

Studies on the Cymothoid Fish Symbionts of
the Eastern Pacific (Crustacea: Isopoda: Cymothoidae)
II. Systematics and Biology of *Lironeca vulgaris*
Stimpson 1857

by Richard C. Brusca
Allan Hancock Foundation
University of Southern California
Los Angeles, California

ABSTRACT. *Lironeca panamensis* Schioedte and Meinert 1884 is synonymized with *L. vulgaris* Stimpson 1857, and detailed descriptions are presented for the male, female, and juvenile stages. Taxonomic characters of the genus *Lironeca* are discussed, and a key to the eastern Pacific species (including Hawaii) is given. Marsupial and postmarsupial development, fecundity, and general life history of *L. vulgaris* are elucidated and the ecology of the host-parasite relationship is discussed. Male *Lironeca vulgaris* are parasitic, feeding on red blood cells from the host fish's gills or the inner surface of the opercle (although saprophagy may also occur under certain conditions); females are primarily nonfeeding commensals in the host's buccal chamber, although may occasionally feed in a manner similar to males. Host specificity is primarily a matter of ecological preference, rather than taxonomic preference, preferred fish groups being benthic and/or schooling species. Transition from male to female takes place (superficially) in a single molt. Fecundity is greater than described for any other flabelliferous isopod (440-540 eggs; 375-435 manca released). It appears probable that only a single brood is normally produced by each female.

INTRODUCTION

Brusca (1975, 1977, 1978) has discussed the general state of affairs as regards the knowledge of the family Cymothoidae in the eastern Pacific. The present paper follows the recommendations and format of those papers. *Lironeca* is one of the better known cymothoid genera in the eastern Pacific (yet it still remains poorly known, most of its species having been described before or near the turn of the century). It is the only genus in the family having had recent taxonomic and ecological work published on its eastern Pacific species (Menzies *et al.*, 1955).

Five species of *Lironeca* have been reported from the eastern Pacific: *L. californica* Schioedte and Meinert 1883, *L. convexa* Richardson 1905, *L. vulgaris* Stimpson 1857, and *L. panamensis* Schioedte and Meinert 1884. The Indo-Pacific species *L. raynaudi* Milne Edwards 1840 was reported from southern Chile by Menzies (1962). This number is herein reduced to four by synonymy of *L. panamensis* with *L. vulgaris*. *Lironeca puhi* Bowman 1960 is known only from the Hawaiian Islands.

The most significant study of this century on eastern Pacific *Lironeca* is that of Menzies, *et al.* (*op. cit.*) for *L. convexa*. Their attempt to establish a life cycle (through secondary data) was a great step forward and should be compared to conclusions drawn in this paper and Brusca (1978). The present study has resulted from the examination of types of *L. panameusis*, and over 400 additional adult individuals from over 75 discreet localities throughout the range of *L. vulgaris*. Most of these specimens are deposited at the Allan Hancock Foundation, University of Southern California (Los Angeles, California). In addition, a culture of *L. vulgaris* (from southern California) was monitored daily in the laboratory during a two-month period, using the California killifish (*Fundulus parvipinnis*) as a host. Scientific and common names of fishes are based on Miller and Lea (1972) and Bailey, *et al.* (1970).

SYSTEMATICS

Taxonomic Characters of the Species
of *Lironeca*

Historically, isopod taxonomists have emphasized the following characters in their descriptions of eastern Pacific species of this genus: width vs. length ratios of head and pleotelson; shape and length of uropods and pleotelson; presence or absence of a carina on the pereopod bases; size and position of the eyes; width and length of the pereonites and pleonites; position of coxal plates (= "epimeres"); concealment of the pleonites by the pereon; and, total length-width ratios of adults. In addition, most older descriptions repeat numerous generic characters, which are of no value for specific identification. Of the above-listed attributes, the first three are of taxonomic utility; the remainder are all highly variable and of little or no use in distinguishing the eastern Pacific species of *Lironeca*. In addition to the three significant characters mentioned above, pleopod morphology and appendage ornamentation have been found to have high diagnostic credibility.

Character states vary considerably in *L. vulgaris*. Data from other eastern Pacific species of Cymothoidae suggest that these variations are probably common in most species in this family.

- A. Antennae: the number of articles in antenna 1 varies from 7 (in juveniles) to 8 (in adults); in antenna 2 from 10 to 11 (in adults). It is not uncommon, however, to find individuals with fewer than the normal number of articles due to loss of the terminal ones from damage—possibly inflicted by predators (cleaning fishes, etc.).
- B. Length-width ratios of body, pereonites, pleonites, and coxal plates: as *Lironeca vulgaris* matures its width-length ratio decreases. Once the female stage is achieved the onset of oostegite formation and brooding tends to accentuate this trend. Further, gravid females usually develop a strongly convex dorsum, resulting in a distortion of the lateral margins of the pereon and coxal plates. The twisting of the body, to the left or right, also distorts the "normal" length to width ratios and coxal configuration. The high degree of variability in these body size ratios is reflected in the body index (length divided by width), which varies in adult *L. vulgaris* from 1.6 to 2.2. These variables also affect the first pleonite, which may be entirely exposed, or only partly exposed.
- C. Appendix masculinum of the female: once thought to be a reliable taxonomic character, this structure actually decreases in size with succeeding molts. Young slender females have an appendix masculinum as large as adult males, whereas in older, larger females (over 20 mm in length), it may be reduced to a minute, barely discernible, spine-like flap.
- D. Pereopods: the spines of the pereopodal articles are easily eroded or rubbed off, and it is common to find individuals with fewer than the "normal" number. It would appear that in *L. vulgaris* erosion (or reduction) of the pereopodal spines proceeds concurrently with growth. The spines are robust and acute in juveniles, appear considerably eroded or reduced in young males, and are absent in old males and all females. It has been shown that similar structures (pereopodal bristles) play a role in pre-copulatory behavior in other groups of isopods (Solignac 1972a, 1972b, 1975), and the possibility of this function in *L. vulgaris* is discussed in a subsequent section of this paper. The shape of the carina on the bases of the pereopods is also somewhat variable, ranging from a long, smooth, gradual elevation to a short, pronounced hump.
- E. Accessory gill of pleopodal basis: this structure varies from a minute flap to a large lamella, two-thirds the size of the exopod. Larger sizes may be related to increased oxygen demand and the size may thus eventually be shown to be predictable from host fish and/or water depth and temperature data. No correlation between latitude or host species and size of this structure has been evident from this study.
- F. Pleotelson shape: the posterior border of the pleotelson often shows signs of damage, probably due to predation, occasionally presenting a somewhat crenulate appearance (note figure 250 in Schultz, 1969).

Synonymy

- Lironeca vulgaris*: Stimpson, 1857:508; Stimpson, 1859:88; Schioedte and Meinert, 1884:344; Calman, 1898:261; Richardson, 1899:830; Richardson, 1899:172; Richardson, 1900:221; Richardson, 1904:214; Richardson, 1904:659; Richardson, 1905:258; Nierstrasz, 1931:144; Hatch, 1947:211; Menzies, *et al.*, 1955:288; Schultz, 1969:165; Turner, *et al.*, 1969:89; Hobson, 1971:504; Crane, 1972:152; Brusca, 1973:205; Miller, 1975:297.
- Lironeca panamensis*: Schioedte and Meinert, 1884:349; Richardson, 1899:830; Richardson, 1899:172; Richardson, 1905:257; Nierstrasz, 1931:144; Menzies, 1962:345; Schultz, 1969:167; Brusca, 1973:205.
- Anilocra occidentalis*: Richardson, 1899:830; Richardson, 1899:172; Richardson, 1900:220.

Description, *Lironeca vulgaris*

ADULT FEMALE

Body: Width 6.3-19.1 mm (mean = 9.0); length 11.4-43.0 mm (mean = 18.5); body index 1.6-2.18 (mean, non-ovigerous females 1.91; standard deviation .13; mean, ovigerous females 1.84; standard deviation .12); body occasionally twisted to right or left (fig. 1).

Cephalon: About two-thirds as wide as long (length to width ratio .41-.73; mean .66); front weakly truncate. Eyes well developed. Antenna 1 separated by approximately 1 mm, of 8 articles, reaching posterior border of cephalon (fig. 4); antenna 2 of 10-11 articles, extended $\frac{1}{2}$ - $\frac{1}{2}$ distance into first pereonite (fig. 5). Mouthparts reduced; maxilliped with 2 terminal, recurved spines (fig. 16); maxilla 1 styliform, with 1 large and 3 smaller terminal spines (fig. 13); maxilla 2 with 2 terminal spines, palp with 1 terminal spine (fig. 14); mandible without lacinia mobilis, incisor blade-like and curved (fig. 15).

Pereon: Pereonite 1 longest; anterolateral angles produced forward to border posterior quarter of

cephalon. Pereonites 4-5 widest. Coxal plates 2-7 visible in dorsal aspect; 4-7 or 5-7 free distally and with posteriorly directed subacute angles; all at least reaching posterior margin of respective pereonite, and occasionally beyond (fig. 2). Pereopods similar, increasing gradually in length posteriorly; inside borders without spines (figs. 10 to 12); 4-7 with a carina on basis, increasing in size posteriorly (fig. 12).

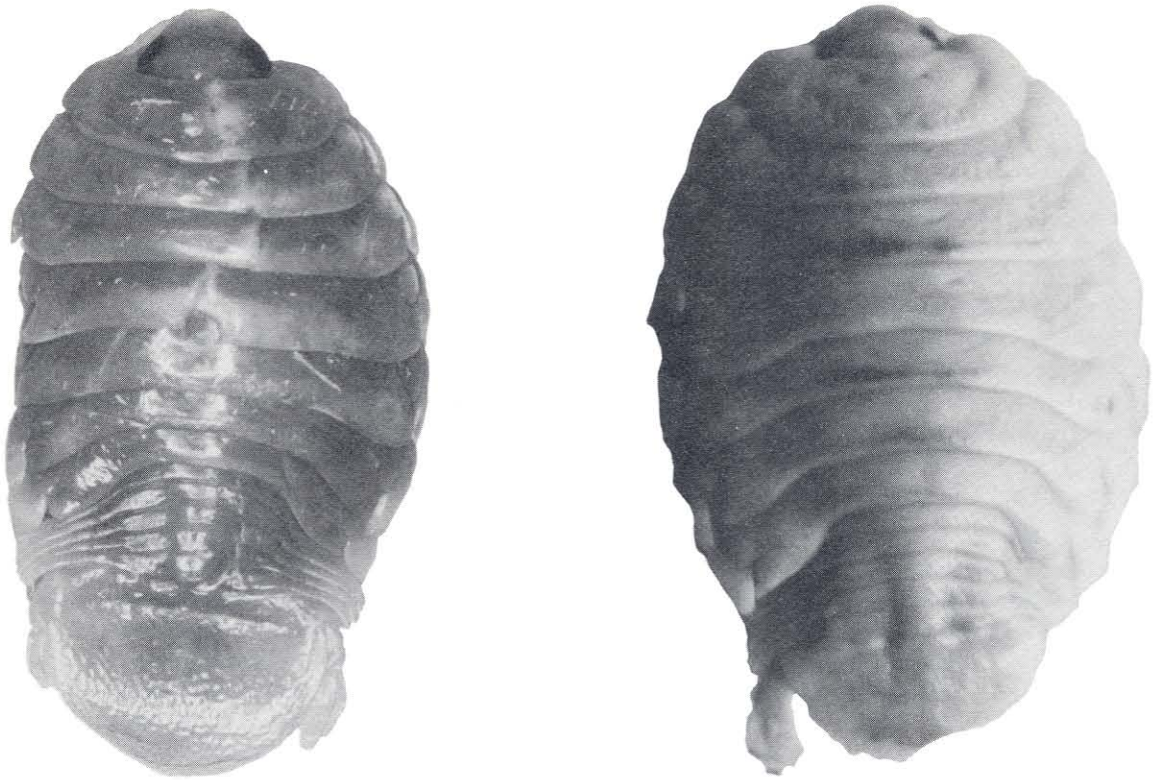
Pleon: Pleonites subequal in length; all more-or-less visible in dorsal aspect; strongly twisted individuals may have portions of 1 or more pleonites hidden under pereon. Midline of pleon more-or-less elevated, forming a slight median rise. Pleotelson evenly rounded; width approximately 2 times length (length to width ratio .47-.78; mean .52). Pleopods with accessory lobe (epipod) on basis, of variable size (figs. 6 to 8); pleopods 3-5 with accessory lobe on endopod (fig. 8); pleopod 2 with at least a remnant of the male appendix masculinum (fig. 7). Exopod and endopod of uropods subequal (fig. 9).

ADULT MALE

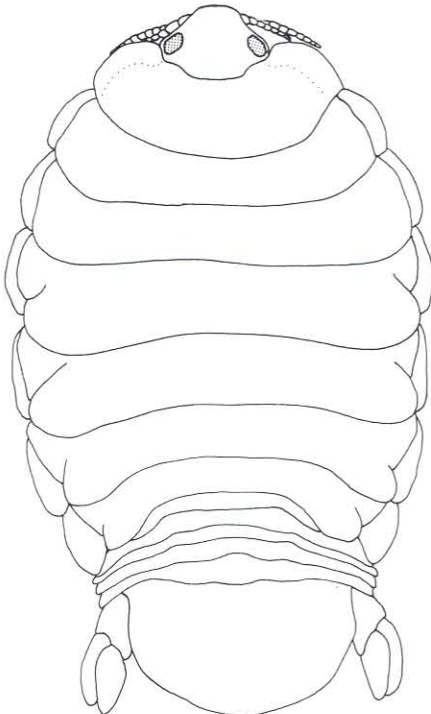
Width 3.2-16.2; (mean 6.5; standard deviation 2.5); length 6.9-31.0 (mean 11.9; standard deviation 4.2); body index 1.7-2.2 (mean 1.97; standard deviation .14). Similar to female except for the following: body smaller and narrower (fig. 3); with a more distinctly truncate cephalon; coxal plates generally less acute; young males with spines on propus and carpus of pereopods (as in juveniles, figs. 20 to 22); and, posterior pereopods bear somewhat more distinct carina on bases.

JUVENILE ("aegathoid" stage)

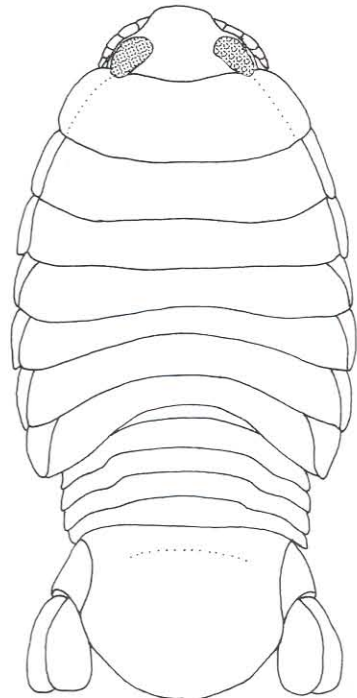
Always with darker pigmentation than adults, especially on uropods and margins of pereonites and pleonites. Cephalon width about 1.5 times length, front broadly and roundly truncate; eyes very large, $\frac{1}{2}$ total cephalon length. Antenna 1 of 7 articles; extended to posterior border of cephalon. Antenna 2 of 10-11 articles; extended to posterior border of pereonite 1. Pereonite 1 longest; pereonites 3 and 4 widest. All coxal plates visible in dorsal aspect; extended to or falling short of posterior border of respective pereonite. Propus and carpus of pereopods with robust, acute spines on inside margin (figs. 20 to 22); pereopods 1-4 with 4 spines on propus and 2 on carpus; pereopods 5-6 with 3 spines on



1



2



3

Fig. 1. Top left and right. *Lironeca vulgaris*, female. (Note variation in body morphology, particularly width vs. length.) Fig. 2. *Lironeca vulgaris*, female. Fig. 3. *Lironeca vulgaris*, male.

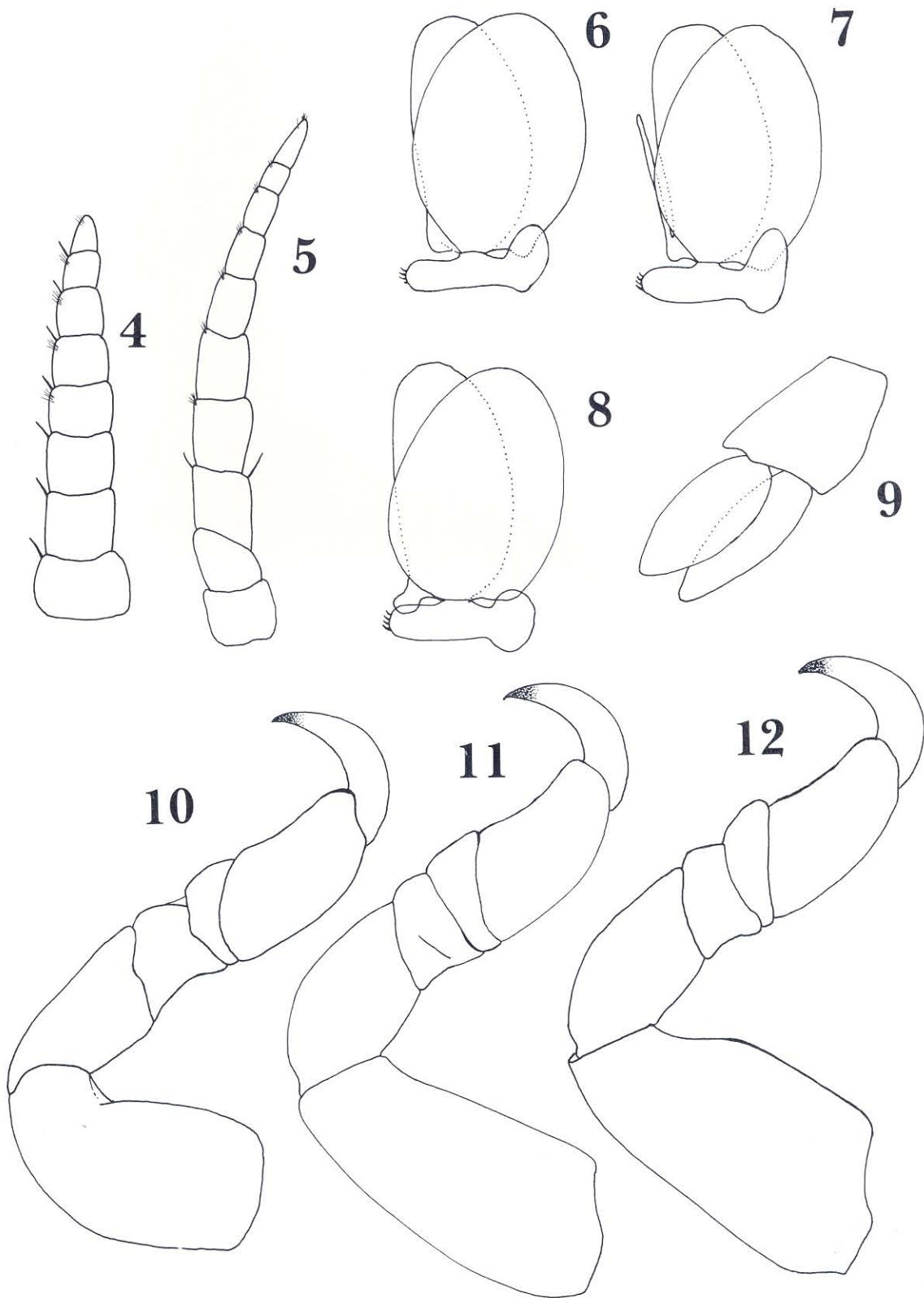


Fig. 4. Antenna 1, female. Fig. 5. Antenna 2, female. Fig. 6. Pleopod 1, female. Fig. 7. Pleopod 2, female. Fig. 8. Pleopod 3, female. Fig. 9. Uropod, female. Fig. 10. Pereopod 1, female. Fig. 11. Pereopod 5, female. Fig. 12. Peropod 7, female.

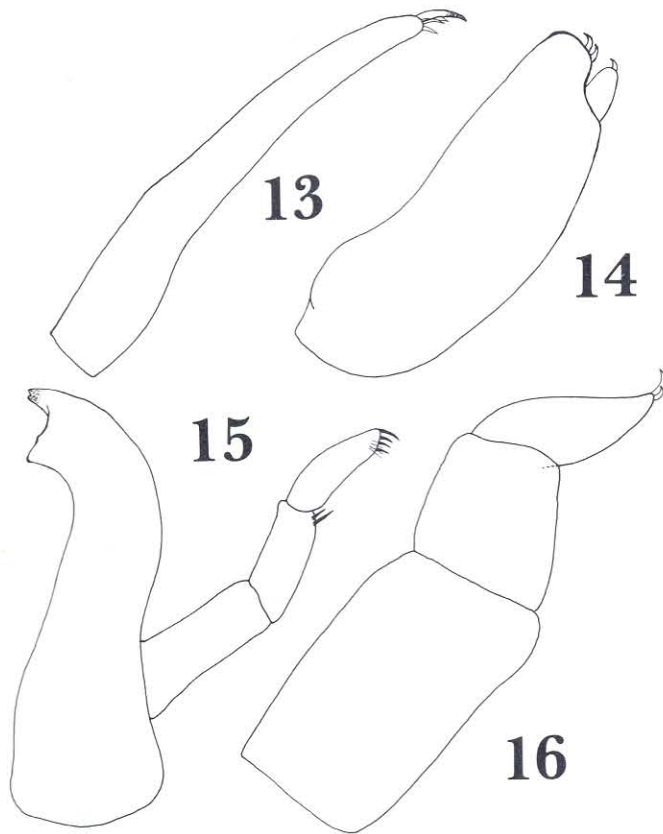


Fig. 13. Maxilla 1, female. Fig. 14. Maxilla 2, female. Fig. 15. Mandible, female. Fig. 16. Maxilliped, female.

propus and 3 on carpus; pereopod 7 with 5 spines on propus and 8 on carpus. Carinae well developed on bases of all pereopods. Pleon symmetrical; margins even. All pleopods as in adults, but with marginal setae and without a well developed accessory gill on the basis. Uropods angular and setose (fig. 19).

Remarks

Specimens of *L. vulgaris* I have examined are identical to the description of this species (and *L. panamensis*) given by Richardson (1905) in all but 3 respects: (1) the cephalon of *L. vulgaris* is said to be widely rounded, although she figured it as truncate (after Schioedte and Meinert, 1884 and Stimpson, 1857), as it is in all specimens I have observed; (2) the fifth and sixth coxal plates of *L. panamensis* are said not to reach the posterior margin of their respective pereonites, whereas in most specimens I have examined they not only reach but in some cases extend slightly beyond the margin; and, (3) the first pleonite of *L. panamensis* is said to have its posterior border hidden by pereonite 7, but in specimens I have examined it is obvious that this is a variable character, in that some are hidden while most

others are not. The lateral edges of pleonite 1 are similarly occasionally hidden but more often not. Clearly, these characters of the coxal plates and first pleonite are unreliable for use in species identification. The use of the pleopods as diagnostic taxonomic characters in this genus appears to be significant, although the only other new world species of *Lironeca* that have had the pleopods fully described are *L. convexa* and *L. puhi*. Richardson's (1899) *Anilocra occidentalis* is actually a young male *L. vulgaris*, recently having molted out of the juvenile (natatory) instar (Richardson, 1905), and personal observation.

There seems to be no question that isopods described as *L. panamensis* are simply specimens of *L. vulgaris* collected in the southern extent of the range. There are no significant differences between any measurable characters from specimens collected in the northern, central and southern localities of this isopod. Also, there are no clinal or latitudinal trends discernible for any character studied. The difficulty in distinguishing between these two species has long vexed workers with this taxon, and I suspect that many previous identifications must have been based ultimately upon geographic data, rather than morphological criteria.

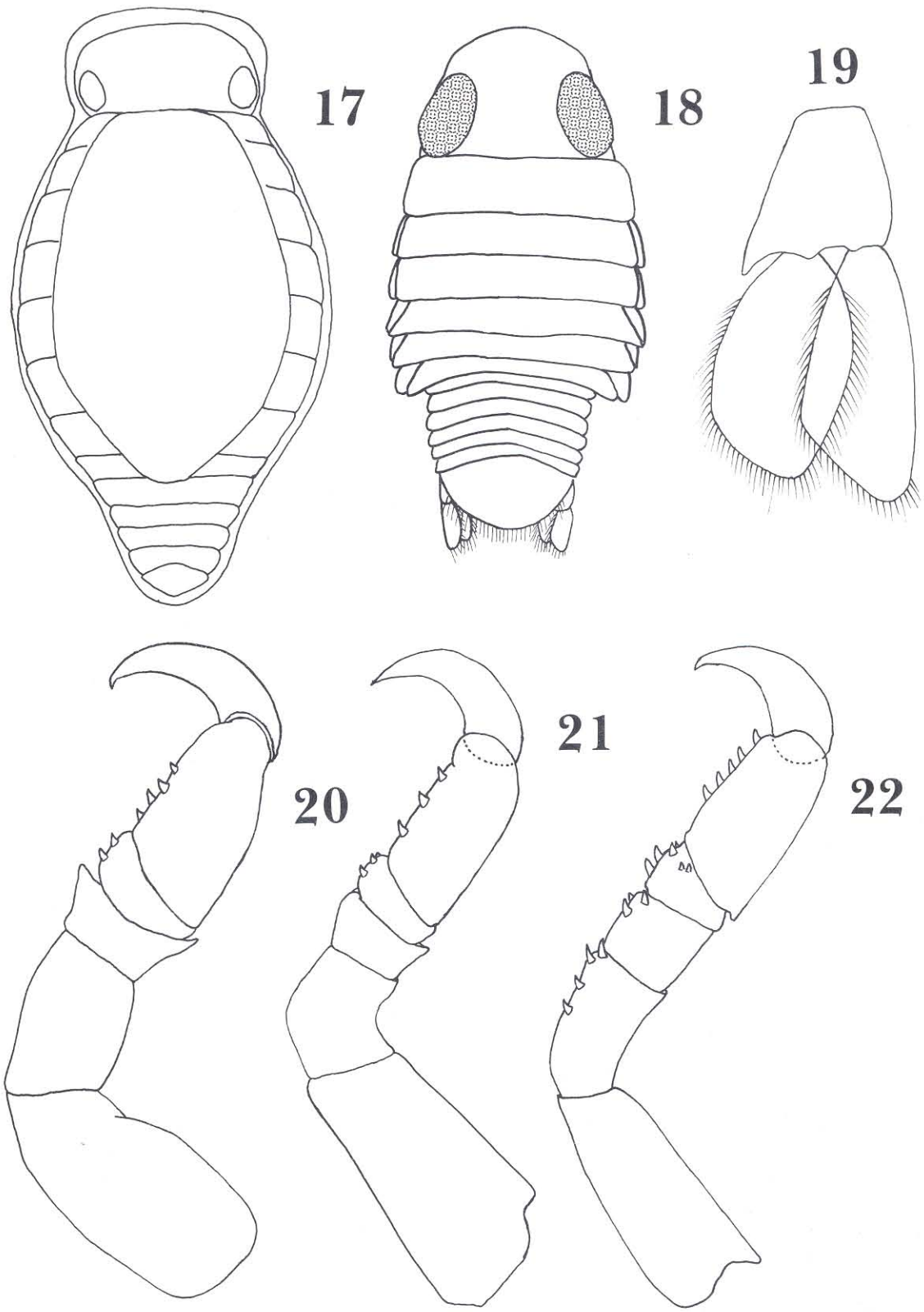


Fig. 17. First visible segmentation stage. Fig. 18. Manca stage. Fig. 19. Uropod, juvenile. Fig. 20. Pereopod 1, juvenile. Fig. 21. Pereopod 5, juvenile. Fig. 22. Pereopod 7, juvenile.

DEVELOPMENT AND LIFE HISTORY

Marsupial Development

Little work has been done on the development and life histories of cymothoid isopods. Brusca (1978) and Strombert (1965a, 1965b, 1967, 1971) have briefly reviewed these works. Stromberg's excellent papers present some of the best modern accounts of isopod development, treating *Idotea*, *Limnoria*, and selected bopyrids. With the exception of Nair (1956), the most significant papers dealing with cymothoid embryology are all nineteenth century works (Bullar, 1878; Patten, 1890; Nusbaum, 1898).

A model for the life cycle of *Lironeca vulgaris* is proposed (fig. 23), based on 60 individuals from the upper Gulf of California. Marsupial development is similar to that of *Irona* (Nair, 1956) and *Nerocila* (Brusca, 1978), and the stages are nearly identical in appearance. The large, yolky egg is subspherical, becoming progressively more ovoid as development ensues. Two transparent egg membranes are apparent in the early stages (in fertilized eggs), the outermost chorion and the inner vitelline membrane. These are shed as the first segmented marsupial stage is formed¹. The first two segmented marsupial stages (marsupial stages 3 and 4) are enclosed by the embryonic membrane and are similar to those of *N. californica* except that segmentation appears somewhat more distinct (fig. 17).

Thus marsupial development in *L. vulgaris* may be considered composed of five distinguishable stages: (1) subspherical to ovoid egg, including the earliest cleavage stages not yet visible superficially (equivalent to developmental stage 1 of Kjennerud, 1950, for *Idotea neglecta*); (2) late cleavage and development to first visible body segmentation stage, wherein the embryo appears as an undifferentiated ovoid mass (this stage was not recognized by Kjennerud, although it was recognized by Holdich (1968) for *Dynamene bidentata*); (3) first segmentation stage, in which somite formation appears largely superficial (equivalent to Kjennerud's stage 2) and considerable yolk is still present (fig. 17); (4) second segmentation stage, in which segmentation ap-

proaches completion and distinct limbs are obvious (equivalent to Kjennerud's stage 3); and, (5) the pre-hatch or manca stage, in which six pairs of pereopods are present (fig. 18). This pattern is consistent with that described for *Idotea emarginata* (Naylor, 1955), *Lironeca convexa* (Menzies, Bowman and Alverson, 1955), *Irona* (Nair, 1956), *Anilocra* spp. (Montalenti, 1941), *I. neglecta* (Kjennerud, 1950), *Jaera albifrons* (Forsman, 1944), and *Nerocila californica* (Brusca, 1978). Holdich (1968) described five marsupial stages for *Dynamene bidentata*, which were similar to those described above (except that author recognized two rows of limb buds prior to any visible segmentation).

Postmarsupial Development

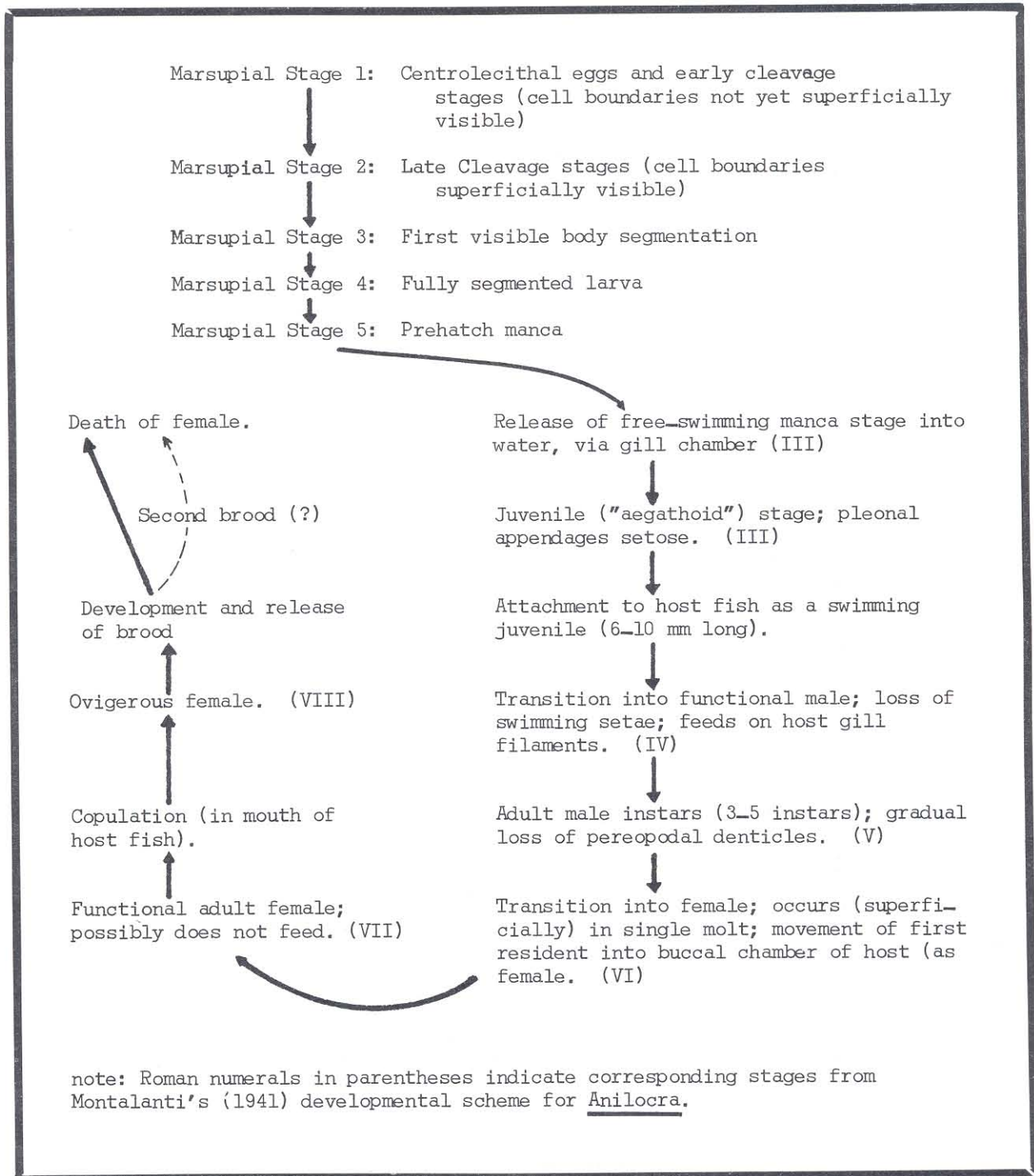
The largest single series of *L. vulgaris* present in this study consists of 60 individuals from the northern Gulf of California. Although these probably represent a sample of a single interbreeding population, this is still too few specimens to get a precise picture of all the details of postmarsupial growth, although some generalizations can be made. No juveniles are present in this series, the smallest individual being a fully developed male (3.2 x 7.1 mm; body index 2.22). The largest male is an extraordinarily robust specimen (12.3 x 21.3 mm; body index 1.73) that obviously either never received, or missed, his cue to enter the first female instar. With this single exception, all other large males from the Gulf of California average 8-9 mm in width and 18-19 mm in length. The smaller females average 11.5 mm in length, the larger 22.7 mm.

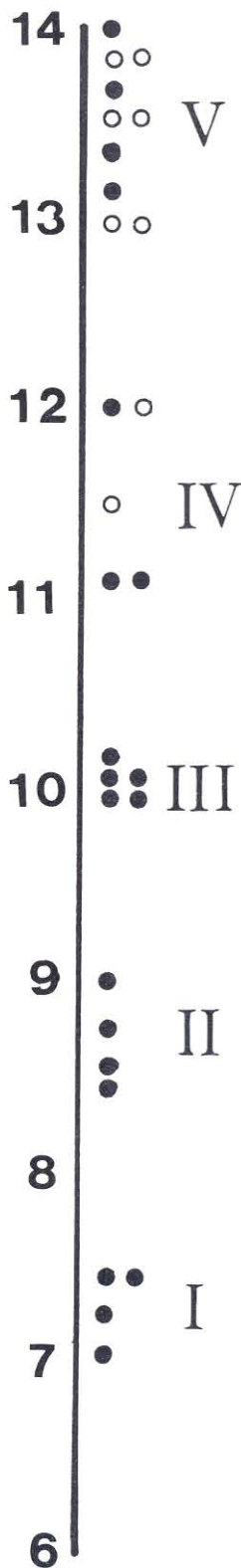
The major changes in morphology from the juvenile (= "aegathoid" stage) to the young adult male stages are: (1) loss of natatory setae on pleopods, pleotelson, and uropods; (2) reduction in size of carinae on bases of pereopods; (3) reduction in size of eyes; (4) reduction in pigmentation; (5) increase in number of antenna 1 articles from 7 to 8; and (6) progressive reduction in size of spines on pereopods.

When the sizes (total body length) of these individuals are plotted (against their frequency) the data suggest that there are 5 male instars represented by the series (fig. 24). The third and

¹The term "segmented", in this paper, refers to the body segmentation, and is not used in the embryological sense as synonymous with "cleavage."

Fig. 23. Proposed life cycle for *Lironeca vulgaris*.





fourth male instars molt into either another male or a female. Beyond the fifth instar all individuals are normally female, assuming they receive their cue to undergo the sex-change molt. Discrete instars are not recognizable in the data for individuals greater than 14 mm in length. Again, these data compare favorably with data presented for *Nerocila californica* (Brusca, 1978) and *Lironeca convexa* (Menzies, *et al.*, 1955), and it is probable that any instars preceding these (recorded from this population of *L. vulgaris*) would be juveniles.

As with *N. californica*, the existence of midmolt individuals demonstrates that the sex reversal from male to female occurs in a single molt, at least superficially. The stimulus for the sex reversal may be either the presence of a new male entering the gill chamber, or the absence of a resident female on the host fish when the young male first attached (or subsequent death of the resident female). Size alone cannot account for the timing of the sex change, as large males (to 16.2 x 31 mm) do exist, albeit in relatively low numbers. It is not uncommon to find fishes infested with isopods of one sex only. The fact that adult females vary so greatly in size suggests that the male grows and remains masculine until a second male attempts to establish residence in the same gill chamber. The first male then, regardless of its size, undergoes a sex-change molt and moves into the buccal region to establish a new residence on the base of the host fish's tongue. After that time the continuing presence of the female may prolong the new male's masculine stage, as in *Anilocra physodes* (Legrand, 1951, 1952).

A recent paper by Charnov, *et al.* (1978) states that the age at which the protandrous shrimp *Pandalus jordani* changes sex is dependent upon the age composition of the local shrimp population. Once a juvenile cymothoid isopod has attached to its host fish, however, it becomes effectively isolated from the rest of its "population," making such a strategy unlikely in these parasites.

Fig. 24. Size frequency data for *Lironeca vulgaris*, from a population occurring in the northern Gulf of California. Only individuals smaller than 14 mm are plotted; above this size no distinct instars were discernable (arabic numerals = total length in mm.; solid circles = males; open circles = females; roman numerals indicate instar number). See text for further discussion.

Copulation and Broods

Laboratory studies have shown that adult *L. vulgaris* possess very little motility beyond the young male stages (6-10 mm in length). Although older males (10-30 mm) can slowly crawl about the substratum, gravid females must struggle to move even a few millimeters. Directed swimming maneuvers occur only in the juveniles and very young male stages. Because of these, and the following observations, it appears that copulation and insemination must occur on the host fish itself. I have recorded several instances of a male found in the host's buccal cavity, clinging to a female. In most cases the female is attached at the base of the fish's tongue, while the male sits atop her, his venter to her dorsum and his cephalon to her pleotelson. To my knowledge the actual copulatory act has not been witnessed in this species, or any other cymothoid isopod; however, these observations suggest a copulatory position similar to that recorded for species of *Jaera* (Solignac, 1972a, 1972b, 1975). Moreira (1973) described the copulatory position of 3 species of *Serolis* also as male venter to female dorsum, but head to head. Markus (1930) described a similar situation in *Lirceus macrourus*. In all of these cases the male is known to slide alternately onto one side, then the other, of the clasped female, with actual insemination presumed to occur as his venter lies adjacent to her lateral margin. The presence of strong spines on the inside margin of the pereopods of juveniles and young males, and their subsequent loss in older males and all females, suggests a possible copulatory or precopulatory function for these structures. It is possible that they are used by the male to stroke the female in some manner, as part of a precopulatory stimulation behavior. Solignac (1972a, 1972b, 1975) found this behavior in various species of *Jaera*, in which the male strokes the dorsum of the female. The particular pereonites stroked on the female, and the pattern of the male's pereopodal bristles were shown to be species specific (thus possibly the principal isolating mechanism) in the *Jaera* complex investigated by Solignac. It may be equally likely, however, that the spines merely assist the male in clinging to the female during copulation.

Ovigerous females of *L. vulgaris* have been collected in all months of the year. In the northern-most parts of the range (Oregon to the Mexican border), they have been recorded from February through September; in the more southern regions (Central and South America) from June through September and in December. In the central part of the range (western Mexico) ovigerous females have been recorded during every month of the year.

Females from both coasts of Baja California (ranging from 18 to 20 mm in length) carry 440-540 eggs, of which roughly 90 percent develop into stage 4 embryos. No data are available on how many mancae are released from the marsupium, or the percentage survival from stage 4 embryos to manca stage. An overall marsupial mortality of 36.4 percent was found for *Dynamene bidentata* by Holdich (1968), 12 percent of which occurred during the last molt into the manca stage. Based on these figures *L. vulgaris* appears to have a better overall marsupial survival (15-20 percent mortality), and to produce more offspring (estimated 375-435 released) than the free-living sphaeromatid isopod *D. bidentata*. Egg production in *L. vulgaris* is also well above that described for any other flabelliferous isopod.

The question now arises, do repeated copulations or broods occur, or do the females produce a single brood, then die? Assuming that the females are principally non-feeding commensals (see following discussion) and lack seminal receptacles or other sperm storage organs (Montalenti, 1941), it might at first appear that females would produce a single brood and then die, as demonstrated for *Paragnathia formica* by Monod (1926), and *Dynamene bidentata* by Holdich (1968). The great range in size of females (in various populations), however, indicates that a number of molts probably occur during the female phase of the life cycle. These size differences could, however, be attributed to varying numbers of preovigerous instars, or to size differences at the time of the sex reversal. These data suggest that female *L. vulgaris* probably produce but a single brood, although conclusive evidence must await further experimentation.

ECOLOGY

Capture data available for this study indicate *Lironeca vulgaris* displays a weak host fish preference, based more upon the habits of the host than upon their taxonomic affiliation. Richardson (1905) stated this isopod was a parasite of "rock cod, flounder, lingcod (*Ophiodon elongatus*), and walleye surfperch (*Hyperprosopon argenteum*)."² She also reported it as a parasite on *Steindachneri* sp. (*sic*). This latter record is unclear. Species bearing this generic name are either deep-water ratfishes (= *Steindachnerella* Eiglmann, 1897) or freshwater South American catfishes (by Eiglmann and Eiglmann, 1888), both of which appear to be unlikely host fishes. Hobson (1971) reported *L. vulgaris* from the California blue rockfish (*Sebastes mystinus*), and Turner, *et al.* (1969) reported it from 9 species of reef fish (see Table 1). These appear to be the only published host fish records for this isopod.² The host(s) of "*L. panamensis*" have never been recorded in the literature. Materials examined during this study have revealed *L. vulgaris* to be a common inhabitant of certain species of the families Embiotocidae and Scorpaenidae, and occasional parasites of numerous other taxa (see Table 1). All of the host species are widely distributed, no doubt contributing, in part, to the wide distribution of this isopod (Table 1). Host fishes in the extreme southern range of this isopod are still not known.

In all cases male isopods normally attach within the gill chamber of the host fish, and feed upon the gill filaments or inner surface of the opercle. Varying degrees of gill and opercle damage have been recorded. Gut analyses (using a Zeiss phase contrast microscope) of males taken directly from the host's gills have shown the intestine and midgut diverticula to be packed with lysed red blood cells. Females normally attach at the base of the tongue, deep within the buccal cavity. Gut analyses of females taken directly from the mouths of their hosts have consistently shown the entire digestive system to be empty. Keusink (*pers. comm.*), however, has found occasional feeding females attached within the gill chamber of *Ophiodon elongatus*.

Multiple infestations by males (1 in each gill chamber) occur, but are rare (less than 2 percent of the fishes I have examined). I have seen no records or instances of multiple infestations by females. Induced multiple infestations by males, when monitored under laboratory conditions, are excessively harmful to *Fundulus parvipinnis*, resulting in lethargy and eventually death of the host. This is obviously disadvantageous to a weakly motile (or non-motile) adult isopod and should not be considered as reflecting a normal or advantageous strategy. Bowman (1960) came to a similar conclusion in regard to *L. puhi* and Sadzikowski and Wallace (1974) have shown that infestation by *L. ovalis* (Say) on the white perch (*Morone americana*), in the Delaware River, results in reduced growth of the host. Turner, *et al.* (1969) noted that, in regards to *L. vulgaris* infestations on California reef fishes, "heavily parasitized fishes [multiple infestations] appeared gaunt and barely able to swim; mortality seemed inevitable for these." The authors did not state the nature of these multiple infestation (males and/or females?). Observations of isopods that have abandoned their regular host under stress conditions have shown that erroneous records of multiple infestations (as well as erroneous host fish data) could be easily made (Brusca 1977, 1978). Such a phenomenon regularly occurs when otter trawls are made, the fugitive isopods then being seen (and often recorded) crawling about the trawl catch at random. Female *L. vulgaris*, lacking the ambulatory capabilities of males, rarely do this, and fugitive males in a trawl catch are often a sign that one or more of the captured fishes will contain a female, still attached in the buccal cavity of the proper host.

It can be seen from the host data presented that *L. vulgaris* prefers demersal fishes (cod, flat fishes, sculpin and rockfish), particularly those that school (perch and sanddab). As with *Nerocila californica* (Brusca, 1978), *L. vulgaris* is found on fishes whose behavior serves to facilitate dispersal of the young (manca and juvenile stages). Thus, it appears that host preference in *L. vulgaris* is largely a function of utility (or ecological preference), rather than taxonomic preference.

²G. Robinson (*pers. comm.*) states he has collected *L. vulgaris* (in central California) from the following fishes: *Neoclinus blanchardi*, *Damalichthys vacca*, *Scorpaenichthys marmoratus*, *Citharichthys stigmatæus*, *Sebastes rastrelliger*, *S. carnatus*, *S. caurinus*, *S. mystinus*, and *S. vexillaris*.

TABLE 1. HOST FISH DATA FOR *L. VULGARIS*

Host Fish	Host Range	Host Family	Geographic	Depth	Source
"Rock cod" ¹		Scorpaenidae	—	—	Richardson (1905)
"Flounder" ²		Bothidae (?) Pleuronectidae (?)	—	—	Richardson (1905)
<i>Hyperprosopon argenteum</i> (walleye surfperch)		Embiotocidae	Vancouver Isl., British Columbia to Rio San Vicente, Baja Calif.	Surface to 60'	Richardson (1905)
<i>Ophiodon elongatus</i> (lingcod)		Hexagrammidae	Alaska to Baja Calif.	Juveniles: shallow beach to 100'; Adults: surface to 1400'	E. Iverson (pers. comm.) Richardson (1905), Turner, <i>et al.</i> (1969) (this investigation)
<i>Sebastes mystinus</i> (California blue rockfish)		Scorpaenidae	Alaska to northern Baja	Surface to 300'	Hobson (1971)
<i>Embiotoca jacksoni</i> (black surfperch)		Embiotocidae	Monterey, Calif. to Pt. Abrejos, Baja Calif.	Surface to 130'	(this investigation)
<i>Citharichthys sordidus</i> (Pacific sanddab)		Bothidae	Alaska to Cabo San Lucas, Baja Calif.	30' to 1800'	(this investigation)
<i>Citharichthys stigmatus</i> (speckled sanddab)		Bothidae	Alaska to SW Baja Calif.	10' to 1200'	(this investigation)
<i>Amphistichus rhodoterus</i> (redtail surfperch)		Embiotocidae	Vancouver Isl., British Columbia to Monterey, Calif.	Surface to 24'	E. Iverson (pers. comm.)
<i>Synodus lucioceps</i> (California lizardfish)		Synodontidae	San Francisco, Calif. to Gulf of California	5' to 150'	Turner, <i>et al.</i> (1969) (this investigation)
<i>Trachurus symmetricus</i> (jack mackerel)		Carangidae	Alaska to S. Mexico, plus offshore islands S. to Galapagos	Surface to 150'	Turner, <i>et al.</i> (1969)
<i>Sebastes serranoides</i> (olive rockfish)		Scorpaenidae	Del Norte Co., Calif. to NW Baja Calif.	Surface to 480'	Turner, <i>et al.</i> (1960)
<i>Damalichthys vacca</i> (pile perch)		Embiotocidae	Alaska to Guadalupe Isl., Mexico	Surface to 150'	Turner, <i>et al.</i> (1960) E. Iverson (pers. comm.)
<i>Paralabrax nebulifer</i> (barred sand bass)		Serranidae	Santa Cruz, Calif. to SW Baja Calif.	Shallow to 600'	Turner, <i>et al.</i> (1960)
<i>Neochinus blanchardi</i> (sarcastic fringedhead)		Clinidae	San Francisco, Calif. to central west Baja Calif.	10' to 200'	Turner, <i>et al.</i> (1960)
<i>Scorpaena guttata</i> (sculpin)		Scorpaenidae	Santa Cruz, Calif. to Baja Calif.	Shallow to 600'	Turner, <i>et al.</i> (1960)
<i>Palaerodon farcatus</i> (white surfperch)		Embiotocidae	Vancouver Isl., British Columbia to Baja Calif.	Surface to 140'	Turner, <i>et al.</i> (1960)

¹ 55 species of "rock fish" or "rock cod" occur in California waters, most belonging to the genus *Sebastes*.² Two "true flounder" occur in California waters: *Platichthys stellatus* (the starry flounder) and *Atheresthes stomias* (the arrowtooth flounder), plus 25 other species of flatfishes.

It would further appear that this isopod is a regular resident only on such ecologically preferred fish groups, and only an occasional resident on some others (jack mackerel, California lizardfish, clinids, etc.). Isopods occurring on fishes of the latter group are probably not contributing significantly to local gene pools.

Laboratory experiments have shown that *L. vulgaris* possesses two distinct modes of host fish location. The first is to actively swim about in the water column. Juvenile *L. vulgaris* are quite adept at this and invariably strike downward onto the potential host fish, attaching subdorsally near the gill aperture. In the second mode of locating a host the isopod lies on its back on the substratum, and in this position waits until the fish passes overhead. It then swims quickly upward (usually a distance of 1 to 15 centimeters) to attach subventrally, near the gill aperture. Within a few hours to a few days the isopod enters the gill chamber of the host. It will be noticed that these two distinct host locating strategies lend themselves perfectly to the two ecological host categories utilized by these isopods (demersal and schooling fishes).

Juvenile *L. vulgaris* (6-10 mm in length) that still possess the natatory setae on the appendages are quite good swimmers. Beyond this stage, concurrent with loss of the swimming setae, the isopods become successively less adept at directed movement. Larger males can still actively crawl about the substratum but females with developed marsupia can do little beyond lie on their backs. In laboratory experiments adult males dislodged from their host fish crawl about the bottom of the tank, but are rarely able to reattach on a living fish. They will, however, attach to the skin of a dead fish placed in their vicinity. Gut analyses of these saprophagous individuals revealed only lysed red blood cells. Whether this

was residue left from a former infestation on a living fish (24-72 hours previously) or whether the isopods were actually extracting blood from recently killed fish was not determined. Detached females, on the other hand, simply lie on their backs with the pleopods beating. They have been kept in this state (without food) for up to 40 days. Neither sex has been observed molting.

Thus it appears that *L. vulgaris* rarely feeds (or at least may not need to feed) during the female period of its life. With this consideration females might best be considered as commensals, rather than parasites, as are the males. This is not an unexpected conclusion. Holdich (1968) noted that ovigerous female *Dynamene bidentata* retire to the shelter of crevices and empty barnacle shells where they do not feed and, upon release of the young, die. Monod (1926) described a similar behavior for *Paragnathia formica*. Menzies (1954) noted that the increased volume of maturing eggs in female *Limnoria tripunctata* compressed the other internal organs to the extent that females did not feed prior to egg deposition. Moreira (1973) showed that both male and female *Serolis polaris* and *S. laevis* cease feeding during the entire breeding period. Although Menzies, *et al.* (1955) stated that female *Lironeca convexa* positioned herself in the buccal cavity in such a manner as to have the mouthparts close to the gill rakers (to facilitate feeding on food particles strained by them), they did not perform gut analyses. Bowman (1960) stated that (in regards to *Lironeca puhi*, a parasite on *Gymnothorax eurostus* in Hawaii) "whether the isopod feeds at the expense of its host is not known." Stromberg (pers. comm.) has pointed out, however, that should female *L. vulgaris* eventually be shown to undergo multiple broods (or a series of ecdyses) the energy demands may exceed that available from stored energy reserves from the male instars, thus necessitating feeding.

ZOOGEOGRAPHY

Lironeca vulgaris is now known from Coos Bay, Oregon to Colombia (near Malpelo Island). It occurs in abundance in the Gulf of California and appears to be relatively common throughout its range, although records north of San Francisco are considerably less common. This is an extremely broad distribution (approximately 5° to 43°N latitude), extending through five zoogeographic provinces (Oregonian, Californian, Cortez, Mexican and Panamic; by Briggs, 1974 and Brusca and Wallerstein, in press). (See fig. 25.)

The range of *L. vulgaris* can be conveniently divided into four component regions, corresponding to these zoogeographic provinces. The northern component lies within the Oregonian Province (cool temperate), north of Point Conception, California. Moving southward, the next component is within the Californian Province (warm temperate), extending from Point Conception to the outer coast of southwest Baja California. The next component lies within the Cortez-Mexican Provinces (subtropical) and extends south to Tangola-Tangola, Mexico. The southernmost component is within the Panamic Province (tropical), and extends to Colombia,

South America. Samples examined independently from these four component regions revealed that morphological variations within each geographic region are as great as those between any of the regions.

Over 50 species in this large genus have been described from warm temperate and tropical regions around the world. Adequate descriptions of many species are lacking, however, and until the group is treated as a whole it seems unlikely that the phylogeny and paleozoogeography will be well understood. The only other species of *Lironeca* in the east Pacific that bears carinae on the bases of the pereopods is *L. convexa*, a distinctly tropical species that is sympatric with *L. vulgaris* between southern California and Colombia. Until the west Atlantic species in this genus (of which there are 9) are better known, the affinities of *L. vulgaris* and *L. convexa* must remain speculative. The genus as a whole appears to represent a facet of the early Tethyan Track fauna. Whether *L. vulgaris* and/or *L. convexa* are remnants of the New World Panamanian transisthmian track, or whether they are derived trans-Pacific species, cannot be said at this time.

KEY TO THE SPECIES OF *LIRONECA*
KNOWN FROM THE EAST
PACIFIC OCEAN (INCLUDING HAWAII)

- | | |
|---|--|
| <p>1 — Bases of pereopods 4-7 with carinae2
— Bases of pereopods 4-7 without carinae . .4
2 — Antenna 2 of 12 articles; reported only from southern Chile (a west Pacific species)<i>L. raynaudi</i>
— Antenna 2 of 9-11 articles3
3 — Pleotelson about as wide as long; body with dorsum strongly convex; body tapering abruptly posteriorly; uropods extended to or beyond posterior border of pleotelson <i>L. convexa</i></p> | <p>— Pleotelson about twice as wide as long; body not as above; uropods extended to or falling short of posterior border of pleotelson <i>L. vulgaris</i>
4 — Pereonites with well developed posterolateral lobes; antenna 2 of 8-13 articles; cephalon wider than long; known only from Hawaii <i>L. phui</i>
— Pereonites without posterolateral lobes; antenna 2 of 8 articles; cephalon width subequal to length; known from coastal North America <i>L. californica</i></p> |
|---|--|

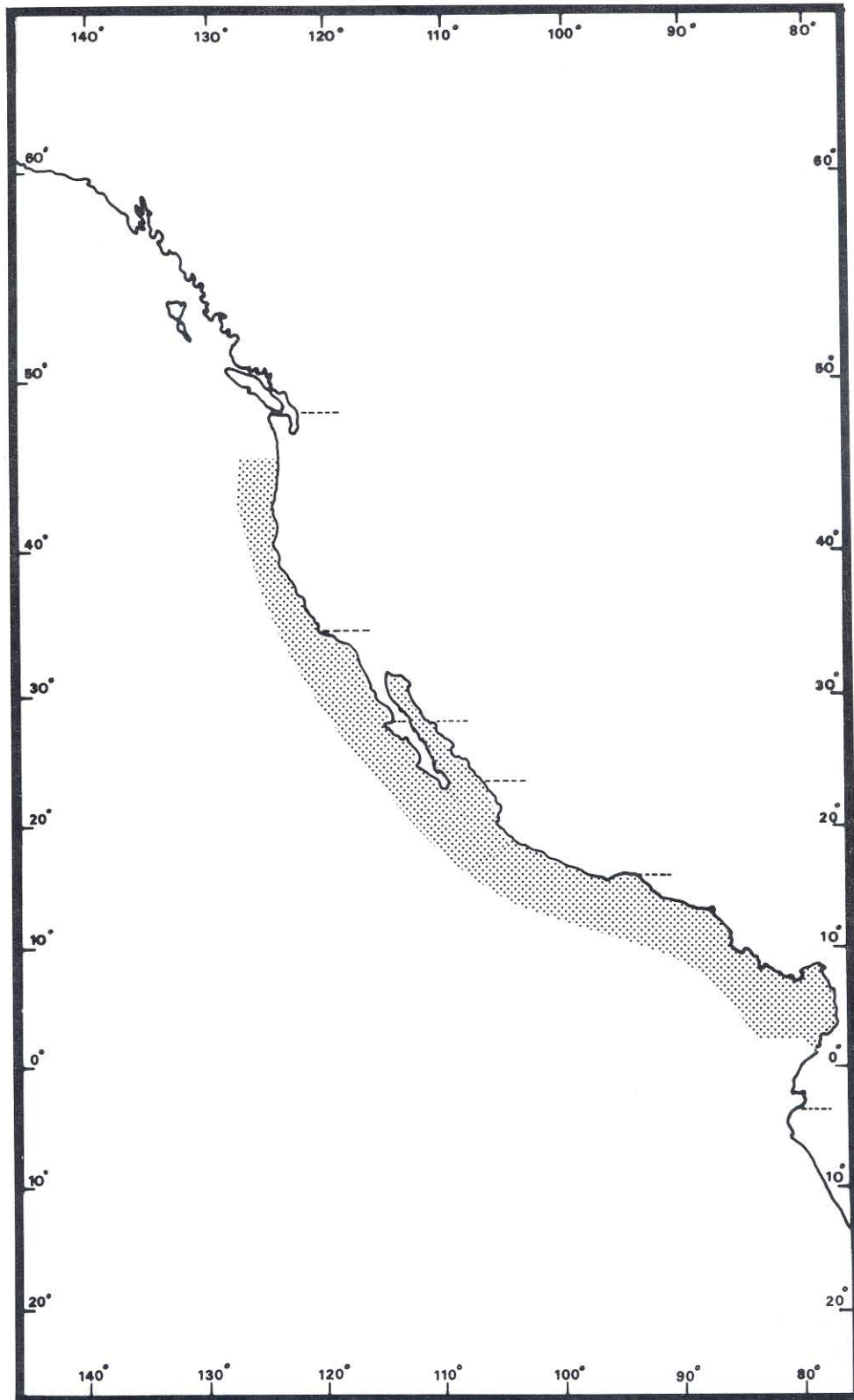


Fig. 25. Zoogeographic distribution of *Lironeca vulgaris*. Dashed lines along coast indicate regions of major faunal breaks associated with recognized zoogeographic province boundaries. See text for further discussion.

ACKNOWLEDGEMENTS

This work would not have been possible without a great deal of assistance from many fine people. I am especially indebted to Drs. Thomas Bowman (U.S. National Museum), Jarl-Ove Stromberg (Zoological Institute, University of Lund, Sweden), Robert Lavenberg (Los Angeles County Museum of Natural History), G. Brusca (Humboldt State University, California), and R.K. Allen (California State University, Los Angeles), for the time and careful attention they gave the manuscript. Acknowledgements are also extended to Barry Wallerstein, Gene

Kramer, Anna Mary Mackey, Gary Robinson, Chris Keusink, Ernest Iverson, and Lloyd Findley for reviewing the manuscript. Special thanks go to Chris Keusink for making available his unpublished data on feeding behaviors of *L. vulgaris*.

This research was supported, in part, by grants from Sigma Xi, the National Science Foundation (Alpha Helix Program), California State Department of Fish and Game, and the University of Southern California.

LITERATURE CITED

- BAILEY, R.M., J. E. FITCH, E.S. HERALD, E.A. LACHNER, C.C. LINDSEY, C.R. ROBINS and W.B. SCOTT. 1970. A list of common and scientific names of fishes from the United States and Canada. (third edition). Amer. Fish. Soc., Spec. Publ. No. 6. 150 pp.
- BOWMAN, T.E. 1960. Description and notes on the biology of *Lironeca puhi*, n.sp. (Isopoda: Cymothoidae), parasite of the Hawaiian moray eel *Gymnothorax eurostus* (Abbott). Crustaceana 1(2): 82-91.
- BRIGGS, J.C. 1974. Marine zoogeography. McGraw-Hill, New York. 475 p.
- BRUSCA, R.C. 1973. Handbook to the common intertidal invertebrates of the Gulf of California. Univ. Ariz. Press, Tucson. 427 p.
- BRUSCA, R.C. 1975. Isopoda Cymothoidae of the Gulf of California. (Ph.D. Thesis, Univ. Arizona).
- BRUSCA, R.C. 1977. Range extensions and new host records of cymothoid isopods (Isopoda: Cymothoidae) in the east Pacific. Bull. So. Calif. Acad. Sci. 76(2): 128-131.
- BRUSCA, R.C. 1978. Studies on the cymothoid fish symbionts of the eastern Pacific (Crustacea: Isopoda: Cymothoidae). I. Biology of *Nerocila californica*. Crustaceana, 34(2): 141-154.
- BRUSCA, R.C. (in press). A handbook to the common intertidal invertebrates of the Gulf of California, 2nd ed., Univ. Ariz. Press.
- BRUSCA, R.C. and B. WALLERSTEIN. Preliminary comments on zoogeographic patterns of idoteid isopods in the northeast Pacific, with a review of shallow water zoogeography for the region. (In press. Bull. Biol. Soc. Wash.).
- CALMAN, W.T. 1898. On a collection of Crustacea from Puget Sound. Ann. New York Acad. Sci. 11: 259-292.
- CHARNOV, E.L., D.W. GOTSHALL and J.G. ROBINSON. 1978. Sex ratio: adaptive response to population fluctuations in pandalis shrimp. Science 200: 204-206.
- CRANE, J.W. 1972. Systematics and new species of marine Monogenea from California. Wasmann Jour. Biol. 30: 109-166.
- FORSMAN, B. 1944. Beobachtungen über *Jaera albifrons* Leach an der Schwedischen Westküste. Ark. f. Zool. 35a(11): 1-33.
- HATCH, M.H. 1947. The Chelifera and Isopoda of Washington and adjacent regions. Univ. Wash. Publ. Biol. 10(5): 155-274.
- HOBSON, E.S. 1971. Cleaning symbiosis among California inshore fishes. Fish. Bull. 69(3): 491-523.
- HOLDICH, D.M. 1968. Reproduction, growth and bionomics of *Dynamene bidentata* (Crus-

- tacea: Isopoda). Proc. Zool. Soc. Lond. 156: 137-153.
- JORDAN, D.S. and B.W. EVERMANN. 1969. American food and game fishes. Doubleday, Doran and Co., New York. 574 p.
- KJENNERUD, J. 1950. Ecological observations on *Idothea neglecta* G.O. Sars. Univ. Bergen Arb. Natur. 7: 1-47.
- LEGRAND, J.J. 1951. Etude statistique et experimentale de la sexualite d'*Anilocra physodes* L. (Crustace Isopode Cymothoide). Bull. Soc. Hist. Nat. Toulouse 86(1/2): 176-183.
- LEGRAND, J.J. 1952. Contribution a l'etude experimentale et statistique de la biologie d'*Anilocra physodes* L. Arch. Zool. Exper. et Generale 89(1): 1-55.
- MARKUS, H.C. 1930. Studies on the morphology and life history of the isopod *Mancasellus macrourus*. Trans. Amer. Micros. Soc. 49: 220-237.
- MENZIES, R.J. 1954. The comparative biology of reproduction in the wood-boring isopod crustacea *Limnoria*. Bull. Mus. Comp. Zool. 112(5): 363-388.
- MENZIES, R.J. 1962. The marine isopod fauna of Bahia de San Quintin, Baja California, Mexico. Pac. Naturl. 3(11): 337-348.
- MENZIES, R.J., T.E. BOWMAN, and F.G. ALVERSON. 1955. Studies of the biology of the fish parasite *Lironeca convexa* Richardson (Crustacea, Isopoda, Cymothoidae). Wassmann Jour. Biol. 13(2): 277-295.
- MILLER, D.J. and R.N. LEA. 1972. Guide to the coastal marine fishes of California. State of Calif., Dept. Fish and Game.
- MILLER, M.A. 1975. Phylum Arthropoda: Crustacea, Tanaidacea and Isopoda. In, R.I. Smith and J.T. Carlton, Light's Manual: Intertidal Invertebrates of the Central California Coast. Third Ed. Univ. Calif. Press, Los Angeles, pp. 277-312.
- MONOD, T. 1926. Les Gnathiidae, essai monographique (morphologie, biologie, systematique). Mem. Soc. Sci. Nat. Maroc. 13: 1-668.
- MONTALENTI, G. 1941. Studi sull'ermafroditismo dei Cimotoide. I. *Emetea audouinii* (M. Edw.) e *Anilocra physodes* (L.). Pub. della Stazione Zool. Napoli 18(3): 337-394.
- MOREIRA, P.S. 1973. The biology of species of *Serolis* (Crustacea, Isopoda, Flabellifera): reproductive behavior of *Serolis polaris* Richardson 1911. Bolm Inst. Oceanogr., Sao Paulo 22: 109-122.
- NAIR, S.G. 1956. On the embryology of the isopod *Irona*. J. Embryol. Exp. Morph. 4(1): 1-33.
- NAYLOR, E. 1955. The life cycle of *Idotea emarginata* (Fabricus). Jour. Anim. Ecol. 24: 270-281.
- NIERSTRASZ, H.F. 1913. Die Isopoden der Siboga-Expedition. I. Isopoda Chelifera. Siboga-Expeditie 32a: 1-56. E.J. Brill, Leiden.
- RICHARDSON, H.R. 1899. Key to the isopods of the Pacific coast of North America, with descriptions of twenty-two species. Proc. U.S. Nat. Mus. 21: 815-869.
- RICHARDSON, H.R. 1899. Key to the isopods of the Pacific coast of North America, with descriptions of twenty-two new species. Ann. Mag. Nat. Hist. (7)4: 157-187, 260-277, 321-338. London.
- RICHARDSON, H.R. 1900. Synopses of North American invertebrates. VIII. The Isopoda. Amer. Natural. 34: 207-230, 295-309.
- RICHARDSON, H.R. 1904. Isopod Crustaceans of the northwest coast of North America. Harriman Alaska Expedition, Crustacea, 10: 213-230.
- RICHARDSON, H.R. 1905. A monograph on the isopods of North America. Bull. U.S. Nat. Mus. 54: 1-727.
- SADZIKOWSKI, M.R. and D.C. WALLACE. 1974. The incidence of *Lironeca ovalis* (Say) (Crustacea, Isopoda) and its effects on the growth of white perch, *Morone americana* (Gmelin) in the Delaware River near Artificial Island. Chespk. Sci. 15(3): 163-165.
- SCHIOEDTE, J.C. and F. MEINERT. 1884. Symbolae ad monographiam Cymothoarum, Crustaceorum Isopodum Familiae. IV. Cymothoidae. Naturhistorisk Tidsskift. Ser. III. Vol. XIV: 221-454.
- SCHULTZ, G.A. 1969. How to know the marine isopod Crustaceans. Dubuque, Iowa: Wm. C. Brown. 359 pp.
- SOLIGNAC, M. 1972a. Comparaison des comportements sexuels specifiques dans la super-espece *Jaera albifrons* (Isopodes Asellotes). C.R. Acad. Sci. Paris 274: 2236-2239.
- SOLIGNAC, M. 1972b. Le comportement sexuel des *Jaera (albifrons) posthirsuta* (Isopodes Asellotes). C.R. Acad. Sci. Paris 274: 1570-1572.

- SOLIGNAC, M. 1975. Isolement reproductif entre les membres de la super-espece d'Isopode littoral *Jaera albifrons* Leach. VIII European Mar. Biol. Symp. (Naples, 1973), Pubbl. Staz. Zool. Napoli 39 (Suppl.): 696-716.
- STIMPSON, W. 1857. The Crustacea and Echinodermata of the Pacific shores of North America. Boston Jour. Nat. Hist. 6: 503-513.
- STIMPSON, W. 1859. Notices of new species of Crustacea of western North America; being an abstract from a paper to be published in the journal of the society. Proc. Bost. Soc. Nat. Hist., 6: 88-89.
- STROMBERG, JARL-OVE. 1965. On the embryology of the isopod *Idotea*. Arkiv for Zoologi (2)17(5): 421-473.
- STROMBERG, JARL-OVE. 1967. Segmentation and organogenesis in *Limnoria lignorum* (Rathke) (Isopoda). Arkiv for Zoologi (2)20(5): 91-139.
- STROMBERG, JARL-OVE. 1971. Contribution to the embryology of bopyrid isopods, with special reference to *Bopyroides*, *Hemiarthrus*, and *Pseudione* (Isopoda, Epicaridea). Sarsia 47: 1-46.
- TURNER, W.R. and R.B. ROE. 1967. Occurrence of the parasitic isopod *Olencira praegustator* in the yellowfin menhaden, *Brevoortia smithi*. Trans. Amer. Fish. Soc. 96(3): 357-359.
- TURNER, C.H., E.E. EBERT and R.R. GIVEN. 1969. Man-made reef ecology. State of Calif., Dept. Fish and Game, Fish Bull. 146. 221 pp.