. For instance, in some species of Hippolytidae, the palp may not appear until as late as the third or fourth juvenile stage (Lebour 1936), and in some genera, such as *Hippolyte*, the absence of the palp in the adult may mean the palp is absent in the larvae also. The palp eventually becomes three segmented in the Pandalidae and two segmented in the Hippolytidae.

Maxillules

Lebour (1930) stated that *Pandalus* larvae have no subterminal seta (Fig. 1F, st) on the basipodite of the maxillule (Fig. 1F, Mx_1, b). Yet, the seta is present in some or all larval stages of *Pandalus kessleri*, *P. tridens*, *P. stenolepis*, *P. borealis*, *P. goniurus*, *P. jordani*, *P. hypsinotus*, and *Pandalopsis coccinata*. The seta is also present in the early stages of *Pandalus montagui*, *P. propinquus*, *Pandalina brevirostris*, and *Dichelopandalus bonnieri* that were collected from waters off Great Britain (Needler 1938; Kurata 1955, 1964a; Pike and Williamson 1964; Modin and Cox 1967; Lee 1969; Haynes 1976, 1978a, 1979, 1980a). The subterminal seta is absent in hippolytid and crangonid larvae described from the North Pacific Ocean but is present in larvae of *Hippolyte inermis* and *H. varians* from waters off Great Britain (Lebour 1931). According to Gurney (1942) and Pike and Williamson (1964), the seta is probably the vestige of an exopodite; however, Williamson (1982) regards it as a vestigial epipodite or pseudoepipodite.

Maxillae

Development of the scaphognathite (exopodite) of the maxilla (Fig. 1G) is related to development of the larvae. Most species that lack precocious development have a scaphognathite that is not lobed proximally and has only a few (usually ⩽ 12) plumose setae only on its outer margin. The scaphognathite gradually becomes lobed proximally in subsequent stages, and the outer margin becomes fringed with many plumose setae. In species with precocious development, the scaphognathite is lobed proximally and fringed with many plumose setae in Stage I.

The number of plumose setae is sometimes used for distinguishing Stages I or II of similar species. For instance, Stage I zoeae of *Pandalus borealis* and *P. goniurus* are similar morphologically, and in these species the scaphognathite has 12 and 5 plumose setae, respectively. In later stages, however, the number of plumose setae fringing the scaphognathite becomes too great to be practical for distinguishing zoeae of similar species.

Maxillipeds

The number of natatory setae on the exopodite of each maxilliped (Fig. 1H-J) is helpful for distinguishing Stage I hippolytid and crangonid zoeae from Stage I pandalid zoeae. All Stage I hippolytid and most Stage I crangonid zoeae have 4, 5, 5 natatory setae on the exopodites of maxillipeds 1-3. In the Pandalidae, all Stage I pandalid zoeae, except *Pandalus stenolepis*, have ⩾ 8 natatory setae on the exopodites of at least two pairs of maxillipeds. Stage I *P. stenolepis*, however, cannot be differentiated from Stage I hippolytid and crangonid zoeae based only on natatory setae because Stage I *P. stenolepis* also has 4, 5, 5 natatory setae on the exopodite of each maxilliped.

The absence or reduction in numbers or size of natatory setae on the exopodites of maxillipeds is associated with markedly precocious development. This is especially true for *Pandalopsis coccinata*, *Sclerocrangon boreas*, and *S. zenkevitchi*. Each of these species has only one zoeal stage before molting to the megalopa. In *P. coccinata*, the natatory setae are absent from the third maxilliped. In *S. boreas*, the number of natatory setae on maxillipeds 1-3 is 2, 3, 4, respectively; and the setae are reduced in size. *Sclerocrangon zenkevitchi* zoeae do not have natatory setae on the maxillipeds.

Apparently, the absence or reduction in size of natatory setae prevents zoeae from being planktonic. Zoeae of *S. boreas* and *S. zenkevitchi* (collected at sea) cling to the pleopods of the adult (Birshteyn and Vinogradov 1953; Makarov 1968). Zoeae of *P. coccinata* are rarely, if ever, taken in plankton tows (Kurata 1964a).

Pereopods

The presence of exopodites (Fig. 1J, ex) on certain pereopodal pairs is an important morphological character for identifying shrimp larvae. Exopodites are present on pereopods 1, 1 and 2, 1-3, or 1-4, depending on genus or species (Fig. 1K-M).

Species with unabbreviated development usually develop an exopodite on each pereopod. In most species with ⩾ 5 zoeal stages, the exopodites are characteristically small, naked, and nonfunctional at Stage I but functional (have natatory setae) at Stage II or III. Development of exopodites on pereopods tends to be suppressed in species with < 5 zoeal stages.

In the Pandalidae, species that have segmented pereopods directed vertically under cephalothorax (i.e., developed pereopods) in Stage I–*Pandalopsis coccinata*, *Pandalopsis dispar*, *Pandalus kessleri*, *Pandalus danae*, *Pandalus hypsinotus*, and *Pandalus prensor*–also have exopodites or vestigial exopodites on pereopods 1 and 2. Species that have unsegmented pereopods directed anteriorly under cephalothorax (i.e., undeveloped pereopods) in Stage I–*Pandalus tridens*, *P. stenolepis*, *P. borealis*, *P. goniurus*, and *P. jordani*–also have exopodites on pereopods 1-3 (the exopodites are undeveloped in Stage I and develop in later stages). An exception is *P. platyceros*, which in Stage I has developed pereopods and exopodites on pereopods 1-3 (Haynes 1980b).

Of the Hippolytidae, only larvae of the genus *Lebbeus* have developed pereopods in Stage I. *Lebbeus polaris* has vestigial exopodites on pereopods 1 and 2 in Stage I and on pereopod 1 in Stage II. *Lebbeus groenlandicus* has vestigial exopodites on pereopods 1 and 2 in Stage I and no exopodites on pereopods in Stages II or III (Haynes 1978b, 1981).

In the Crangonidae, most species with developed pereopods in Stage I (*Argis crassa*, *A. lar*, *A. dentata*, *Sclerocrangon boreas*, and *S. salebrosa*) are either without exopodites or have rudimentary exopodites. An exception is *S. zenkevitchi*, which has an exopodite on pereopod 1 in Stage I (Birshteyn and Vinogradov 1953).

Which pereopods have exopodites can differ for different species of a genus. For example, the genus *Pandalus* includes larvae that have exopodites on pereopods 1 and 2 or 1-3 (Haynes 1980a). The genus *Eualus* includes larvae that have exopodites on pereopods 1-3 or 1-4 (Haynes 1981). Larvae of *Crangon* typically have an exopodite only on pereopod 1; however, larvae of *C. franciscorum angustimana* have exopodites on pereopods 1 and 2 (Haynes 1980b).

Abdomen

The presence or absence of posterolateral spines (Fig. 1A, pl) on the abdomen is often an important character for identifying the families of caridean larvae. Specimens of pandalid larvae from the northern North Pacific Ocean do not have posterolateral spines. Crangonid larvae, however, usually have posterolateral spines on somite 5, except for larvae of *Sclerocrangon boreas* and *S. zenkevitchi* (Birshteyn and Vinogradov 1953; Makarov 1968). Larvae of Hippolytidae also have posterolateral spines. Posterolateral spines are present on somites 4 and 5 in *Lebbeus* larvae and on somite 5 in *Hippolyte* larvae, but are absent in *Heptacarpus* larvae.

The number of abdominal somites with posterolateral spines is not always the same for all species of a genus. For instance, *Spirontocaris* larvae and most *Eualus* larvae have posterolateral spines on somites 4 and 5, or 5. In some species of *Eualus*, the posterolateral spines may be absent.

Most pandalid and hippolytid larvae lack dorsal spines or teeth on the abdomen. The only known exception is *Spirontocaris spinus*, which has a distinct dorsal tooth on the posterior margin of abdominal somite 3 in the megalopa (Stage VI) (Pike and Williamson 1961).[5]

Of the described crangonid larvae of the northern North Pacific Ocean, only *Crangon septemspinosa*, *C. affinis*, *C. alaskensis*, and *C. franciscorum angustimana* have a dorsal spine (Fig. 1A, ds) on somite 3 (Makarov 1967; Loveland 1968; Haynes 1980b). *Paracrangon echinata* has dorsal spines on somites 1-5 (Kurata 1964b).

Some zoeae have spinules on the posterior margins of abdominal somites. These spinules are present in zoeae of *Pandalus platyceros*, *P. tridens*, *P. stenolepis*, *Eualus suckleyi*, *E. fabricii*, *Argis crassa*, *A. dentata*, and *Crangon communis*. The number and size of spinules decrease in later stages.

[5]This spine is present in all subsequent stages (juvenile and adult) and should probably not be regarded as a larval character.

Telson

The shape of the telson is useful in determining the stage of development of caridean larvae. For most Stage I-III pandalid and hippolytid larvae, the posterior margin of the telson is about twice the width of the anterior margin. At about Stage IV, the shape of the telson narrows posteriorly, and from Stage IV on, the posterior margin of the telson is noticeably less than twice the anterior width. Eventually, the telson narrows posteriorly, as in the adult. Although the telson remains triangular in all stages of crangonid larvae, it is somewhat narrower in the megalopa or first juvenile stage than in earlier stages.

For caridean larvae with unabbreviated development, the typical number of telsonic setae (Fig. 1O, ts) is 7 + 7 in Stage I and 8 + 8 in later stages. These numbers of telsonic setae are seldom exceeded in later stages and are often reduced by either loss or transformation of certain pairs (usually pairs of 2 or 3) into small setae or hairs.

A larger number of telsonic spines are more commonly associated with abbreviated development than with unabbreviated development (Gurney 1942; Pike and Williamson 1964), and this is generally true for caridean larvae of the North Pacific Ocean. For example, *Pandalus kessleri*, a species with four larval stages, has 16 + 16 telsonic setae in Stage I, and *Pandalopsis coccinata*, a species with three (or two) larval stages, has 28 + 28 telsonic setae in Stage I (Haynes 1980a). Examples can also be found in the other families of Caridea. In the Crangonidae, *Sabinea septemcarinata* has 16 + 16 telsonic setae in Stage I and three larval stages, whereas *Sclerocrangon salebrosa* has 22 + 22 telsonic setae in Stage I and one larval stage (Williamson 1960; Makarov 1968). In the Hippolytidae, *Lebbeus polaris* has 9 + 9 telsonic setae in Stage I and four larval stages; *L. groenlandicus* has a total of 21 telsonic setae in Stage I and three larval stages (Haynes 1978b, 1981).

All larvae of Hippolytidae except larvae of the genus *Hippolyte* have an anal spine (Fig. 1O, al). For *Hippolyte* larvae, the anal spine is absent in all described stages. When pandalid and crangonid larvae have unabbreviated development, the anal spine usually appears at about Stage II in pandalid larvae and about Stage IV in crangonid larvae.

However, the presence of an anal spine has little value in the identification of pandalid and crangonid larvae with abbreviated development. In pandalid larvae with abbreviated development, the anal spine first appears at different stages in different species.

For example, the spine is present in Stage I *Pandalus kessleri*, but absent in *P. hypsinotus* until Stage III. The stage at which the anal spine first appears in crangonid larvae with abbreviated development has not been reported.

KEY TO STAGE OF DEVELOPMENT

Larvae of most of the species in this report can be keyed to stage based on development of the eyes and tail fan (Key I; Table 1). Key I is mostly applicable to species whose larval development is not markedly abbreviated (i.e., those with ≥ 5 zoeal stages). In species with unabbreviated development, exopodites on pereopods are characteristically undeveloped in Stage I and usually have natatory setae beginning at Stage II or III. Most of the species excluded from the key (Table 2) have ≤ 4 zoeal stages, and exopodites on pereopods are either absent in all stages, vestigial in Stages I and II, or have natatory setae as early as Stage I. Key I is limited because it does not differentiate between the latest stages and uses only one or two characters, which may be absent in damaged specimens.

For pandalid shrimp, Key I can be supplemented by keys to stages for each species (i.e., Keys IV and VI-XI, which have characters not given in Key I and distinguish between the latest stages). With a few

TABLE 1.—Species included in keys.

Pandalidae Haworth 1825	Hippolytidae Bate 1888	Crangonidae White 1947
Pandalopsis Bate 1888	*Eualus* Thallwitz 1892	*Argis* Krøyer 1842
P. coccinata Urita 1941	*E. barbatus* (Rathbun 1899)	*A. crassa* (Rathbun 1899)
P. dispar Rathbun 1902	*E. fabricii* (Krøyer 1841)	*A. dentata* (Rathbun 1902)
Pandalus Leach 1814	*E. gaimardii* (H. Milne Edwards 1837)	*A. lar* (Owen 1839)
P. borealis Krøyer 1838	*E. herdmani* (Walker 1898)	*Crangon* Fabricius 1798
P. danae Stimpson 1857	*E. macilentus* (Krøyer 1841)	*C. affinis* de Haan 1849
P. goniurus Stimpson 1860	*E. pusiolus* (Krøyer 1841)	*C. alaskensis* Lockington 1877
P. hypsinotus Brandt 1851	*E. suckleyi* (Stimpson 1864)	*C. communis* Rathbun 1899
P. jordani Rathbun 1902	*Heptacarpus* Holmes 1900	*C. dalli* Rathbun 1902
P. kessleri Czerniavski 1878	*H. brevirostris* (Dana 1852)	*C. franciscorum angustimana* Rathbun 1902
P. platyceros Brandt 1851	*H. camtschaticus* (Stimpson 1860)	*C. septemspinosa* Say 1818
P. prensor Stimpson 1860	*H. paludicola* (Holmes 1900)	*Mesocrangon* Zarenkov 1965
P. stenolepis Rathbun 1902	*H. tridens* (Rathbun 1902)	*M. intermedia* (Stimpson 1860)
P. tridens Rathbun 1902	*Hippolyte* Leach 1815	*Paracrangon* Dana 1852
	H. clarki Chace 1951	*P. echinata* Dana 1852
	Lebbeus White 1847	*Sabinea* J. C. Ross 1835
	L. groenlandicus (Fabricius 1775)	*S. septemcarinata* (Sabine 1824)
	L. polaris (Sabine 1821)	*Sclerocrangon* G. O. Sars 1883
	Spirontocaris Bate 1888	*S. boreas* (Phipps 1774)
	S. arcuata Rathbun 1902	*S. salebrosa* (Owen 1839)
	S. lilljeborgii (Danielssen 1859)	*S. zenkevitchi* Birstein and Vinogradov 1953
	S. murdochi Rathbun 1902	
	S. ochotensis (Brandt 1851)	
	S. phippsii (Krøyer 1841)	
	S. spinus (Sowerby 1805)	
	S. spinus var. *intermedia* Makarov 1941	

TABLE 2.—Species that cannot be keyed to stage of development using Key I.

Pandalidae	Hippolytidae	Crangonidae
Pandalopsis	*Lebbeus*	*Argis*
P. coccinata	*L. groenlandicus*	*A. crassa*
P. dispar	*L. polaris*	*A. dentata*
Pandalus		*A. lar*
P. danae (Stage III)		*Sclerocrangon*
P. hypsinotus (Stage III)		*S. boreas*
P. kessleri		*S. salebrosa*
P. platyceros		*S. zenkevitchi*
P. prensor		*Sabinea*
P. stenolepis (Stage III)		*S. septemcarinata*

exceptions, Key I can be used to identify larval stages of *Pandalus hypsinotus*, *P. danae*, and *P. stenolepis*. The exceptions are in Stage III *P. hypsinotus*, the endopodite of the uropods is setose and nearly the same length as the exopodite, and in Stage III *P. danae* and *P. stenolepis*, the endopodite is setose and somewhat shorter than the exopodite.

Key I.—Generalized key to stages of most species of pandalid, hippolytid, and crangonid larvae described from waters of the northern North Pacific Ocean. (This key cannot be used for all species, see Table 2 for exceptions.)

1. Uropods absent 2
   Uropods present 3

2. Eyes sessile; telson with 7 + 7 setae. . . . Stage I
   Eyes stalked; telson with 8 + 8 setae . . Stage II

3. Posterior width of telson about twice its anterior width. Endopodite of uropod (Fig. 1O, en) with relatively few setae and noticeably shorter than exopodite (Fig. 1O, ex) . . . . Stage III
   Posterior width of telson noticeably less than twice its anterior width. Endopodite of uropod setose and about as long as exopodite . . . . Stage IV and later

LARVAL CHARACTERS OF FAMILIES

Crangonid larvae are relatively easy to distinguish from pandalid or hippolytid larvae; however, pandalid and hippolytid larvae often are difficult to distinguish from each other, especially in the early stages. Briefly, the characteristics of crangonid larvae are 1) the tip of the antennal scale is always unsegmented, 2) the inner flagellum of the antennule is a setose spine or oblong projection, 3) an exopodite is usually only on pereopod 1 and never on pereopods 3-5, and 4) in later stages, pereopod 1 is subchelate, and the telson widens posteriorly. No known pandalid or hippolytid larvae possess this combination of characters.

The following set of characters, although not without exceptions, is probably the most useful set for distinguishing between pandalid and hippolytid larvae of the northern North Pacific Ocean. Pandalid larvae 1) always have a long rostrum (greater than 1/4 carapace length) that has teeth from Stage III on, 2) the basipodite of the maxillule has a subterminal seta, 3) exopodites are only on pereopods 1-2 or 1-3, 4) the abdomen lacks posterolateral spines, and 5) an anal spine is absent in Stage I. On the other hand, hippolytid larvae 1) have a rostrum that is long and without teeth (especially from Stage III on), 2) in all stages, the basipodite of the maxillule lacks a subterminal seta, 3) exopodites are on pereopods 1-2, 1-3, or 1-4 (rather than only on pereopods 1-2 or 1-3), 4) the abdomen has posterolateral spines, and 5) an anal spine is present in Stage I (except larvae of the genus *Hippolyte*).

Late-stage (Stage IV and later) pandalid and hippolytid larvae can often be distinguished from each other by shape of eyes and distance between bases of antennules. The eyes of pandalid larvae taper toward the base, and the distance between bases of antennules is more than the width of an antennule. The eyes of hippolytid larvae are almost cylindrical, and the distance between antennules is less than the width of an antennule. In Stages I-III, distinctions in the shape of eyes and distance between bases of antennules are usually not useful.

Shape of the larva is often helpful in distinguishing between pandalid and hippolytid larvae during the initial sorting. Pandalid larvae, when viewed laterally, have nearly straight antennules, whereas the antennules of many hippolytid larvae curve upward. The abdomen of pandalid larvae appears slightly longer than the abdomen of hippolytid larvae in relation to length of the larva as a whole. These two characters are difficult to quantify and are best learned through examination of specimens of known identity. Additional morphological characters that distinguish larvae of the Pandalidae, Hippolytidae, and Crangonidae are given in the synopsis of each family.

PANDALIDAE

(Genera *Pandalopsis* and *Pandalus*)

In all stages, rostrum long, styliform, or slightly sinuate; plumose seta on inner flagellum of antennule (Fig. 1B, A_1, if); maxillule with or without subterminal seta (Fig. 1F, Mx_1, st) on basipodite; abdomen without dorsal spines, keels, or posterolateral spines; pereopod 1 never subchelate. In Stage I, supraorbital spine absent; rostrum with teeth in some species; anal spine absent in some species. In early stages of most species, antennal scale segmented at tip. In Stages I and II of some species with abbreviated development, vestigial exopodites on pereopods 1 and 2 or 1-3. In later stages, developed exopodites on pereopods 1 and 2 or 1-3, never on 1-4; setose setae on endopodite of each pleopod (Stage V

TABLE 3.—Principal morphological characteristics and number of larval stages of known larvae of pandalid shrimp of the northern North Pacific Ocean. + = yes; − = no.

Species	Pereopods bearing an exopodite	Pereopods poorly developed in Stage I	Spinules on abdominal somites	Denticles on carapace margin	No. of telson spines in Stage I	No. of larval stages
Pandalopsis coccinata	1-2	—	—	—	28 + 28	3
P. dispar	1-2	—	—	—	12 + 12	7
Pandalus kessleri	1-2	—	—	—	16 + 16	4
P. danae	1-2	—	—	—	7 + 7	6
P. hypsinotus	1-2	—	—	—	7 + 7	7
P. platyceros	1-3	—	+	+	8 + 8	5
P. prensor	1-2	—	—	—	9 + 9	5
P. tridens	1-3	+	+	+	7 + 7	8
P. stenolepis	1-3	+	+	+	7 + 7	6
P. borealis	1-3	+	—	—	7 + 7	6
P. goniurus	1-3	+	—	—	7 + 7	6
P. jordani	1-3	+	—	—	7 + 7	13

on); telson does not widen posteriorly, has > 1 pair of lateral spines (Stage IV on).

The principal morphological characters and number of larval stages of known larvae of pandalid shrimp of the northern North Pacific Ocean are summarized (Table 3, modified from Haynes 1980b).

Genus *Pandalopsis* Bate

Larval development abbreviated; larvae relatively large (⩾ 10.0 mm in Stage I). In all described stages, rostrum with teeth; carapace without denticles; antennal flagellum as long as or longer than body; thoracic appendages noticeably long and thin; abdominal somites without spines or spinules, somites not flared laterally. In Stage I, pereopods segmented; telson with at least 12 + 12 setae; telson jointed with abdominal somite 6.

Pandalopsis coccinata **Urita**

Only Stage I described, known parentage; figure 7 in Kurata (1964a).

Eyes partially fused with carapace; antennal flagellum same length as body; mandibular palp with 3 segments; seta on basipodite of maxillule; rudimental exopodite on maxilliped 3 and pereopods 1 and 2; telson discoid with 55 or 56 setae (Fig. 3). Length: Stage I, 15.5 mm. Range: Japan (Kurata 1964a), no depth given.

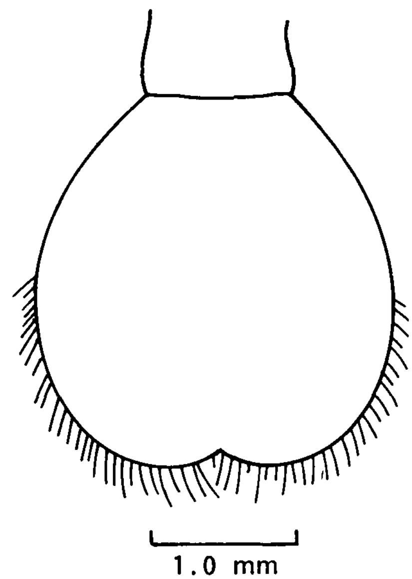

FIGURE 3.—Telson, Stage I zoea of *Pandalopsis coccinata*.

Pandalopsis dispar **Rathbun**

Possibly 7 larval stages.

Stage I, known parentage; Stages II, III, and V?, from plankton; figures 11-13 in Berkeley (1930).

In all stages, basipodite of maxillule without subterminal seta. In Stage I, eyes sessile; antennal flagellum about 1/4 longer than body. Telson fan shaped in early stages. Until at least Stage V, mandibles without palps; developed exopodites on maxilliped 3 and pereopods 1-2. Length: Stage I, 10.0 mm. Range: Pribilof Islands, Bering Sea to Manhattan Beach, OR; depth, 46-649 m (Butler 1980).

Key II.—Larval stages of *Pandalopsis dispar*.

1. Rostrum curves dorsally (Fig. 4); exopodites on pereopods without natatory setae . . . Stage I

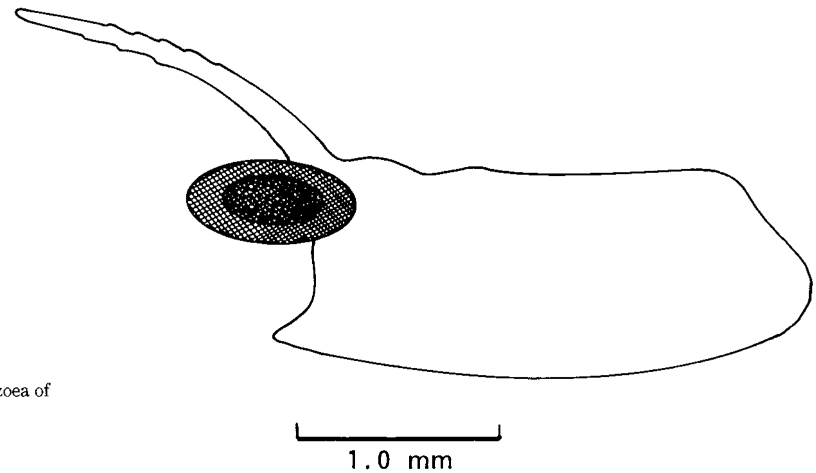

FIGURE 4.–Carapace, Stage I zoea of *Pandalopsis dispar*.

Rostrum horizontal; exopodites on pereopods with natatory setae 2

2. Uropods absent; length of larvae < 13.0 mm . . . . Stage II
Uropods present; length of larvae > 13.0 mm 3

3. Endopodite of uropod noticeably shorter than exopodite; length of larvae ≅ 16.0 mm . . . . Stage III
Endopodite and exopodite of uropod same length; length of larvae > 16.0 mm . . . . Stage IV and later[6]

Genus *Pandalus* Leach

Most species with unabbreviated development. In all stages, thoracic appendages not especially long or thin. In Stage I, larvae usually 5-6 mm long; rostrum usually without teeth; pereopods usually undeveloped and tucked under cephalothorax; telson with 7 + 7 setae; telson not jointed with abdominal somite 6. In early stages of some species, anteroventral margin of carapace with denticles; posterior margin of abdominal somites with spinules.

***Pandalus borealis* Krøyer**[7]

Six larval stages.

Stages I-V, VI (megalopa), and VII and VIII (juveniles); all stages from both known parentage and plankton; figures 1-7 in Haynes (1979).

Stage I, known parentage; Stages II-VII from plankton; figures 1-3 in Kurata (1964a).

Stage I, known parentage; Stages II-VI from plankton; figures 7 and 8 in Berkeley (1930).

Stages I-V from plankton; described as "*P. propinquus* (?)" by Stephensen (1912); figures 22-31 in Stephensen (1912).

Stage III from plankton; described as "*Spirontocaris* larva Nr. 4" by Stephensen (1916); figure 11 in Stephensen (1916). Also described as *P. propinquus*, Stage VI? by Stephensen (1916); figure 17 (chelae only) in Stephensen (1916).

Stage IV from plankton; described as "*Dymas typus*" (?) by Krøyer (1861, as cited in Stephensen 1935). No figures.

"Post larval" from plankton; Plate VII in Sars (1900). Probably megalopa of *P. borealis* (see Haynes 1979).

Not Stages I-VIII *P. borealis* as described by Sars (1900) and figured in Plates I-VI. Correct identity, *Caridion gordoni* (see Berkeley 1930; Lebour 1930).

In all described stages, carapace and abdominal somites not flared laterally; basipodite of maxillule

[6]A later larval stage, probably Stage V or VI, characterized by rostrum with 25 dorsal spines: 1 spine near tip, 14 dorsal spines, 10 ventral spines. Chela of pereopod 2 (Fig. 1, P_2, ch) developed, and carpopodite (Fig. 1, ca) with a few faint segments; abdominal somites and pleopods essentially adult; telson narrows posteriorly and has 7 + 7 slightly plumose, terminal setae and 6 pairs of single lateral spines. Length: 30.0 mm (Berkeley 1930).

[7]Larvae of *Pandalus borealis* and *Pandalus goniurus* are often found together in plankton. They are especially similar in the early stages and are difficult to distinguish. For identification of these two species, I have included Table 4, which lists by larval stage the most readily observable differences for both species. In general, larvae of *P. goniurus* are smaller than those of *P. borealis*. In Stages I-III, *P. goniurus* larvae have fewer setae on the antennal scale and certain mouth parts than *P. borealis* larvae. From Stage IV to megalopa, the rostrum of *P. borealis* has more dorsal teeth, pereopod 2 is more developed, and the pleopods are fringed with more setae than larvae of *P. goniurus* (Haynes 1979).

with subterminal seta. Carapace usually with denticles on anteroventral margins in Stages I-V. Rostrum without teeth until Stage III; rostral tip bifid in Stage V. In Stage I, exopodites of maxillipeds 1, 2, and 3 with 5 or 6, 13 or 14, and 16 natatory setae, respectively; pereopods tucked under carapace; left mandible with a lacinia mobilis; basipodite of maxillule with 9 spinulose spines terminally; scaphognathite of maxilla with 12 setae along outer margin. Length: Stages I-VI, 6.5-20.2 mm. Range: Sea of Japan to Chukchi Sea to Columbia River mouth (northwestern United States); Barents Sea to North Sea; western Greenland to Gulf of Maine; depth, 16-1,380 m (Butler 1980).

Key III.—Larval and first juvenile stages of *Pandalus borealis* (see footnote 7 and Table 4).

1. Eyes sessile; pleopods absent; telson with 7 + 7 setae . . . . Stage I
   Eyes stalked; pleopods present as minute buds; telson with 8 + 8 setae 2

2. Rostrum without teeth; pereopods 4 and 5 tucked under cephalothorax; uropods enclosed . . . . Stage II
   Rostrum with ≥ 1 dorsal tooth at base; pereopods 4 and 5 extend ventrally; uropods free . . . 3

3. Rostrum with 1 or 2 dorsal teeth at base; antennal flagellum with 8 segments and same length as scale; endopodite of uropod about 1/3 length of exopodite . . . . Stage III
   Rostrum with ≥ 4 dorsal teeth; antennal flagellum with ≥ 15 segments and longer than scale; endopodite of uropod > 1/2 length of exopodite 4

4. Rostrum with 4-8 dorsal teeth (usually 6), without ventral teeth; tip of rostrum styliform; pleopods with a few small setae at tip; endopodite of uropod about 2/3 length of exopodite . . . . Stage IV
   Rostrum with > 8 dorsal teeth and ≥ 4 ventral teeth; tip of rostrum bifid; pleopods setose; endopodite of uropod nearly as long as expodite 5

5. Rostrum with 9-12 dorsal teeth and 4 or 5 small ventral teeth; carapace with supraorbital spine; telson with 2 spines on each lateral margin; lateral margins of telson nearly parallel . . . . Stage V
   Rostrum with > 12 dorsal teeth and ≥ 6 distinct ventral teeth; carapace without supraorbital spine; telson with ≥ 4 spines on each lateral margin; lateral margins of telson taper posteriorly 6

6. Mandibles without palps; exopodites on maxillipeds and pereopods reduced in size; lateral margins of telson converge posteriorly but widen slightly at junction with posterior margin . . . . Stage VI (megalopa)
   Mandibles with palps; vestigial exopodites on maxillipeds and pereopods; telson with lateral margins converging to narrow tip, as in adult . . . . Stage VII (first juvenile)

Pandalus danae **Stimpson**

Six larval stages.
Stage I, known parentage; Stages II-VI, from plankton; figures 3-5 in Berkeley (1930).

In all described stages, carapace without denticles on anteroventral margin; basipodite of maxillule without subterminal seta; posterior margins of abdominal somites without spinules. In Stage I, thoracic appendages developed; naked exopodites on pereopods 1 and 2; telson jointed with abdominal somite 6. Length: Stages I-VI, 5.7-17.0 mm. Range: Resurrection Bay, AK, to Point Loma, CA; depth, intertidal to 185 m (Butler 1980).

Key IV.—Larval stages of *Pandalus danae*.

1. Eyes sessile; carapace without supraorbital spine; exopodites on pereopods 1 and 2 without natatory setae . . . . Stage I
   Eyes stalked; carapace with supraorbital spines; exopodites on pereopods 1 and 2 with natatory setae 2

2. Rostrum without teeth; uropods enclosed . . . . Stage II
   Rostrum with teeth; uropods free 3

3. Rostrum with 2 or 3 minute dorsal teeth at base; endopodite of uropods noticeably shorter than exopodite . . . . Stage III
   Rostrum with ≥ 8 teeth dorsally; endopodite of uropods same length as exopodite 4

4. Pleopods small, slightly cleft buds; telson widens slightly posteriorly . . . . Stage IV

TABLE 4.—Morphological characteristics for distinguishing between larvae of *Pandalus borealis* and *P. goniurus* reared in situ in Kachemak Bay, Alaska (from Haynes 1979).

Stage and characteristic	*Pandalus borealis*	*Pandalus goniurus*
Stage I zoea:		
Mean total length	6.7 mm (range 6.5-7.3 mm; 25 specimens)	4.0 mm (range 3.7-4.2 mm; 10 specimens)
Number of plumose setae fringing antennal scale	19	9
Number of spines terminally on basipodite of maxillule	9	5
Number of plumose setae on scaphognathite (in addition to single proximal seta)	11	4
Number of natatory setae on each exopodite:		
maxilliped 1	5-6	4
maxilliped 2	13-14	8
maxilliped 3	16	12
Stage II zoea:		
Mean total length	7.5 mm (range 6.7-8.2 mm; 25 specimens)	5.9 mm (range 4.5-5.3 mm; 10 specimens)
Number of plumose setae fringing antennal scale	about 25	about 19
Number of natatory setae on each exopodite:		
maxilliped 1	7	6
maxilliped 2	16	12
maxilliped 3	18	14
pereopods 1, 2, 3	16, 16, 12	12, 8, 8
Stage III zoea:		
Mean total length	9.5 mm (range 9.0-10.0 mm; 10 specimens)	6.2 mm (range 6.0-6.6 mm; 10 specimens)
Rostrum	1-2 conspicuous teeth	1 inconspicuous tooth
Antennal flagellum	8-segmented	3-segmented
Antennal scale	about 30 setae	about 20 setae
Stage IV zoea:		
Mean total length	13.0 mm (range 12.6-13.2 mm; 10 specimens)	7.7 mm (range 6.8-8.3 mm; 10 specimens)
Rostrum	6-7 dorsal teeth	2 dorsal teeth
Antennal flagellum	about 1½ times length of scale, extending past tips of plumose setae	longer than scale but not extending past tips of plumose setae
Propodite of pereopod 2	projected anteriorly about 1/2 length of dactylopodite	projected anteriorly only slightly
Pleopods	segmented, pleopod 2 about 1/2 height of abdominal somite	unsegmented, pleopod 2 about 1/3 height of abdominal somite
Stage V zoea:		
Mean total length	16.0 mm (range 15.2-17.1 mm; 10 specimens)	10.3 mm (range 8.2-11.3 mm; 10 specimens)
Rostrum	9-12 dorsal teeth; tip bifid; 45 partially developed ventral teeth	5-6 dorsal teeth; tip not bifid (but may show slight protuberance); no ventral teeth
Chela of pereopod 2	fully formed	not fully formed, propodite extension about 1/2 length of dactylopodite
Pleopods	with appendix interna; fringed with plumose setae; 2 as long or longer than height of abdominal somite	without appendix interna; 2-4 simple setae terminally; pleopod 2 about 2/3 height of abdominal somite
Stage VI (megalopa):		
Mean total length	18.5 mm (range 17.4-20.2 mm; 5 specimens)	13.8 mm (range 11.1-15.8 mm; 6 specimens)
Rostrum	13-15 dorsal teeth, 6-7 ventral teeth	8-9 dorsal teeth, 4-5 ventral teeth

Pleopods distinct and biramous; sides of telson parallel or narrow posteriorly 5

5. Carapace with supraorbital spine; exopodites on maxillipeds and pereopods have natatory setae . . . . Stage V
Carapace without supraorbital spine; exopodites on maxillipeds and pereopods naked and vestigal . . . . Stage VI (megalopa)

Pandalus goniurus Stimpson
(see footnote 7)

Six larval stages.
Stages I-V, VI (megalopa), and VII (first juvenile), all from both known parentage and plankton; figures 1-7 in Haynes (1978a).
Stages I-VII from plankton; figure 2 in Makarov (1967).
Stage I, known parentage; figure 1 in Ivanov (1965).

In all stages, carapace and abdominal somites not flared laterally; subterminal seta on basipodite of maxillule. In Stages I-V, carapace usually with denticles on anteroventral margin. In Stage I, pereopods 1-5 tucked under carapace; exopodites of maxillipeds 1-3 with 4, 8, and 12 natatory setae, respectively; lacinia mobilis on left mandible; 5 spinulose spines terminally on basipodite of the maxillule; 5 setae along outer margin of scaphognathite of maxilla. Rostrum without teeth until Stage IV (in Stage III, rostrum with beginning of a tooth at base); rostral tip becomes bifid in Stage VI. Length: Stages I-VI, 3.7-15.8 mm. Range: Sea of Japan to Chukchi Sea to Puget Sound, WA; 5-450 m (Butler 1980).

Key V.—Larval and first juvenile stages of *Pandalus goniurus* (see footnote 6 and Table 4).

1. Eyes sessile; pleopods absent; telson with 7 + 7 setae . . . . Stage I
Eyes stalked; pleopods present as minute buds; telson with 8 + 8 setae 2

2. Rostrum without teeth; pereopods 3-5 tucked under cephalothorax; uropods enclosed . . . . Stage II
Rostrum either with undeveloped or developed teeth; all pereopods extended ventrally; uropods free 3

3. Rostrum with undeveloped tooth at its base; antennal flagellum 3 segmented and about 2/3 length of scale; endopodite of uropod about 1/3 length of exopodite . . . . Stage III
Rostrum with ≥ 2 dorsal teeth; antennal flagellum with ≥ 6 segments and longer than scale (not including setae); endopodite of uropod nearly same length as exopodite 4

4. Rostrum with 2 dorsal teeth; antennal flagellum does not extend beyond plumose setae of antennal scale; chela of pereopod 2 not formed; width of telson increases posteriorly . . . . Stage IV
Rostrum with > 2 dorsal teeth; antennal flagellum extends beyond plumose setae of antennal scale; chela of pereopod 2 nearly or fully formed; lateral margins of telson nearly parallel or narrow posteriorly 5

5. Carapace with supraorbital spine; rostrum with 5 or 6 dorsal teeth, no ventral teeth; tip of rostrum styliform (may have undeveloped bifid tip); lateral margins of telson nearly parallel . . . . Stage V
Carapace without supraorbital spine; rostrum with dorsal and ventral teeth; tip of rostrum bifid; lateral margins of telson narrow posteriorly 6

6. One or two setae between several posterior dorsal teeth of rostrum; 2-segmented mandibular palp without setae; exopodites of maxilliped 3 and pereopods present but reduced; carpopodite of left and right pereopods 2 with 20-25 and 7-9 joints, respectively . . . . Stage VI (megalopa)
One or two setae between most, if not all, rostral teeth; 3-segmented mandibular palp with spiniform setae; no exopodites on maxilliped 3 and pereopods; carpopodites of left and right pereopods 2 with 29 and 11 joints, respectively . . . . Stage VII

Pandalus hypsinotus Brandt

Seven larval stages.
Stages I-VI, VII (megalopa), and VIII-IX (juveniles), known parentage; figures 1-6 in Haynes (1976).
Stage I, known parentage; Stages II-V, from plankton; figures 5-6 in Kurata (1964a).
Stage I, known parentage; Stages II and III, from

plankton; figures 6 (only Stage I figured) in Berkeley (1930).

In all described stages, carapace without denticles on anteroventral margin; posterior margins of abdominal somites without spinules. In Stage I, thoracic appendages segmented, dactyli undeveloped; naked exopodites on pereopods 1 and 2; telson not jointed with abdominal somite 6. Beginning in Stage III, basipodite of maxillule with subterminal seta; anal spine present. Length: Stages I-VII, 5.5-12.8 mm. Range: Sea of Japan to western Bering Sea; Norton Sound to Puget Sound, WA; depth, 5-460 m (Butler 1980).

Key VI.—Larval stages of *Pandalus hypsinotus*.

1. Eyes sessile; naked exopodites on pereopods ....Stage I
   Eyes stalked; exopodites on pereopods with natatory setae 2

2. Rostrum without teeth; uropods enclosed ....Stage II
   Rostrum with ⩾ 1 dorsal tooth at base; uropods free 3

3. Rostrum with dorsal tooth at base and no ventral teeth; exopodites on maxilliped and pereopods with natatory setae ....Stage III
   Rostrum with ⩾ 11 dorsal teeth and ⩾ 2 small ventral teeth; naked, vestigial exopodites on maxillipeds and pereopods..........4

4. Rostrum with 11-13 dorsal teeth and 2 or 3 small ventral teeth; tip of rostrum not bifid; mandibular palps unsegmented; telson margins nearly parallel but widen slightly posteriorly ....Stage IV
   Rostrum with > 13 dorsal teeth and > 3 ventral teeth; tip of rostrum bifid; mandibular palp with 3 segments; telson slightly wider at midlength or narrows posteriorly 5

5. Bilobed pleopods without setae; telson slightly wider at midlength...............Stage V
   Biramous pleopods with setae; telson narrows posteriorly 6

6. Carpopodite of left and right pereopods 2 with 19 and 7 or 8 joints, respectively; pleopods with setae only at tip; telson with 3 pairs of dorsolateral spines..........Stage VI
   Carpopodite of left and right pereopods 2 with 24 or 25 and 10 joints, respectively; pleopods setose; telson with ⩾ 4 pairs of dorsolateral spines ....Stage VII (megalopa)

Pandalus jordani Rathbun

Thirteen larval stages.

Stages I-XIII, known parentage; figures 1-7 in Modin and Cox (1967).

Stages I-XIII, Stages XIV and XV (juveniles), all from both known parentage and plankton; figures 1-15 in Rothlisberg (1980).

Stages I-VIII, known parentage; figures 5-11 in Lee (1969).

In all described stages, carapace and abdominal somites not flared laterally and lack denticles or spinules; basipodite of maxillule without subterminal seta (except possibly Stage I). Pereopods tucked under carapace in Stage I. Rostrum without teeth in Stage I; rostrum with undeveloped dorsal tooth in Stage II; rostral tip bifid beginning at Stage VIII. Length: Stages I-XIII, 5.1-16.3 mm. Range: Unalaska, AK, to San Nicolas Island, CA; depth, 36-457 m (Butler 1980).

Key VII.—Larval and first juvenile stages of *Pandalus jordani*.

1. Eyes sessile; telson and abdominal somite 6 not jointed ....Stage I
   Eyes stalked; telson and abdominal somite 6 jointed 2

2. Rostrum with precursor of first dorsal tooth; uropods enclosed ....Stage II
   Rostrum with ⩾ 1 movable dorsal tooth; uropods free 3

3. Rostrum with 1 movable dorsal tooth; endopodite of uropod a bud with only a few setae ....Stage III
   Rostrum with > 1 movable tooth; endopodite of uropod > 1/2 length of exopodite and setose.................................4

4. Posterior width of telson about twice anterior width....................Stage IV
   Posterior width of telson noticeably less than twice anterior width 5

5. Lateral margins of telson widen slightly posteriorly ....Stage V

Lateral margins of telson parallel or narrow posteriorly 6

6. Rostrum with 5 developed dorsal teeth and 1 undeveloped dorsal tooth; antennal flagellum with 15 segments and same length as scale . . . . Stage VI
Rostrum with ≥ 5 developed dorsal teeth and > 1 undeveloped dorsal tooth; antennal flagellum with > 20 segments and longer than scale 7

7. Rostrum with 5 developed dorsal teeth and styliform tip; anal spine absent . . . . . . Stage VII
Rostrum with > 5 developed teeth, tip of rostrum with precursor of subterminal tooth; anal spine present 8

8. Rostrum with 7 developed teeth; lateral margin of telson with 2 spines . . . . . . Stage VIII
Rostrum with > 7 developed teeth; lateral margin of telson with ≥ 3 spines 9

9. Rostrum with 9 developed teeth; inner flagellum of antennule with 3 segments; outer flagellum of antennule with 2 segments . . . . Stage IX
Rostrum with > 9 developed teeth; inner flagellum of antennules with ≥ 4 segments; outer flagellum of antennule with 3 segments 10

10. Rostrum with 10 developed teeth; medial pair of terminal telsonic spines shorter than adjacent pair . . . . Stage X
Rostrum with > 10 developed teeth; medial pair of terminal telsonic spines same length or longer than adjacent pair 11

11. Inner flagellum of antennule with 4 segments; medial pair of terminal telsonic spines same length as adjacent pair . . . . Stage XI
Inner flagellum of antennule with 5 segments; medial pair of terminal telsonic spines longer than adjacent pair 12

12. Rostrum with 12 developed dorsal teeth and precursors of 3 ventral spines; terminal margin of telson straight . . . . Stage XII
Rostrum with > 12 developed dorsal teeth and precursors of > 3 ventral teeth; terminal margin of telson convex 13

13. Carapace with supraorbital spine; pereopod 2 with unsegmented carpus . . . . Stage XIII (last larval stage)
Carapace without supraorbital spine; pereopod 2 with segmented carpus . . . . . . Stage XIV (first juvenile stage)

Pandalus kessleri **Czerniavski**

Four larval stages.

Stages I-IV and Stage V (first juvenile), known parentage; figures 2-6 (fig. 6, first juvenile stage) in Kurata (1955). (Stages II-IV have a mixture of zoeal and megalopal characters.)

Abbreviated larval development. In all described stages, carapace without denticles along anteroventral margin; antennal scale not jointed at tip; 2 lateral setae proximally on exopodite of maxilliped 1. Stages II and III with transverse dorsal groove. Rostrum with teeth beginning in Stage II. Supraorbital spines in Stage II only. In Stage I, antennal flagellum 3/4 length of body; antennal flagellum segmented throughout its length; telson with 30-34 setae; anal spine present; zoea longer than 8.1 mm. In Stage III, mandible with unjointed palp. Vestigial exopodites on pereopods 1 and 2 in Stages I and II. Pleopods with plumose setae in Stage II. Length: Stages I-IV, 8.1-10.8 mm. Range: Hokkaido, Japan (no depth given) (Kurata 1955).

Key VIII.—Larval and first juvenile stages of *Pandalus kessleri*.

1. Rostrum without teeth; eyes sessile . . . . Stage I
Rostrum with teeth, eyes stalked 2

2. Mandible without palp; uropods enclosed; carapace with supraorbital spine . . . . . . Stage II
Mandible with palp; uropods free; carapace without supraorbital spine 3

3. Rostral tip not bifid; telson widens posteriorly . . . . Stage III
Rostral tip bifid; telson margins parallel or narrows posteriorly 4

4. Mandibular palp unsegmented; sides of telson parallel; telson with 2 pairs of lateral spines and 11-14 terminal seta . . . . Stage IV
Mandibular palp segmented; telson narrows posteriorly; telson with 3 pairs of lateral spines and several terminal setae vestigial as hairs . . . . Stage V (first juvenile)

Pandalus platyceros **Brandt**

Five larval stages.
Stages I-V and Stages VI-X (juveniles), known parentage; figures 1-6 in Price and Chew (1972).
Stage I, known parentage; Stages II, IV?, and V?, from plankton; figures 9 and 10 in Berkeley (1930).

In all described stages, rostrum with teeth, basipodite of maxillule without subterminal seta. In Stages I-III, carapace flares laterally, lateral margins with denticles; abdominal somites flare laterally, lateral margins with spinules (Fig. 5). In Stage I, pleopods present as buds; telson jointed with abdominal somite 6. In Stages II and III, less flaring of abdominal somites and smaller denticles and spinules than in Stage I. Thoracic appendages developed in Stage I, except naked endopodites on pereopods 1-3. Length: Stages I-V, 8.1-13.0 mm. Range: Sea of Japan, Hokkaido; Unalaska Island, AK, to off San Diego, CA; depth, intertidal to 487 m (Butler 1980).

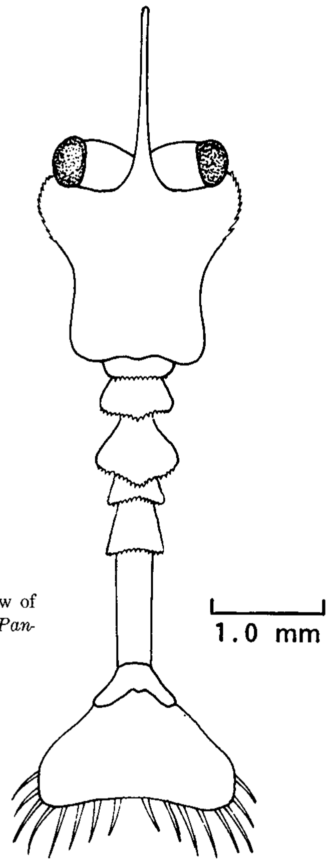

FIGURE 5.–Dorsal view of body, Stage I zoea of *Pandalus platyceros*.

Key IX.—Larval and first juvenile stages of *Pandalus platyceros*.

1. Rostrum without ventral teeth (Fig. 6); eyes sessile; pereopods with naked exopodites . . . . Stage I
   Rostrum with ventral teeth; eyes stalked; pereopods with setose exopodites 2

2. Antennal flagellum with 6 segments and flagellum only slightly longer than plumose setae of scale; uropods enclosed . . . . Stage II
   Antennal flagellum with ⩾ 15 segments and flagellum at least twice length of scale; uropods free 3

3. Antennal flagellum about twice length of antennal scale; telson widens posteriorly; telson with 1 pair of lateral spines . . . . Stage III
   Antennal flagellum ⩾ 3 times length of antennal scale; telson margins parallel or converge posteriorly; telson with > 1 pair of lateral spines 4

4. Carapace with supraorbital spines; mandibles without palps; pereopod 2 with unsegmented carpopodite; telson with 2 pairs of lateral spines . . . . Stage IV
   Carapace without supraorbital spines; mandibles with palps; pereopod 2 with segmented carpopodite; telson with ⩾ 3 pairs of lateral spines 5

5. Telson margins nearly parallel, distal margin concave . . . . Stage V (megalopa)

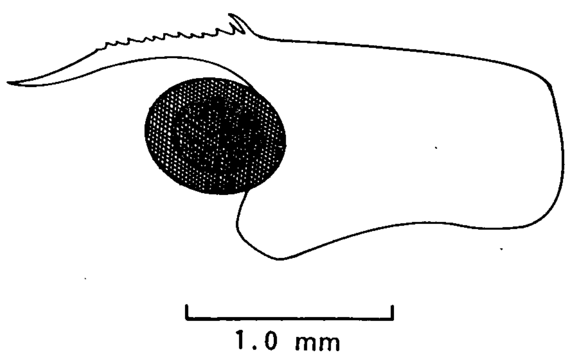

FIGURE 6.–Rostrum, Stage I zoea *Pandalus platyceros*.

Telson narrows posteriorly, distal margin convex .... Stage VI (first juvenile stage)

***Pandalus prensor* Stimpson**

Five larval stages.

Stages I-V (larvae) and VI-IX (juveniles), known parentage; figures 2-7 in Mikulich and Ivanov (1983).

Abbreviated larval development characterized by marked heterochrony in development of appendages. In all described stages, supraorbital spine absent; antennal flagellum segmented; antennal scale not jointed at tip; pereopods developed. In Stage I, rostrum curves ventrally between eyes; telson discoid and jointed with abdominal somite 6; natatory setae on exopodites of maxillipeds 1-3 and pereopods 1-2. Length: Stages I-V, carapace length 1.42-1.75 mm. Range: coastal waters of southern Okhotsk Sea, Sea of Japan, and southeastern Siberia (Vladivostok and Possjet Bay); depth, 2-93 m (Holthuis 1976; Mikulich and Ivanov 1983).

Key X.—Larval stages of *Pandalus prensor*.

1. Eyes sessile; rostrom bends ventrally between eyes .... Stage I
   Eyes stalked; rostrom straight 2

2. Rostrum does not extend to anterior margin of eye; telson discoid; uropods enclosed .... Stage II
   Rostrum extends beyond anterior margin of eye; telson rectangular; uropods free 3

3. Pleopods uniramous and unsegmented; telson with 7 pairs of terminal spines .... Stage III
   Pleopods (pairs II-V) biramous and segmented; telson with ≤ 5 pairs of terminal spines ... 4

4. Ventral rostrum with 4 teeth; telson with 5 pairs of terminal spines .... Stage IV
   Ventral rostrum with 6 teeth; telson with 3 pairs of terminal spines .... Stage V

***Pandalus stenolepis* Rathbun**

Six larval stages.

Stages I and II, known parentage; Stages III-VII (Stage VII, first juvenile), from plankton; figures 1 and 2 in Needler (1938); figure 73 in Gurney (1942; Page 208 verifies subterminal seta on maxillule).

In Stages I-IV, carapace flares laterally, lateral margin with denticles; abdominal somites with spinules and flared laterally. Flaring, size of denticles, and spinules decrease in Stages II-IV. In Stage I, pereopods tucked under carapace; telson not jointed with abdominal somite 6; and flagellum of antenna longer than antennal scale. Pleopods absent until Stage III. Length: Stages I-VI, 6.0-14.0 mm. Range: Unalaska Island, AK, to Hecata Bank, OR; depth, 49-229 m (Butler 1980).

Key XI.—Larval and first juvenile stages of *Pandalus stenolepis*.

1. Eyes sessile; rostrum without teeth .... Stage I
   Eyes stalked; rostrum with teeth 2

2. Rostrum with only dorsal teeth (4-5 teeth); uropods enclosed .... Stage II
   Rostrum with dorsal and ventral teeth; uropods free 3

3. Rostrum with 8 or 9 dorsal teeth and 2 ventral teeth; pleopod buds only slightly cleft .... Stage III
   Rostrum with > 9 dorsal teeth and > 2 ventral teeth; pleopods biramous 4

4. Unjointed pleopods without setae .... Stage IV
   Jointed pleopods with setae 5

5. Right and left pereopods 2 with endopodites of same length; pleopods with a few setae; each endopodite without an appendix interna (Fig. 1N, ai) .... Stage V
   Right and left pereopods 2 with endopodites of different lengths; pleopods setose; each endopodite with an appendix interna 6

6. Carapace with supraorbital spine; setose exopodite on each pereopod .... Stage VI (megalopa)
   Carapace without supraorbital spine; naked, vestigial exopodite on each pereopods .... Stage VII (first juvenile stage)

***Pandalus tridens* Rathbun**

Probably 8 larval stages.

Stage I, known parentage; Stages I-VII, from plankton; figures 1-7 in Haynes (1976).

Stage I, known parentage; figure 1 in Ivanov (1971).

In all described stages, carapace and abdominal somites not flared laterally; antennal scale relatively long and narrow (about 5-7 times as long as wide). In Stages I-III, but rarely in Stage IV, carapace with denticles along anteroventral and posteroventral margins; posterior margin of abdominal somites 1-5 fringed with spinules (Fig. 7). Rostrum sinuate, projects somewhat upwards in Stages I-III, remains shorter than carapace as late as Stage VIII, without teeth until Stage IV. Antennal flagellum shorter than antennal scale through at least Stage V. Length: Stages I-VII, 3.1-13.0 mm. Range: Bering Sea to San Nicolas Island, CA; depth, 5-1,984 m (Butler 1980).

Key XII.—Larval stages (Stages I-VII) of *Pandalus tridens*.

1. Eyes sessile; carapace without supraorbital spine; pereopods 1-3 without exopodites; telson with 7 + 7 setae . . . . Stage I
   Eyes stalked; carapace with supraorbital spine; exopodites on pereopods 1-3; telson with 8 + 8 setae 2

2. Uropods enclosed . . . . Stage II
   Uropods free 3

3. Endopodite of uropod < 1/2 length of exopodite . . . . Stage III
   Endopodite of uropod > 1/2 length of exopodite 4

4. Rostrum with 2 dorsal teeth; endopodite of uropod about 3/4 length of exopodite; telson widens posteriorly . . . . Stage IV
   Rostrum with > 2 dorsal teeth; endopodite of uropod nearly same length as exopodite; lateral margins of telson nearly parallel 5

5. Antennal flagellum with 5 segments and about 2/3 length of antennal scale; chela of pereopod 2 slightly developed (Fig. 8); pleopod 2 about 1/4 height of abdominal somite 2 . . . . Stage V
   Antennal flagellum with ≥ 20 segments and as long as or longer than antennal scale; chela of pereopod 2 well formed (Fig. 9); pleopods 2 at least 1/2 height of abdominal somite 2 6

6. Rostrum with 6 dorsal teeth; pleopods without setae; telson slightly wider near center . . . . Stage VI

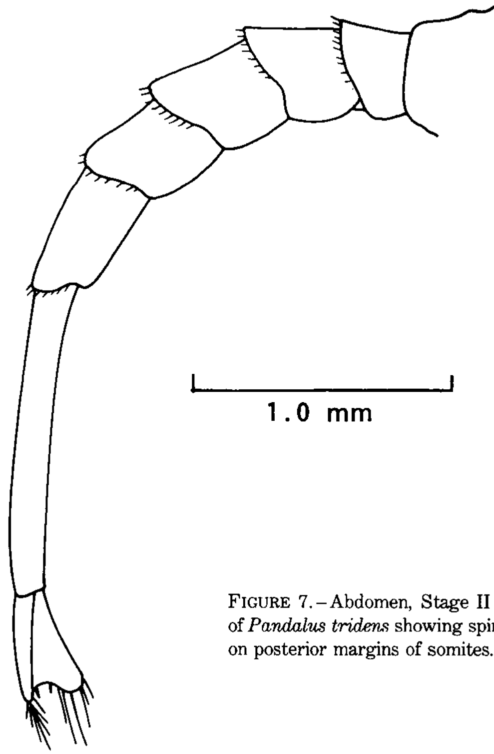

FIGURE 7.–Abdomen, Stage II zoea of *Pandalus tridens* showing spinules on posterior margins of somites.

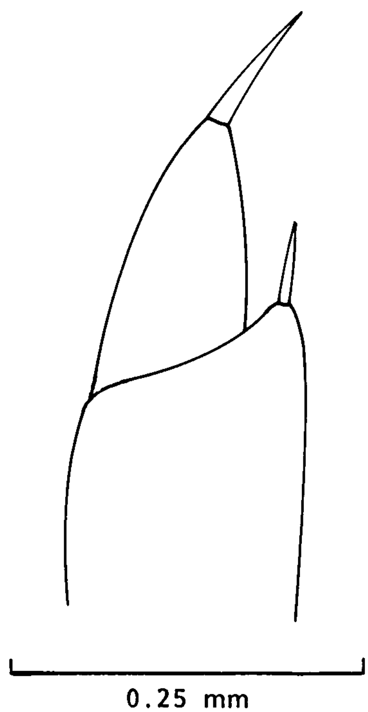

FIGURE 8.–Chela of pereopod 2, Stage V zoea of *Pandalus tridens*.

Rostrum with 7 dorsal teeth; pleopods tipped with a few setae; telson margins nearly parallel . . . . Stage VII

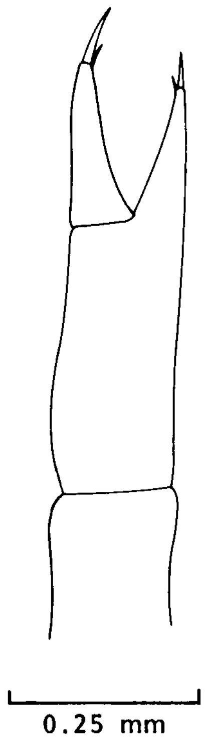

FIGURE 9.–Chela of pereopod 2, Stage VI zoea of *Pandalus tridens*.

HIPPOLYTIDAE

(Genera *Eualus*, *Heptacarpus*, *Hippolyte*, *Lebbeus*, and *Spirontocaris*)

In all described stages, rostrum absent to long, usually spiniform (slightly sinuate in species with abbreviated development); plumose seta rather than long setose spine on inner flagellum of antennule; exopodites on pereopods 1-2, 1-3, or 1-4; abdomen without dorsal spine or keels on somite 3 (megalopa of *Spirontocaris spinus* with a minute dorsoposterior spine on abdominal somite 3); posterolateral spines absent, on abdominal somites 4 and 5, or only on abdominal somite 5 (spines may be lacking in megalopa); pereopod 1 never subchelate; anal spine present in all stages (exception: at least Stage I of *Hyppolyte*). Rostrum may have teeth in last zoeal stage (megalopa); supraorbital spine usually absent in Stage I. Stages I-III, antennal scale nearly always jointed or partially jointed at tip. Stage I, exopodites of maxilliped 1-3 with 4, 5, 5 natatory setae; about Stage V, setose setae on endopodite of each pleopod; telson does not widen posteriorly, has more than 1 pair of lateral spines.

The principal morphological characters and number of larval stages of known larvae of hippolytid shrimp of the northern North Pacific Ocean are summarized in Table 5.

TABLE 5.—Principal morphological characteristics and number of larval stages of known larvae of hippolytid shrimp of the northern North Pacific Ocean. + = yes; – = no; ? = unknown.

Species	Rostrum	Supra-orbital spine in Stage I	Pereopods in Stage I	Pereopods bearing an exopodite in later zoeal stages	Postero-lateral spines on abdominal somites	Telsonic spines in Stage I	No. of larval stages
Eualus barbatus	—	—	—	?	—	7 + 7	?
E. fabricii	+	—	[1]5	1-3	4, 5	7 + 7	?
E. gaimardii	+	—	[1]4	1-3	5	7 + 7	6
E. herdmani	—	—	—	?	—	7 + 7	?
E. macilentus	+[2]	—	—	?	—	7 + 7	?
E. pusiolus	+[2]	?	—	1-4	—	7 + 7	6-7
E. suckleyi	+	—	[1]5	1-3	5	7 + 7	?
Heptacarpus brevirostris	—	—	—	?	—	7 + 7	?
H. camtschaticus	+[2]	—	[1]5	1, 2	—	7 + 7	?
H. paludicola	—	—	—	?	—	7 + 7	?
H. tridens	—	—	—	?	—	7 + 7	?
Hippolyte clarki	+	—	[1]1	?	5	7 + 7	?
Lebbeus groenlandicus	+	—	5	—	4, 5	9(10) + 10(11)	3
L. polaris	+	—	5	—	4, 5	9 + 9	4
Spirontocaris arcuata	+	—	[1]5	1, 2	—	7 + 7	?
S. lilljeborgii	+	+	[1]5	1, 2	4	7 + 7	6
S. murdochi	+	—	[1]5	1, 2	4, 5	7 + 7	?
S. ochotensis	—	+	[1]5	1, 2	4, 5	7 + 7	?
S. phippsii	+	+	[1]5	1, 2	4, 5	7 + 7	6
S. spinus	+	+	[1]5	1, 2	4, 5	7 + 7	6
S. spinus var. *intermedia*	+	—	[1]5	1, 2	4, 5	7 + 7	?

[1]Undeveloped pereopods. [2]Minute.

Genus *Eualus* Thallwitz

In Stage I, rostrum absent to long; carapace without supraorbital spine; tip of antennal scale jointed; pereopods absent or, if present, undeveloped; anal spine present. Exopodites first appear on pereopods 1-3 or 1-4 in Stage III. Posterolateral spines absent, on abdominal somites 4 and 5, or only on abdominal somite 5.

Eualus barbatus (Rathbun)

Only Stage I described, known parentage; figure 3 in Ivanov (1971).

Carapace without rostrum, supraorbital spine, or denticles; pereopods absent; abdominal somites without posterolateral spines or denticles but with isolated hairs on dorsal surface of abdominal somites 3 and 4; abdominal somite 3 with indistinct row of setae on dorsal surface. Length: 4.5 mm. Range: Pribilof Islands, AK, to Hecata Bank, OR; depth, 82-507 m (Butler 1980).

Eualus fabricii (Krøyer)

Only Stages I and II described, known parentage; figure 5 in Haynes (1981).

Not "*Spirontocaris* larva Nr. 3, *Spirontocaris fabricii*?" as described by Stephensen (1916) (see Haynes 1981).

Not "*Spirontocaris*-larvae No. 3? *Spirontocaris fabricii* (Krøyer)" as described by Stephensen (1935) (see Haynes 1981).

Not *Spirontocaris fabricii* as described by Frost (1936) (see Haynes 1981).

Not "*Eualus fabricii* (Krøyer)" as described by Pike and Williamson (1961) (see Haynes 1981).

In all stages, posterolateral spines on abdominal somites 4 and 5. In Stage I, antennal flagellum about 1.5 times length of antennal scale; minute spinules along dorsoposterior margins of abdominal somites 4 and 5 (spinules absent in Stage II); supraorbital spine absent (small in Stage II). In Stages I and II, pereopods 1-3 with undeveloped exopodites. In Stage II, exopodites of maxillipeds 1-3 with 4, 9, and 11 natatory setae, respectively; telson not jointed with abdominal somite 6. Length: Stages I and II, 3.5-4.3 mm. Range: Sea of Japan, Okhotsk Sea; Chukchi Sea to British Columbia; in northwestern Alantic, from Foxe Basin and West Greenland to Massachusetts Bay (eastern United States); depth, 4-255 m (Butler 1980).

Eualus gaimardii (H. Milne Edwards)

Six larval stages.

Stages I-VI, known parentage; also Stages I and II from plankton; figure 2 in Pike and Williamson (1961).

Last zoeal stage from plankton, described as "Spirontocaris-larva No. 2A" by Stephensen (1935), probably *E. gaimardii* forma *gibba* (see Pike and Williamson 1961, p. 198). No figure.

Stage V (?), described as "*Spirontocaris* B" by Frost (1936), probably *E. gaimardii* forma *gibba* (see Pike and Williamson 1961, p. 198); figure 4 in Frost (1936).

Stage I, known parentage; described as *Spirontocaris gaimardii* by Lebour (1940); figure 1 in Lebour (1940).

Stage I, known parentage; figures 21-23 in Williamson (1957a: figures from Lebour 1940).

In all described stages, rostrum long (about 1/3 carapace length); no subterminal seta on maxillule. Rostrum without teeth until Stage V. In Stage V, rostrum with 2 dorsal teeth; in Stage VI, rostrum with 3 dorsal teeth. Supraorbital spine in Stages II-V. Carapace with 3 or 4 denticles on anteroventral margin in Stages I-IV. Antennal flagellum does not extend beyond antennal scale until Stage V. Natatory setae on exopodites of maxillipeds 1-3: 5, 7, 7 natatory setae, respectively, in Stage II; 5, 9, 9 in Stage III; and 5, 10, 10 in Stages IV and V. In Stages I-V, posterolateral spine on abdominal somite 5. Length: Stages I-VI, 2.9-5.4 mm. Range: circumpolar, southward to North Sea; Cape Cod, MA; Sitka, AK; Siberia; depth, 10-900 m (Holthuis 1947).

Eualus herdmani (Walker)

Only Stage I described, known parentage; described as "*Spirontocaris herdmani*" by Needler (1934). No figure.

Stage I, known parentage; Pike and Williamson (1961: description from Needler 1934). No figure.

Carapace without rostrum or supraorbital spine but with 3 anteroventral denticles; abdomen without posterolateral spines; anal spine minute. No length given. Range: Sitka, AK, to Puget Sound, WA; depth, 18-232 m (Butler 1980).

Eualus macilentus (Krøyer)

Only Stage I described, known parentage; figure 2 in Ivanov (1971).

No supraorbital spine; 4 denticles on anteroventral margin of carapace; pereopods absent; abdomen without spines or denticles. Length: 3.0 mm. Range: West Greenland to Nova Scotia; Bering and Okhotsk Seas; depth, 150-540 m (Holthuis 1947).

Eualus pusiolus (Krøyer)

Larvae described from Atlantic specimens.
Seven or eight larval stages.
Stage I, known parentage; Stages I-VII, from plankton; figure 3 in Pike and Williamson (1961).
Last zoeal stage, from plankton, described as "*Spirontocaris* C" by Frost (1936); figure 5 in Frost (1936).
Stage I, known parentage; described as "*Spirontocaris pusiola*" by Bull (1938); figure 1 in Bull (1938).
Stage I, known parentage; figures 27-30 in Williamson (1957a); figures from Bull (1938).

In all described stages, 3 denticles on anteroventral margin of carapace; no spines, denticles, or dorsal setae on abdominal somites. Rostrum minute in Stage I, only slightly larger in other stages, without teeth in all stages. Exopodites of maxillipeds 1-3, with 5, 8, and 8 natatory setae, respectively, in Stage II. In Stages V-VIII, pereopods 1-4 with setae. Length: Stages I-VIII, 2.2-4.8 mm. Range: Sea of Japan to Chukchi Sea and British Columbia; Gulf of St. Lawrence to Cape Cod, MA; Europe from the southwestern Barents Sea to Spain; depth, intertidal to 1,381 m (Butler 1980).

Eualus suckleyi (Stimpson)

Only Stages I and II described, known parentage; figures 3 and 4 in Haynes (1981).

In Stage I, anteroventral margin of carapace with 3 or 4 denticles; undeveloped exopodites on pereopods 1-3. In Stage II, carapace with supraorbital spine, without denticles along anteroventral margin. In Stage II, maxillipeds 1-3 with 4, 5, and 5 natatory setae, respectively; pereopods 1-5 present but undeveloped. Length: Stage I, 3.0-3.5 mm; Stage II, 3.5-4.2 mm. Range: Okhotsk Sea to Chukchi Sea to about Grays Harbor, WA; depth, 11-1,025 m (Butler 1980).

Genus *Heptacarpus* Holmes

Only Stage I described. Rostrum minute to absent; no supraorbital spine; pereopods absent or pairs 1-5 present but undeveloped; abdominal somites without posterolateral spines; exopodites develop on pereopods 1 and 2; tip of antennal scale not always jointed.

Heptacarpus brevirostris (Dana)

Stage I, known parentage; described as *Spirontocaris brevirostris* by Needler (1934). No figures.

Carapace without anteroventral spines; antennal scale partially jointed at tip. Length: Stage I, 1.5 mm. Range: Aleutian Islands, AK, to San Francisco Bay, CA; depth, intertidal to 128 m (Butler 1980).

Heptacarpus camtschaticus (Stimpson)

Stage I, known parentage; figure 8 in Haynes (1981).

Carapace without spines; minute rostrum curves slightly downward following dorsal contour of eyes; undeveloped exopodites on pereopods 1 and 2; abdomen without spines or spinules. Length: Stage I, 2.9 mm. Range: Sea of Japan to Chukchi Sea and Strait of Georgia, WA; depth, intertidal to 108 m (Butler 1980).

Heptacarpus paludicola (Holmes)

Stage I, known parentage; described as *Spirontocaris paludicola* by Needler (1934); figure 1 in Needler (1934).

Antennal scale partially jointed at tip; abdomen without posterolateral spines. Length: Stage I, 2.0 mm. Range: Tava Island, AK, to San Diego, CA; depth, intertidal to 10 m (Butler 1980).

Heptacarpus tridens (Rathbun)

Stage I, known parentage; described as *Spirontocaris tridens* by Needler (1934); figure 1 in Needler (1934).

Carapace without anteroventral spines; antennal scale unsegmented. Length: Stage I, 3.0 mm. Range: Aleutian Islands, AK, to Cape Flattery, WA; depth, intertidal to 110 m (Butler 1980).

Genus *Hippolyte* Leach

Only Stage I described. Antennal scale without joints at tip.

Hippolyte clarki Chace

Stage I, known parentage; described as *Hippolyte californiensis* by Needler (1934); figure 1 in Needler (1934).

Rostrum long; carapace with 4 anteroventral denticles; bud of pereopod 1 present; small posterolateral spines on abdominal somite 5. Length: 1.9 mm. Range: Sheep Bay, AK, to Puget Sound, WA; Santa Catalina Island, CA; depth, intertidal to 30.5 m (Butler 1980).

Genus *Lebbeus* White

In all described stages, posterolateral spines on abdominal somites 4 and 5 (Fig. 2). In Stage I, larvae relatively long (> 5.0 mm); rostrum long, slightly sinuate (Fig. 2), with no supraorbital spine. Abbreviated development.

Lebbeus groenlandicus (Fabricius)

Three larval stages.
Stages I-III from both known parentage and plankton; figures 1-3 in Haynes (1978b).
Stage I, known parentage; figure 5 in Ivanov (1971).
Not "*Spirontocaris*-larva No. 1A." as described by Stephensen (1935) (see Haynes 1978b).

Somewhat more developed in each stage than larvae of *L. polaris*. In Stage II, no vestigial exopodites on pereopods. Telson with about 20 setae in Stages I and II, and 3 + 3 spines in Stage III (megalopa). Length: 6.4-7.6 mm. Range: Sea of Japan to Chukchi Sea to Puget Sound, WA; arctic coast of Canada; Greenland to Cape Cod, MA; depth, 11-518 m (Butler 1980).

Lebbeus polaris (Sabine)

Probably 4 larval stages.
Stages I and II, known parentage; figures 1 and 2 in Haynes (1981).
Neither *Spirontocaris polaris* (= *L. polaris*) as described by Stephensen (1916) nor "*Spirontocaris*-larva No. 1" as described by Stephensen (1935) (see Haynes 1981).

In Stages I and II, telson with 9 + 9 setae. In Stage II, vestigial exopodite on peropod 1. Length: Stage I, 5.2 mm; Stage II, 5.8 mm. Range: circumpolar, southward to the Skagerrak and Hebrides; Cape Cod, MA; Bering and Okhotsk Seas; Aleutian Islands, AK; depth, 0-930 m (Holthuis 1947).

Genus *Spirontocaris* Bate

In all described stages, rostrum absent to long; posterolateral spines on abdominal somites 4 and 5, or 5 only; no minute spines on posterior margins of abdominal somites. In Stage I, supraorbital spine present or absent; all pereopods present but undeveloped. Exopodites only on pereopods 1 and 2 in later stages (usually by Stage IV or V).

Spirontocaris arcuata Rathbun

Only Stage I described, known parentage; figure 6 in Haynes (1981).

Rostrum short (about 1/7 carapace length), projects downward following contour of eyes; 2 or 3 minute denticles on anteroventral margin of carapace; supraorbital spine absent; posterolateral spines on abdominal somites 4 and 5. Length: 4.1-4.4 mm. Range: Sea of Japan to Chukchi Sea to Juan de Fuca Strait, WA; Canadian Arctic; depth, 5-641 m (Butler 1980).

Spirontocaris lilljeborgii (Danielssen)

Larvae described from Atlantic Ocean.
Six larval stages.
Stages I and II, known parentage; Stages I-V, from plankton; Stages VI (megalopa) and VII (first juvenile), reared in laboratory from Stage V; figure 1 in Pike and Williamson (1961).
Stage I, known parentage; described as *S. spinus* var. *lilljeborgi* by Lebour (1937); figure 1 in Lebour (1937).
Stage I; figures 14-16 in Williamson (1957a). Description and figures from Lebour (1937).

In all described stages, posteroanterior margins of carapace smooth; abdominal somite 4 with a dorsal tuft of short setae, without posterolateral spines. Rostrum long (about 3/4 length of antennular peduncle), deepens slightly in later stages but does not develop teeth until megalopa. Supraorbital spine rudimentary in Stage I, clearly defined in later stages. Posterolateral spines on abdominal somite 5 becoming smaller in later stages and may be absent in Stages V and VI. Megalopa and first juvenile stage without dorsal tooth on posterior margin of abdominal somite 3. Length: Stages I-VI, 4.8-8.5 mm. Range: From Spitsbergen and southwestern

Barents Sea south to south coast of England; Iceland; Greenland; east coast of North America from Nova Scotia to Massachusetts Bay; arctic Alaska; depth, 20-1,200 m (Holthuis 1947).

Spirontocaris murdochi Rathbun

Only Stages I-III described, known parentage; figures 1-3 in Haynes (in press).

Rostrum about 1/4 carapace length, supraorbital spine in Stage III; posterolateral spine on abdominal somite 5 longer than posterolateral spine on abdominal somite 4; dorsal surface of abdominal somite 4 without tuft of setae. Length: Stages I-III, 3.2-4.3 mm. Range: Arctic to southeastern Alaska, Kamchatka, Sea of Okhotsk, Patience Bay (Sakhalin); depth, 18-50 m (Holthuis 1947; Haynes in press).

Spirontocaris ochotensis (Brandt)

Only Stage I described, known parentage; figure 7 in Haynes (1981).

No rostrum; carapace usually with only 1 denticle along anteroventral margin; supraorbital spine minute; posterolateral spines on abdominal somites 4 and 5. Length: 2.8 mm. Range: Sea of Japan to Bering Sea and western coast of Vancouver Island, British Columbia; depth, intertidal to 247 m (Butler 1980).

Spirontocaris phippsii (Krøyer)

Larvae known from Atlantic Ocean.
Stage II, from plankton; Pike and Williamson (1961). No figure. Identity assumed from distribution of adults.
Stage III, from plankton; described as "*Sprionto-caris*-larva Nr. 2," ("*Sp. turgida*?"); figure 6 in Stephensen (1916). Not figure 7 in Stephensen (1916), "last stage"; probably *Eualus macilentus* (see Pike and Williamson 1961) (Pike and Williamson identified figure 7 as *E. macilentus* based on identity of *S. spinus* and *S. lilljeborgii* and distribution of *Eualus* spp. in Greenland waters).
Stage V, from plankton; described as "*Spirontocaris*-larva No. 2 (? *Sp. turgida* (Krøyer))" and "*Spirontocaris*-larva No. 2B" in Stephensen (1935) (see Pike and Williamson 1961 for identification).

Spines on abdominal somites 4 and 5; abdominal somite 4 without dorsal tuft of setae. Length: Stage II, 6.0 mm. Range: circumpolar, southward to northern Norway; Cape Cod, MA; Shumagin Islands, AK; and Plover Bay, Siberia; depth, 11-225 m (Holthuis 1947).

Spirontocaris spinus (Sowerby)

Larvae described from Atlantic Ocean only.
Six larval stages.
Stages I and II, known parentage; Stages III-VII (Stage VII, first juvenile), from plankton; figure 1 in Pike and Williamson (1961).
Stage IV, from plankton; described as "*Spirontocaris* A" by Frost (1936); figure 3 in Frost (1936) (see Pike and Williamson 1961 for identification).
Stage I, probably from known parentage; Stage V, probably from plankton (see Pike and Williamson 1961); figures 17-20 in Williamson (1957a).

Larvae and juvenile stages very similar to those of *S. lilljeborgii*. In all described stages, abdominal somite 4 with a dorsal tuft of short setae; abdominal somites 4 and 5 with posterolateral spines; posterolateral spines on abdominal somite 5 remain same size in all zoeal stages. Posterior margin of abdominal somite 3 with distinct dorsal tooth in megalopa and first juvenile stage. Length: Stages I-VI, 4.3-8.0 mm. Range: Circumpolar, southward to the northern North Sea, Massachusetts Bay (eastern United States), Alaska Peninsula, and eastern coast of Siberia; depth, 16-400 m (Holthuis 1947).

Spirontocaris spinus var. *intermedia* Makarov[8]

Only Stage I described, known parentage; figure 4 in Ivanov (1971).
Not *S. spinus intermedia* as described by Makarov (1967) (see Ivanov 1971).

Rostrum long (> 1/3 carapace length); no supraorbital spine; abdominal somite 4 with dorsal tuft of setae; posterolateral spines on abdominal somites 4 and 5. Length: Stage I, 5.0 mm. Range: (see *S. spinus*); depth, 9-1,380 m (Hayashi 1977).

[8]According to Ivanov (1971), V. V. Makarov, rather than Z. I. Kobjakova, is the author of the subspecies *S. spinus* var. *intermedia* based on Article 51(c) of Chapter XI of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1964). The subspecies *S. spinus* var. *intermedia*, however, may be identical to *S. spinus*. Hayashi (1977) believed that the morphological criteria used by Kobjakova (1937) to distinguish *S. spinus* var. *intermedia* from *S. spinus* were too small and variable to be valid.

CRANGONIDAE

(Genera *Argis*, *Crangon*, *Mesocrangon*, *Paracrangon*, *Sabinea*, and *Sclerocrangon*)

Rostrum nearly always present and long (at least 1/4 length of carapace), spiniform, and always without teeth (rostrum spinulose in Stage I larvae of *Paracrangon echinata*); supraorbital spine absent; inner flagellum of antennule a setose spine or oblong projection rather than a plumose seta; tip of antennal scale never segmented; exopodite usually only on pereopod 1 (rarely on pereopod 2); maxillule without subterminal seta on basipodite; dorsal spine may be on abdominal somite 3 or keels on both abdominal somites 2 and 3; usually posterolateral spines on abdominal somite 5; endopodite of pleopods undeveloped; usually telson widens posteriorly, never with more than 1 pair of lateral spines. Pereopods 1 subchelate at about Stage V. Anal spine absent until about Stage IV.

The principal morphological characters and number of larval stages of known larvae of crangonid shrimp of the northern North Pacific Ocean are summarized in Table 6.

Genus *Argis* Krøyer

In Stage I, rostrum styliform; pereopods and pleopods developed but not functional; exopodite on pereopod 1 rudimentary or absent; abdominal somite 3 without dorsal spine; abdominal somite 5 with posterolateral spine (posterolateral spine absent in megalopa of *A. dentata*).

Argis crassa[9] (Rathbun)

Only Stage I described, known parentage; figure 2 in Ivanov (1968).

Not Stage I *A. crassa* as described by Makarov (1967) in figure 21.

Antennal scale without distal spine on outer margin; endopodite of maxillule with 5 setae; scaphognathite of maxilla with 9 setae; abdominal somites 2-5 fringed dorsally with small spinules; telson and abdominal somite 6 jointed; telson with 8 + 8 setae. Length: 7.5 mm. Range: Sea of Japan to Bering Sea to San Juan Islands, WA; depth, 4-125 m (Butler 1980).

Argis dentata (Rathbun)

Three larval stages. Stage I described, known parentage from Pacific Ocean; Stage I-III described, from plankton from Atlantic Ocean.

Stages I-III, from plankton; figures 1-6 in Squires (1965).

Stage I, known parentage; figure 3 in Ivanov (1968).

Megalopa, from plankton; described as "*Necto-*

[9]Makarov (1967) described a crangonid larva from plankton that has a short rostrum flattened dorsoventrally. He assumed it was *Argis* (= *Nectocrangon*) *crassa*. According to Ivanov (1968), who reared Stage I *A. crassa* from known parentage, the larva described by Makarov is neither *Argis crassa* nor a later stage of *Argis crassa*. The short flattened rostrum, however, is typically a postlarval (juvenile) characteristic of crangonid shrimp. The specimen described by Makarov, therefore, is probably a juvenile rather than a larva.

TABLE 6.—Principal morphological characteristics and number of larval stages of known larvae of crangonid shrimp of the northern North Pacific Ocean. + = yes; – = no; ? = unknown.

Species	Rostrum	Pereopods in Stage I	Pereopods bearing an exopodite in later zoeal stages	Postero-lateral spines on abdominal somite	Dorsal spine on abdominal somite	Telsonic spines in Stage I	No. of larval stages
Argis crassa	+	5	1	5	—	8 + 8	[1]2 or 3
A. dentata	+	5	1	5	—	8 + 8	3
A. lar	+	5	—	5	—	7 + 7	[1]3
Crangon alaskensis	+	—	1	5	3	7 + 7	5
C. communis	+	[2]1	1	5	—	7 + 7	[1]5
C. dalli	+	[2]5	1	5	—	7 + 7	5
C. franciscorum angustimana	+	[2]4	1, 2	5	3	7 + 7	[1]5
C. septemspinosa	+	—	1	5	3	7 + 7	5-6
Mesocrangon intermedia	+	[2]5	1	5	—	8 + 8	5
Paracrangon echinata	+	?	1, 2	1-5	1-5	?	7+
Sabinea septemcarinata	+	?	1	5	—	16 + 16	[1]4
Sclerocrangon boreas	—	5	—	—	—	12 + 12	2
S. salebrosa	+	5	—	5	—	22 + 22	1
S. zenkevitchi	—	5	—	—	—	—	[1]2

[1]Estimated.
[2]Undeveloped pereopods.

crangon lar?, young stage" by Stephensen (1916); figure 3 in Stephensen (1916).

In Stage I, antennal scale with distal spine on outer margin; endopodite of maxillule and scaphognathite of maxilla with 6 setae each; abdominal somites 3-5 fringed dorsally with small spinules (spinules not mentioned for Atlantic specimens); telson and abdominal somite 6 jointed; telson with 8 + 8 setae. In megalopa, short, pointed rostrum extends to middle of eye; carapace with 2 dorsal teeth, ventral edge fringed with short plumose setae; abdominal somite 5 without posterolateral spines. Length: Stages I-III, 8.0-12.0 mm. Range: Sea of Japan to Anadyr Gulf, Gulf of Georgia, and San Juan Islands, WA; arctic Canada to Nova Scotia, Canada; depth, intertidal to 2,090 m (Butler 1980).

Argis lar (Owen)

Probably 3 larval stages.
Stages I and II, from plankton; described as *Nectocrangon lar* by Makarov (1967); figure 22 in Makarov (1967).
Not Crangonidae "Species F" (described by Kurata 1964b), as assumed by Makarov (1967).[10]

In Stage I, telson and abdominal somite 6 not jointed; telson with 7 + 7 setae. In Stage II, telson with 8 + 8 setae. Abdominal somites without spinules. Length: Stages I and II, 6.2-7.5 mm. Range: Sea of Japan to Chukchi Sea to Strait of Georgia, WA; depth, 10-280 m (Butler 1980).

Genus *Crangon* Fabricius (= *Crago* Lamarck)

Five or six zoeal stages. Anteroventral margin of carapace denticulate in most if not all larval stages. In all described stages, rostrum about 1/3 carapace length, spiniform, without teeth; posterolateral spines on abdominal somite 5; exopodites develop on either pereopod 1 or pereopods 1 and 2; abdominal somite 3 usually with dorsal spine; telson always widens posteriorly, with setae and $\leqslant 8 + 8$ spines.

[10]Morphological differences are too great for Makarov's *Nectocrangon lar* larvae and Kurata's "Species F" larvae to be identical. Makarov's larvae lack exopodites on pereopods in all stages and, in Stages I and II, have posterolateral spines on abdominal somite 5. Kurata's "Species F" larvae, known only in Stage II, have an exopodite on pereopod 1 and posterolateral spines on abdominal somites 5 and 6.

Crangon alaskensis Lockington

Five larval stages.
Stages I-VII (Stage VI, first juvenile), known parentage; illustrations 1-79 in Loveland (1968).

In all described stages, rostrum barely reaches beyond eyes; dorsal spine on abdominal somite 3. Length: Stages I-V, 2.0-3.3 mm. Range: Kuril Islands; Bering Sea to Puget Sound, WA; depth, intertidal to 275 m (Butler 1980).

Crangon communis Rathbun[11]

Only Stage I described, known parentage; described as *Sclerocrangon communis* by Ivanov (1968); figure 1 in Ivanov (1968).
Not Stages II-V *C. communis* from plankton; described by Makarov (1967) as *Sclerocrangon communis*.[12]

Antennal flagellum about 3/4 length of antennal scale; antennal scale with 14 setae; abdominal somites without keels; spinules on posterior margins of abdominal somites 3-5. Length: Stage I, 4.8 mm. Range: Sea of Japan to Chukchi Sea to San Diego, CA; depth, 16-1,537 m (Butler 1980).

Crangon dalli Rathbun

Five larval stages.
Stage I, known parentage; Stages II-V and VI (first juvenile, "postlarval"), from plankton; figure 18 in Makarov (1967). Larvae figured in part but not described. Larvae thought to be identical morphologically to *C. allmani* larvae from the Atlantic Ocean (Makarov 1967).
Stage I from plankton; figures 7-9 in Birshteyn (1938).
Not "last (?) stage" as described by Birshteyn (1938) (see Makarov 1967).

Typical unabbreviated crangonid development. In all described stages, carapace without dorsal, lateral, or supraorbital spines; anterior margin of carapace denticulate; rostrum spiniform, without teeth;

[11]Zarenkov (1965) proposed placing *C. communis* in a new subgenus, *Neocrangon*. Butler (1980) has shown that Zarenkov's diagnosis for *Neocrangon* is invalid, at least for British Columbia species. Based on Butler's findings, I have retained *C. communis* in the genus *Crangon*.

[12]It is unlikely that Makarov's (1967) larvae and Ivanov's (1968) larvae are the same species because Makarov's larvae have keels on abdominal somites 2 and 3, whereas Ivanov's larvae do not.

posterolateral spines on abdominal somite 5; abdominal somites without spinules or keels; telson always widens posteriorly, never with > 1 pair of lateral spines. In Stage V, pleopods uniramous, with buds of endopodites. Length: Stages I-V, 2.8-7.0 mm. Range: Sea of Japan to Chukchi Sea, to Puget Sound, WA; depth, 3-630 m (Butler 1980).

Crangon franciscorum angustimana Rathbun

Only Stage I described, known parentage; figure 1 in Haynes (1980b).

Rostrum extends beyond eyes; carapace without shallow transverse groove; antennal scale with 10 plumose setae including subterminal seta along outer margin; endopodite with 4 segments on maxilliped 1, and 5 segments on maxilliped 3; exopodites of maxillipeds not jointed; pereopods 1-4 present but undeveloped; buds of exopodites on perepods 1 and 2; median dorsal spine on abdominal somite 3; posterolateral spines on abdominal somite 5; fifth pair of telsonic spines about equal in length to fourth and fifth pairs. Length: Stage I, 2.8-3.3 mm. Range: Kachemak Bay, AK, to Tillamook Rock, OR; depth, 18-183 m (Butler 1980).

Crangon septemspinosa Say

Described from specimens from both Atlantic and Pacific Oceans.
Five or six larval stages.
Stages I and II, known parentage; Stages III-VI, from plankton; described as *C. affinis* by Kurata (1964b); Pacific specimens; figures 1-29 in Kurata (1964b).
Stage I, known parentage; Stages II-V, from plankton; Atlantic specimens; described as *Crago septemspinosus* Say by Needler (1941); figures 1 and 2 in Needler (1941).
Stages I-X (Stage X, first juvenile stage), known parentage (larval series likely includes extra stages); Atlantic specimens; figures 1-51 in Tesmer and Broad (1964).
Stages I-V, from plankton; Pacific specimens; figure 20 in Makarov (1967).

Discrepancies among descriptions may result, at least in part, from geographical variations in morphology. The following synopsis is based on specimens from off Hokkaido, Japan (Kurata 1964b). In all described stages, shallow transverse groove in carapace; dorsal spine on abdominal somite 3, posterolateral spines on abdominal somite 5. Exopodite only on pereopod 1. In Stage I, antennal scale with 11 setae, including 2 subterminal setae along outer margin; endopodites of maxillipeds 1-3 with 4 segments; exopodites of maxillipeds jointed; fifth pair of telsonic spines distinctly shorter than fourth or sixth pairs. Length: Stages I-V, 1.9-5.0 mm. Range: Prince Edward Island, Canada (Needler 1941); Beaufort, NC (Tesmer and Broad 1964); an estuarine, subarctic boreal species, Sea of Okhotsk (Makarov 1967); Hokkaido, Japan (Kurata 1964b); depth, 0-90 m, rarely to 440 m (Holthuis 1980).

Genus *Mesocrangon* Zarenkov

Largest larvae of Crangonidae with unabbreviated development. From Stage III on, posterior margin of telson straight or slightly concave.

Mesocrangon intermedia (Stimpson)

Five larval stages.
Stages I-V, from plankton; described as *Sclerocrangon intermedia* by Makarov (1967); figure 24 in Makarov (1967).

In Stage I, antennal flagellum about half as long as antennal scale; antennal scale with 11 setae; abdominal somites 2-3 with keels; abdomen apparently without spinules. Length: Stages I-V, 4.5-9.0 mm. Range: Sea of Okhotsk to St. Lawrence Island (Bering Sea); depth, 18-180 m (Makarov 1967).

Genus *Paracrangon* Dana

In all described stages, rostrum long, spiniform, spinulose, directed upwards about 45°; carapace with denticulate anteroventral margin; basipodite of maxilliped without subterminal seta; exopodites on pereopods 1 and 2; exopodites of pereopods 1 and 2 with ≤ 6 natatory setae; protopodite of antenna with 2 spines – one at base of flagellum, other a long spine at base of scale.

Paracrangon echinata[13] Dana

At least 7 larval stages.

[13]A diagnostic character of adult *Paracrangon* is the absence of pereopods 2 (Rathbun 1904). Kurata's (1964b) description of *Paracrangon echinata* shows pereopod 2 fully developed as late as the seventh larval stage. Either Makarov's (1967) identification of these larvae as *P. echinata* is incorrect, or *P. echinata* must have at least 3 or 4 more larval stages before pereopod 2 becomes reduced or absent.

Stages II, IV-VII, from plankton; tentatively identified as *Glyphocrangon* sp. by Kurata (1964b); figures 103-130 in Kurata (1964b).
Stages II and IV; Makarov (1967) based identity on known distribution of adults and morphology of embryo of *Glyphocrangon granulosis* (see Bate 1888); figure 28 in Makarov (1967).

Most spinose of crangonid larvae known from northern North Pacific Ocean (Fig. 10). Length: Stage II, 5 mm; Stage VII, 13.8 mm. Range: Sea of Japan; Okhotsk Sea; Port Etches, AK, to La Jolla, CA; depth, 7-201 m (Butler 1980).

Genus *Sabinea* J. C. Ross

Probably 4 larval stages. In all described stages, telson relatively wide, with shallow indentation; pereopods 2-5 without exopodites.

Sabinea septemcarinata (Sabine)

Probably 4 larval stages.
Prezoeal telson and Stages I and III, probably known parentage; Atlantic specimens: plate V, figures 1-23, and plate VI, figures 1-13, in Sars (1890).
Stages I and III, probably known parentage; described as *Crangon septemcarinatus* by Williamson (1915); figures 167-172 in Williamson (1915). Williamson's figures from Sars (1890).
Stages I and III, from plankton; figure 12, "last stage" (= Stage III), in Birshteyn (1938).
Stage I (whole larva) and Stage III (telson); origin of specimens not given; figures 1 and 2 in Williamson (1960).
Stages and origin of specimens not given, described as *Myto gaimardi* by Birshteyn (1938); plate 7, figure 1 (Krøyer 1846 in Birshteyn 1938).

In all described stages, anteroventral margin of carapace with about 7 denticles. Abdominal somites 1-4 with 1, 2, 1, and 1 ventral spines, respectively; abdominal somite 5 with posterolateral spine. Telson with 16 + 16 setae in Stage I, 13 + 13 setae in Stage III. Length: Stages I-III, 7.7-11.5 mm. Range: area of Iceland and Faroe Islands (Williamson 1960); Barents and Norwegian Seas (Williamson 1960); Chukchi Sea (Birshteyn 1938); eastern coast of North America from mouth of St. Lawrence River to Massachusetts Bay; Arctic Ocean to Point Barrow (Alaska), White Sea, and northern Europe (Williams 1974); depth, 10-240 m (Williams 1974).

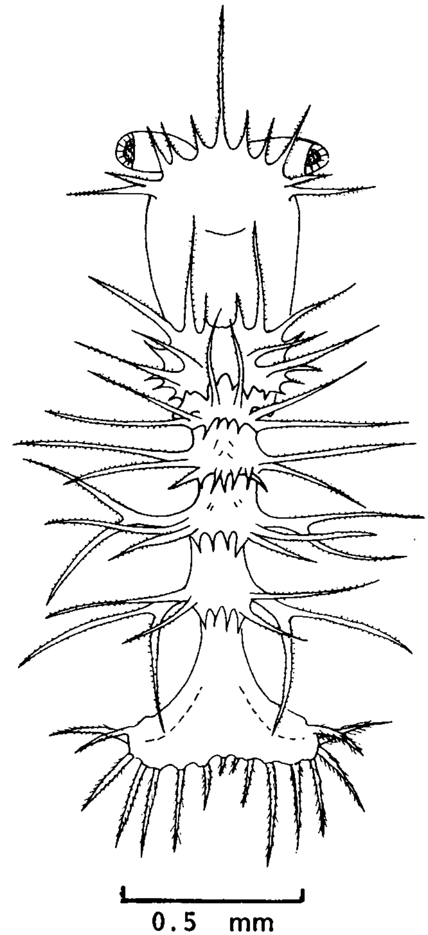

FIGURE 10.–Dorsal view of body, Stage I zoea of *Paracrangon echinata*.

Genus *Sclerocrangon* G. O. Sars

Not more than 2 larval stages. Appendages resemble adult except uropods enclosed and pleopods not fully setose. Pereopods without exopodites; pereopods 4 and 5 have characteristic sickle-shaped dactyli (Fig. 11).

Sclerocrangon boreas (Phipps)

Two larval stages.
Late embryo extracted from egg; plate VI, figures 14-28, in Sars (1890, as cited in Williamson 1960).
Stage not specified, known parentage (Makarov 1967). No figures.
Stage I and Stage II ("postlarval"), known parentage; figures 1-3 in Makarov (1968).

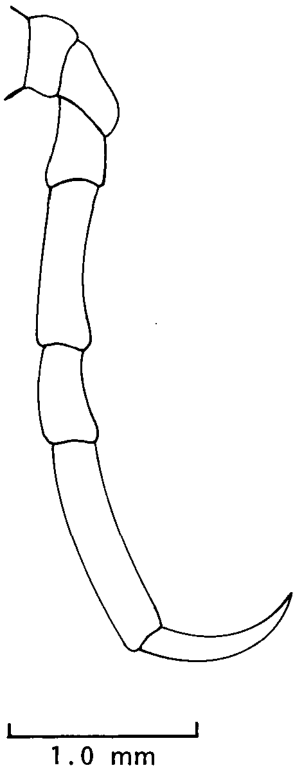

FIGURE 11.–Pereopod 4 or 5 of *Sclerocrangon* larva with characteristic sickle-shaped dactyl.

Larvae not free living but cling to pleopods of female. In all described stages, carapace without anteroventral denticles; flagellum of antennule segmented; basal portion of antennule shaped as in adult; maxillipeds with undeveloped exopodites; exopodites with a few feeble natatory setae; pereopods segmented, without exopodites. In Stage I, rostrum absent; carapace covers sessile eyes; telson and abdominal somite 6 jointed. In Stage II, rostrum short, triangular, flattened dorsoventrally. Length: Stage I, 9.0 mm; Stage II, 11.5 mm. Range: Sea of Japan to Chukchi Sea to Bare Island, WA; arctic Canada to Cape Cod, MA; North Atlantic Ocean and arctic Europe; Spitsbergen to Faroe Islands; depth, 0-366 m (Butler 1980).

Sclerocrangon salebrosa (Owen)

One larval stage.
Stage I, from plankton; figure 27 in Makarov (1967).
Embryos, from female; Stage I and Stage II ("postlarval"), from plankton; figures 1 and 2 in Makarov (1968). Larvae from plankton identified by comparison with embryos dissected from eggs.

Larvae free living. In Stage I, rostrum spiniform; carapace with anteroventral denticles; exopodites of maxillipeds fully developed, each exopodite with 5 natatory setae; telson exceptionally wide with 22 + 22 setae. Length: Stage I, 10.3-10.5 mm. Range: Okhotsk Sea; Hokkaido; no depth range (Kurata 1964b; Makarov 1967).

Sclerocrangon zenkevitchi Birstein and Vinogradov

Only Stage I described, known parentage; figure 5 in Birshteyn and Vinogradov (1953).

Carapace nearly circular laterally, without rostrum; cephalothorax and abdomen without spines or denticles; telson ovoid. Length: Stage I, 7.2 mm. Range: Bering Sea; depth, 2,995-3,940 m (Birshteyn and Vinogradov 1953).

BIOLOGY

Although pandalid, hippolytid, and crangonid larvae are common inhabitants of the neritic meroplankton of temperate and arctic waters of the North Pacific Ocean, only a few studies on their biology have been published. The most complete studies are those of Haynes (1983), Makarov (1967), and Rothlisberg (1975). Haynes described the relative abundance and distribution of pandalid shrimp larvae in the lower Cook Inlet-Kachemak Bay area, Alaska; Makarov (1967) described the distribution of decapod shrimp larvae of the West Kamchatkan shelf; and Rothlisberg (1975) discussed larval ecology of *Pandalus jordani* off the Oregon coast. In this section, I review the findings of these authors and supplement their findings with information from the literature. To avoid redundancy of citation, only information in addition to that given by Haynes, Makarov, and Rothlisberg is cited by author and date. This section does not include every known facet of the biology of decapod shrimp larvae of the northern North Pacific Ocean; however, more information can be acquired from the papers of Haynes, Makarov, and Rothlisberg and from their bibliographies.

Areas of high abundance of Stage I larvae apparently indicate areas where females are releasing larvae. For example, in Kachemak Bay in 1972, Stage I larvae of *Pandalus borealis*, *P. goniurus*, *P. hypsinotus*, and *Pandalopsis dispar* were most abundant in plankton samples collected in the same area where females were releasing larvae (for these 4 species, females were releasing larvae at depths of about 85, 35, 50, and 100 m, respectively, based on a trawling survey).

Time of release of pandalid larvae varies with species. In Kachemak Bay in 1972, Stage I larvae of *Pandalus borealis* were not caught until the first half of April; Stage I larvae of *P. goniurus* and *P. hypsinotus* were caught later, in the latter half of April. In British Columbia waters, *P. borealis* larvae are also released earlier than larvae of either *P. goniurus* or *P. hypsinotus* (Berkeley 1930; Butler 1964).

Time of larval release is also related to water temperature. For example, a residual layer of relatively cold (sometimes subzero) water remains on the central West Kamchatkan shelf at a depth of 50-150 m throughout the summer. Decapods living in this layer of cold water release their larvae later than decapods living in warmer waters to the north and south. In the western North Atlantic Ocean, pandalid shrimp also release their larvae later in colder waters than in warmer waters (Haynes and Wigley 1969).

Depth distributions of larvae of *P. borealis* and *P. goniurus* in Kachemak Bay, 1972, were usually similar. Few larvae were in the 0-10 m stratum; most were between about 10 and 40 m. The abundance of larvae remained relatively constant below about 50 m. Numbers of Stage I *P. borealis* larvae, however, increased below about 70 m, possibly reflecting their recent release. These depth distributions differ from the depth distribution of *P. jordani* off the Oregon coast. Younger (Stages V-X) *P. jordani* larvae were found closer to the surface (0-10 m stratum) than older (Stages XI-XV) larvae (to 160 m).

Water temperature has profound effects on larval survival, growth, and size at metamorphosis. For example, survival of *P. jordani* larvae (Stages I-III) is markedly less at 17° than at 5°C. For the oldest stage (Stages IX-XIII), the relation between survival and temperature is reversed, and survival is lowest at 5°C (Rothlisberg 1979). For larvae of *P. platyceros*, survival is reduced by sudden changes in temperature, particularly about 20°C and below 9°C (Wickins 1972). At a given temperature (range 5°-14°C), growth increments for all larval stages of *P. jordani* decrease with increasing size; however, the higher the temperature, the more rapid the molting frequency (Rothlisberg 1979).

Shrimp larvae can probably influence the direction and extent of their dispersal. For instance, in Kachemak Bay, 1972 and 1976, pandalid shrimp larvae were released in the central portion of the outer bay. Some of these larvae were carried northward out of the bay in the direction of the current, but others were dispersed southwestward in a direction opposite the current. In the southern area of the western Kamchatka shelf, *Crangon* larvae released close to shore with larvae of other species, such as king crab, *Paralithodes camtschatica*, remained close to shore. Larvae of the other species, however, were carried seaward. In the northern area of the western Kamchatka shelf, where currents are faster than in the southern area, *Crangon* larvae were carried seaward (Makarov 1967). The causes for dispersal of larvae against known water currents are unknown, but dispersal may be dependent, at least in part, on the swimming capability of the larvae.

Some pandalid shrimp larvae migrate vertically in a diel cycle. In Kachemak Bay in 1972, Stages I and II larvae of *P. borealis* and *P. goniurus* were most abundant between the surface and 15 m during low light levels (1800-0800 h); however, during high light levels (1000 and 1600 h), they were most abundant between 30 and 60 m. Although present, a pronounced thermocline did not prevent larvae from moving vertically. Whether later stages of *P. borealis* and *P. goniurus* migrate similarly is unknown; however, in waters off Oregon, only Stages XII-XVI larvae of *P. jordani* migrate vertically in a diel cycle. During the day, these *P. jordani* larvae are distributed from the surface to 150 m by age: the deeper the water, the older the larvae. At night, *P. jordani* larvae migrate upwards in the water column, and the stages remain somewhat uniformly distributed with depth.

Foods of pandalid larvae have been determined during attempts to rear the larvae in the laboratory and from examination of shrimp stomachs. Larvae of *P. jordani* and *P. platyceros* have been reared on brine shrimp, *Artemia salina* nauplii (Modin and Cox 1967; Lee 1969; Price and Chew 1972), *P. hypsinotus* larvae have been reared on brine shrimp nauplii and algae (Haynes 1976), and *P. kessleri* larvae have been reared on small pieces of crab, shrimp, and mussel tissue (Kurata 1955). In 1976, I made a preliminary study (unpublished) on foods eaten by pandalid shrimp larvae in Kachemak Bay by examining their gut contents. The larvae mostly ate diatoms, especially *Coscinodiscus* types, and larval crustaceans. Many of the guts also contained black pigment and ommatidia. The assumption that pandalid larvae feed on eyes of other decapod larvae was subsequently confirmed when I observed a *P. borealis* zoea ingesting the eye of a live king crab zoea. Calcareous fragments (probably molluscs), coccolithophores, spines of larval echinoderms, and bits of diatoms have been found in guts of *Pandalus* larvae from European waters (Lebour 1922).

Some species of pandalid larvae are sustained by their internal yolk for several days after hatching without feeding; others must feed immediately after hatching or die. *Pandalus platyceros* larvae can live 11-13 d on stored yolk with no food (Price and Chew 1972); however, when food is offered, they feed immediately after hatching. In Price and Chew's (1972) study, the starved larvae ate their dead relatives, but did not actively prey on them. Larvae of *P. jordani*, however, if not fed soon after hatching, starve and die regardless of later increases in prey concentrations (Modin and Cox 1967). In another study, 40% of Stage I zoeae of *P. borealis* without prey died in 5 d, and 100% died in 13 d (Paul et al. 1979).

The relationship between food and survival in captivity has been determined for some North Pacific Ocean larvae; however, little is known about this relationship in nature. For instance, year-class strength may be influenced or even largely determined by the quality and quantity of food available during the larval period. Unfortunately, there is virtually no information on the types and quantities of food needed for survival of shrimp larvae in nature. Until this information is available, the relation between food and survival of shrimp larvae at sea will remain unknown.

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