STUDIES ON THE CYMOTHOID FISH SYMBIONTS OF THE EASTERN PACIFIC (ISOPODA, CYMOTHOIDAE) I. BIOLOGY OF NEROCILA CALIFORNICA

BY

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INTRODUCTION

Man has probably been noticing and observing parasitic isopods on fishes for a much longer time than he has been aware of other crustaceans of comparable size and occurrence. It could well be assumed, in fact, that ever since man took up the endeavor of fishing in the sea he has been aware of these interesting creatures. It is partly for this reason, no doubt, that the majority of the cymothoids were described so many years ago. The cymothoids at present known from the eastern Pacific were all described between the years 1766 and 1918. As is often the case in older taxonomic works, the descriptions of most eastern Pacific cymothoids are essentially typological. In most cases species were probably originally described from a single female specimen. This in itself is not inherently bad and is, in fact, occasionally a necessity. The basis of most of these older typological descriptions, however, is not consistent with modern population systematics (the "new systematics" of Mayr, 1969) and did not anticipate the future discovery of new material and new congeners. Published descriptions are largely cursory and often inadequate, lacking information beyond that needed to distinguish the proposed species from those previously described, resulting in a need to more fully document generic and specific taxa. Illustrations are often superficial and inadequate for positive identification. Ecological data are usually entirely absent or are based on casual observations. Host data are sparse, at best. The genus Nerocila, in the eastern Pacific, reflects this state of affairs.

The characters classically used to distinguish the species of this genus are known to be somewhat unreliable. Such features as the visibility of the coxae or coxal plates (epimera) in dorsal aspect, the length of the body, the size of the eye, or the length of the various pereonites are highly variable and should not be used in a species diagnosis or a dichotomous key. There was, in years past, also a tendency to include various generic characters in the species descriptions, such as the shape of the pereopods and the presence of the three-lobed posterior border of the cephalon. Further, it is not known precisely what characters are and are not consistent throughout the genus.

Most species of *Nerocila* known to science at this time show only subtle distinctness. The characters of the species occurring in the eastern Pacific that have been

found to be the most taxonomically reliable are the morphology of the mandible, maxilliped, uropoda and pleotelson. Workers are warned, however, that the pleotelson and uropoda are the most likely part of a cymothoid's anatomy to be damaged and thus bear artificial contours. Approximately 20 per cent of the specimens I have examined, in this genus, have had damaged pleotelson and/or uropoda, presumably from predation (e.g., by cleaner fishes, etc.).

One objective of this paper, and subsequent papers on this family of isopods, is to establish a format which will hopefully help future workers with this group to better document and describe the members of this interesting taxon of fish symbionts.

DESCRIPTIONS

Nerocila californica Schioedte & Meinert, 1881

Schioedte & Meinert, 1881: 72; Richardson, 1899a: 172; Richardson, 1899b: 830; Richardson, 1900: 220; Richardson, 1905: 221; Nierstrasz, 1915: 73; Hale, 1926: 208; Nierstrasz, 1931: 126; Schultz, 1969: 151.

Female

Body: Width 7-12 mm, length 14-24 mm; body index (length divided by width) 1.85-2.51 (mean 2.08) for non-ovigerous females, 1.75-2.26 (mean 1.99) for ovigerous females. General color tan to yellowish, with 3 longitudinal dorsal bands of dark chromatophores (a median and two lateral) (pl. 1).

Cephalon: About as wide as long, 3 mm \times 3 mm. Front rounded; eyes oval, set in posterolateral corners, moderately large to small. Antenna 1 (fig. 1b) of 8 articles; antenna 2 (fig. 1a) of 10-11 articles, about 1 mm longer than antenna 1. Mandible as in fig. 1c, terminal article of palp setose; maxilliped as figured by Richardson (1905: 222), with two stout apical hooks.

Pereon: Pereonite 6 widest and longest; pereonites 1, 5 and 7 subequal, next longest; pereonites 2-4 subequal and shortest. Posterolateral corners of all, or any number of posterior pereonites, produced into acute angles, those of pereonite 7 extended ½ to ½ the length of the pleon. Pereonites 4-7 with a shallow, transverse groove in each lateral quarter. Epimera (coxae) of pereonites 2-7 usually all visible in dorsal aspect, although if dorsal surface of body is more strongly convex epimera tend to be directed more ventrally and thus are less easily seen; epimera 4-7 (or occasionally 5-7) forming sharp posterolateral points, increasing in overall size and length posteriorly (pl. 1).

Pleon: Pleonites subequal in length, first and second with long posterolateral processes (those of pleonite 1 extended at least to pleonite 4, usually to anterior margin of pleotelson; those of pleonite 2 extended to midline of pleotelson). Pleopoda as in fig. 1e-f (note retention of masculine appendix masculina on pleopod 2); inner margin of basis with four stout spines. Pleotelson slightly acuminate on posterior margin. Posterior margin of peduncle of uropod (fig. 1g) produced into a single, large, medial spine and 2 smaller spines; exopod of uropod lanceolate, distal end narrowly rounded; endopod subpyriform, shorter than exopod; exopod and endopod extended beyond posterior border of pleotelson.

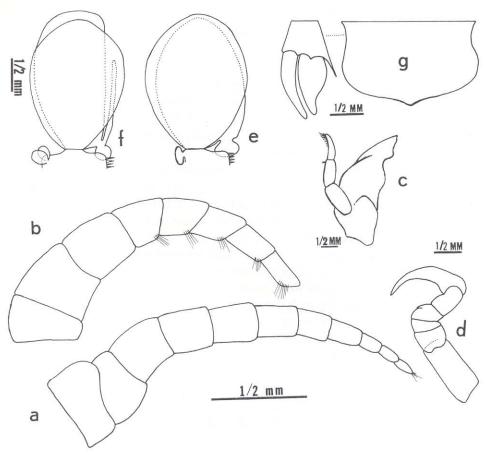


Fig. 1. Nerocila californica Schioedte & Meinert, 1881, adult female. a, antenna 2; b, antenna 1 (to same scale as a); c, mandible; d, pereopod 5; e, pleopod 1 (same scale as f); f, pleopod 2; g, pleotelson with left uropod separated.

Male

Width 3-10 mm, length 10-20 mm; body index 1.87-2.61 (mean 2.26). Similar to female except for the following: usually considerably smaller and more slender (note body indices); anterior margin of cephalon slightly more acute; eyes about twice size of female's; body usually more heavily pigmented; pereonite 1 longest; pereonite 5 widest; posterolateral corners of pereonite 7 barely extended into pleon; lateral extensions of pleonite 1-2 shorter, directed ventrally and not visible in dorsal aspect.

Juveniles ("aegathoid" stages)

In general the juveniles of most species of Cymothoidae look very much alike and resemble slender versions of the adult males. The primary differences between the adult males and juveniles is the presence of marginal setae on certain appendages and the larger eyes of the latter. In addition to these characters the juveniles of *Nerocila californica* show distinct differences in uropod and pleonite morphology.

Examination of 85 specimens of *N. californica* from the northern Gulf of California has revealed the existence of at least three juvenile (post-manca) instars. The juveniles, or "aegathoid" stage cymothoids, resemble adult males in the shape and numbers of articles in the pereopoda and antennae and the shape of the pleopods, including the possession of an appendix masculina (figs. 2d-g). They differ from adult males in the following ways.

First juvenile instar: Eyes very large in proportion to the head, covering about one-third the dorsal surface of the cephalon (fig. 2c). Medial and distal articles of antennae setose (fig. 2d, e); third article of antenna 2 with several long, plumose hairs. Pereopoda with numerous short spines and setae on inside margin (fig. 2f). Uropoda quite different in shape from adults and highly setose on margins (fig. 2g); endopod and exopod with terminal spine. Distal margin of pleotelson highly setose (fig. 2c). Posterolateral angle of pereonite 7 not produced, but rounded. Lateral margins of pleonites 1-2 just barely extended (becoming longer with each succeeding molt). Body very slender, length 10 mm, width of pereonite five 3.1 mm; body index 3.23.

Second juvenile instar: Identical to first instar but wider; length 11.5-12 mm, width of pereonite five 3.6-3.8 mm; body index 3.13.

Third juvenile instar: Similar to first two instars but with a slight reduction of setae; incipient shape of adult uropoda visible within uropoda of premolt individuals; length 12.2-13.6 mm, width of pereonite five 4.1-4.8 mm; body index 2.83. This juvenile molts into a functional adult male.

Distribution. — Nerocila californica is now known to range from Los Angeles, California to Peru, including the Gulf of California (Brusca, in press). There appears to exist, in the northern Gulf of California, a very large and thriving population of this isopod, subsisting largely upon the anchovy Cetengraulis mysticetis (Günther).

Remarks. — Specimens in the author's collections are similar to Richardson's (1905) description in nearly all respects. The 120 specimens examined during this study (including material from California, Panama and Peru) indicate that there exists a fairly wide spectrum of variability, which includes some of the characters upon which the original description, and Richardson's subsequent redescription were based. Specimens I have examined differ from previously published descriptions in the following ways: the eyes are generally larger and more distinct, even in the females; the degree to which both the epimera and the pereonites are extended is quite variable, particularly on the more anterior segments: antenna 2 is composed of 10 or 11 articles; the length of the appendix masculina, on females, is highly variable, and pereonite 6 is the longest, not pereonite 1. These differences are not taxonomically significant and are no doubt



Top: Adult female of Nerocila californica Schioedte & Meinert, 1881, dorsal aspect. Note left uropod is missing (figured in fig. 1g).

Bottom: Two Nerocila californica on their host fish Cetengraulis mysticetus (Günther); note tissue damage; from the upper Gulf of California.

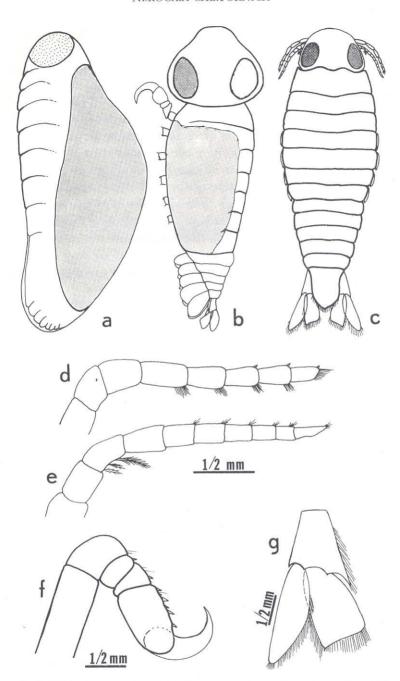


Fig. 2. Nerocila californica Schioedte & Meinert, 1881. a, developing embryo, first visible segmentation stage; actual length 1.45 mm; b, second visible segmentation stage, or prehatch stage; note large amount of yolk still remaining; actual length 3 mm; c, juvenile or "aegathoid" stage; actual length 12 mm; d, antenna 1 of juvenile; e, antenna 2 of same; f, pereopod 5 of same; g, left uropod of same.

the result of simple polymorphism and growth variations. There is evidence that the number of facets in the eye and the length of the appendix masculina (in females) both tend to diminish with successive molts. Significant changes in morphology, due to normal growth, have also been recorded in the valviferan isopods (Kjennerud, 1950; Howes, 1939; Menzies & Waidzunas, 1948; and others). The characters figured by Schioedte & Meinert (1881), and passed on by Richardson, were in obvious need of reexamination with modern microscopy. For this reason entirely new drawings have been made of these and other important characters. The number of flagellar articles of the antennae, the shape of the endopod of the uropoda and the shape of the posterior margin of the pleotelson are all highly variable in nature, this particular variability apparently being due to damage, quite likely inflicted by predators. As a result of this type of variation I have found antenna 1 to have from 6 to 8 articles, and antenna 2 to have from 7 to 11 articles. The normal, bluntly acuminate pleotelson may appear indented or crenulate, and the uropodal endopod may vary from ovate to subpyriform on damaged specimens.

Development and life history. — The life history of members of the family Cymothoidae has often been alluded to but rarely studied in depth. The work of Montalenti (1941), Menzies, Bowman & Alverson (1955), Bowman (1960) and Trilles (1964, 1968, 1969) are the only recent papers giving any details on the subject.

A model for the life cycle of *Nerocila californica* has been established, based on material from a large population in the upper Gulf of California, representing nearly all developmental stages (fig. 3). Beginning with the fertile egg, retained in the marsupium of the female, it is as follows.

Marsupial development: The egg is centrolecithal, having a very large, centrally placed yolk mass. The egg is itself large and subspherical (.98 × 1.05 mm), becoming progressively more ovoid as development ensues. This corresponds to what Kjennerud (1950) has called developmental stage 1 (in the development of Idotea neglecta Sars). Once the egg membrane ruptures the developing embryo lies enclosed in the embryonic membrane. Two distinct prehatch stages are evident beyond the marsupial egg stage. The first of these (fig. 2a) shows visible signs of early segmentation, and all 7 pereonal somites are distinct. This corresponds to Kjennerud's developmental stage 2. Figure 2b depicts the next stage, the marsupial instar prior to the hatch, or manca stage. It has lost the embryonic membrane and resembles the manca in possession of 6 pairs of pereopods, but lacks visible appendage setation. A large yolk supply still exists at this point. This corresponds to Kjennerud's developmental stage 3. This stage molts, in the marsupium, into the manca stage. It is at this point that the typical manca setation is developed. The marsupial development of Nerocila californica is similar to that described for other isopods, as Idotea emarginata (Fabricius) (Naylor, 1955), Lironeca convexa Richardson (Menzies, Bowman & Alverson, 1955), Anilocra (Montalenti, 1941), and Idotea neglecta G. O. Sars (Kjennerud, 1950).

PROPOSED MODEL OF THE LIFE CYCLE AND DEVELOPMENT OF Nerocila californica (BASED ON A LARGE POPULATION IN THE NORTHERN GULF OF CALIFORNIA)

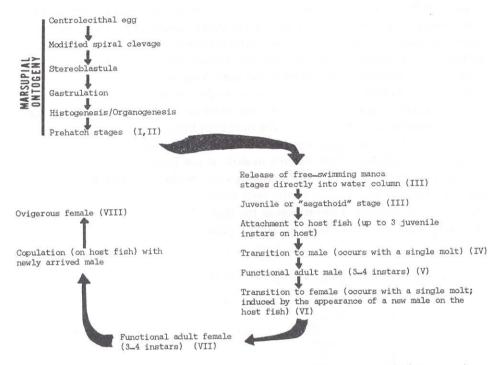


Fig. 3. Proposed life cycle and development of Nerocila californica. Roman numerals in parentheses indicate corresponding stages from Montalenti (1941).

Postmarsupial development: The hatch stage, or the "marsupial posthatch", is referred to as a manca. It is presumed that the mancae do not feed, but probably rely on a large supply of yolk material and their strategy of locating a suitable host fish as quickly as possible. The large number of well-developed eye facets on mancae and juveniles suggest a fairly good visual capability at this stage. The mancae represent the first free-living stage in the life of a cymothoid, during which time they swim about freely in the water column. This posthatch swimming behavior has been witnessed by Segal (pers. communication) in other species of cymothoids. The manca stage is characterized principally by the absence of the seventh pair of pereopods and the possession of numerous marginal setae on the appendages. Once the last pair of pereopods have appeared the isopod is referred to as a juvenile (fig. 2c).

The juveniles possess a well developed appendix masculina. Members of this juvenile stage had previously been placed in the genus Aegathoa, a polyphyletic genus now known to consist solely of juvenile members of other genera of

cymothoids. Because of the distinctness of this developmental stage from all the others and the consistency in appearance of all species in the family during this period, I have referred to this juvenile period as the "aegathoid" stage. Descriptions of juvenile instars have been given above.

During the juvenile, or "aegathoid" stage, the isopod attaches to the proper host. The location of a suitable host is no doubt enhanced by the possession of extremely large eyes and the fact that preferred hosts are apparently always either schooling or demersal fishes. During this period also the antennae, pereopoda, uropoda and pleotelson are all provided with long setae (fig. 2), which aid in buoyancy and swimming. Once attachment to the proper host has taken place the juvenile continues to molt until a maximum width of 4.1-4.5 mm is attained (resulting in a mean body index of 2.83). The next molt brings on the normal, adult male characters and corresponding loss of setae. Whether or not size is the determining factor in the transition from juvenile to male is not known at this time.

The adult male N. californica undergoes 2-3 molts (3-4 instars). As can be seen in table I, during each molt the body becomes progressively broader (that is, the body index drops). Termination of the male phase in the life of N. californica is accompanied by a molt into the female phase.

TABLE I

Data on instars of Nerocila californica in the northern Gulf of California

Instar Number	Sex	Mean Body Index	Width of pereonite 6
1	juvenile	3.23	3.0
2	juvenile	3.13	3.6— 3.8
3	juvenile	2.83	4.1— 4.8
4	male	2.61	5.1— 6.1
5	male	2.33	6.5— 7.0
6	male	1.90	7.6— 7.9
	female	2.07	7.0— 7.5
7	male	2.05	8.5— 9.1
	female	2.05	7.6— 8.6
8	female	1.97	8.7—10.0
9	female	1.94	10.2-12.2

Numerous mid-molt individuals substantiate the fact that this sex reversal occurs during a single molt. The stimulus for this reversal may be either endogenous (age or body size), exogenous (a stimulus from the host fish of the environment, or the appearance of a new male isopod on the same host fish), or both. The fact that two different and succeeding male instars, of different sizes, can undergo the sex reversal lends evidence in favor of an exogenous stimulus, quite likely the appearance of the second male on the host fish. Trilles (1969) has commented briefly on the probable existence of neurohormonal control over the sex change itself, and Romestand (1971) has undertaken electrophoretic studies of cymothoid hemolymph proteins in relation to the phases of sexual development.

Burbanck (1974), and others have demonstrated that most (if not all) members

of the Anthuridae undergo an opposite transition, from female to male. This is referred to as protogynic hermaphroditism, as opposed to the protandric hermaphroditism seen in the family Cymothoidae. Protandrous hermaphroditism is also known to occur in certain species of the group Epicaridea.

The upper Gulf of California population of *Nerocila californica* has females that appear to belong to four different instars. Table I gives the data on these instars. It is impossible to determine which group of females were derived from males, and which groups from other females (without actually rearing the animals), and for this reason the data on female instars remain somewhat clouded.

Copulation and insemination probably occur on the host fish itself, and male-female pairs have been found in contact a number of times, although never actually in copula. The fact that no occurrences of copulation have been reported for cymothoids may attest to the rapidity with which the act is consumated. Members of the genus *Lironeca* have, however, been found in what appears to be a copulatory position on their host fishes (Brusca, in preparation). Copulatory behavior has been described for *Asellus aquaticus* (L.) (by Unwin, 1920) and *Idotea neglecta* (by Kjennerud, 1950). In these species copulation takes place as the female is molting, while the posterior half of her body is still soft and before the anterior half has molted and developed the oostegites (which cover the oviducts on fully developed females).

The appendix masculina of *Nerocila californica*, and all other members of the family Cymothoidae I have examined from the eastern Pacific, is extremely simple and unadorned with any sort of groove, hooks, etc., leading one to suspect it may play no direct role in spermatophore transfer.

Host-parasite relationships. — At the present time Nerocila californica has been recorded from 21 different species of fishes. Many of these records appear questionable for one or more reasons. Some of the records quite likely reflect the occurrence of "fugitive" isopods in trawl or seine collections, where the parasites have abandoned their dying or stressed host and crawled off to search for better hunting grounds, as it were. I have witnessed this phenomenon many times and it would appear that members of this genus abandon their host fish immediately upon cessation of swimming activity of the latter. This behavior was briefly discussed by Brusca (in press), and it seems likely to be directly related to the sudden reduction or absence of water currents across the pleopods, upon which the isopod depends for its oxygen supply (i.e., an oxygen stress behavior). The frequency with which this occurs leads one to suspect those host fishes that have been recorded but once in the literature or are represented by only a single record in available museum and collection material. For this reason I have established two criteria to which one may adhere in the recording of host fish records. These are: (1) obvious tissue damage present on the fish, and (2) the finding of the isopod repeatedly on the same species of fish.

Bearing these facts in mind, the 21 species of fishes that have been recorded in association with *Nerocila californica* are listed below with comments as to the likelihood of their reliability as preferred or "regular" hosts.

Unlikely regular host fishes:

Myliobatis sp. (by Schioedte & Meinert, 1881). An eagle ray; there have been no records from this fish subsequent to the original one nearly 100 years ago.

Triakis semifasciata (Girard) (by Schioedte & Meinert, 1881). The leopard shark; no record subsequent to the original nearly 100 years ago.

Gyropleurodus francisi (Girard) (by Richardson, 1905). A horn shark; no subsequent records. The extremely tough skin and placoid scales of this, and the above species would seem unsuitable for prolonged attachment by a cymothoid isopod.

Sphoeroides annulatus (Jenyns) (by Brusca, in press). The bullseye puffer; no tissue damage evident; single record.

Umbrina roncador Jordan & Gilbert (by Brusca, in press). The yellowfin croaker; no tissue damage present; single record.

Stereolepis gigas Ayres (by Brusca, in press). The giant sea bass; no records of host fish damage; single record.

Istiophorus platypterus (Shaw & Nodder) (by Brusca, in press). Sailfish; no records of host fish damage; single record.

Cynoscion macdonaldi Gilbert (by Brusca, in press). The totuava; no records of host fish damage; single record.

Mycteroperca xenarcha Jordan (by Brusca, in press). The broomtail grouper; no records of host fish damage; single record.

Possible regular host fishes:

"cat fish" (by Richardson, 1905). Probably a marine catfish, family Arridae (possibly *Bagre panamensis*, the Chihuil, which ranges from Peru to southern California, including the Gulf of California); a demersal fish; no subsequent records.

Paralabrax clathratus (Giard) (by Schioedte & Meinert, 1881). A kelp bass; demersal; no subsequent records.

Embiotoca jacksoni Agassiz (by Brusca, in press). The black surfperch; a schooling fish; no tissue damage present; single record.

Atherinops affinis (Ayres) (by Brusca, in press). The topsmelt; a schooling fish; no records of host fish damage; single record.

Atherinops californiensis (Girard) (by Brusca, in press). The jacksmelt; a schooling fish; no tissue damage evident on fish; single record.

Scorpaena guttata Girard (by Schioedte & Meinert, 1881). The California spotted scorpion fish; demersal; no subsequent records.

Promicrops guttatus (L.) (by Richardson, 1905). Probably a misidentification of the similar appearing members of the family Serranidae (sea basses), genus Epinephelus; demersal; no subsequent records.

Positive host fishes:

Mugil cephalus L. (by Brusca, in press; and Nierstrasz, 1915, Mugil mexicana). The striped mullet; a demersal, schooling fish; tissue damage evident; repeated occurrences (Gulf of California and Peru).

Syacium ovale (Günther) (by Brusca, in press). A left-eyed flounder; demer-

sal; tissue damage evident; repeated occurrences.

Cetengraulis mysticetus (Günther) (by Brusca, in press). An anchovy; a pelagic, schooling fish; tissue damage evident, repeated occurrences.

Oligoplites mundus Jordan & Starks (by Brusca, in press). The leather jack;

a pelagic, schooling fish; tissue damage evident; repeated occurrences.

Micrometrus minimus (Gibbons) (by Brusca, in press). The dwarf surfperch;

a schooling fish; tissue damage present.

It can be seen from these data and comments that there are five positive hosts for N. californica and seven additional possible hosts. All twelve of these species fall into one (or both) of two ecological categories: schooling fishes or demersal fishes. It is readily apparent that both these types of fishes would be conducive to the spread of an infestation of external parasites such as cymothoid isopods. The seemingly random occurrence of this parasite on fishes not considered to be regular host fish is here explained as: (1) an artifact of trawl or seine sampling, wherein the isopod has abandoned its true host and been found crawling about on some other fish, or (2) the chance meeting of collector and fish, the latter in the process of being temporarily examined by an isopod in the process of seeking out a preferred host. It may well be that Nerocila californica, when young and first seeking a proper host, or upon being dislodged from its regular host, has a behavior of attaching temporarily to any number of passing fishes until it senses the proper host fish, at which time it takes up permanent residence. It seems apparent, at any rate, that some degree of host specificity does occur with this parasite, but that specificity remains at a low level of discrimination. It is unlikely that adult cymothoids, of any species, make a habit of dislodging themselves of their own volition to change host fishes unless some stress factor is present, as they are quite poorly adapted to swimming.

Nerocila californica is usually found attached near the base of a fin, either on the fin itself or on the body of the fish. In the case of the anchovy host (Ceten-

graulis mysticetus) the isthmus is also a favored place of attachment.

Infestation rates on anchovy in the northern Gulf of California have been recorded as high as 85 to 90 per cent (per cent of fishes infested in a single trawl sample; over the delta of the Rio Colorado; July). Infestation rates for other host fishes are not known but appear to be considerably lower than that of anchovy.

Tissue damage was nearly always evident in specimens I captured, with both male and female isopods. In the case of the anchovy infestations, tissue damage was extensive; in some cases several patches, each several square centimeters across, were found on both sides of the fish. Erosion commonly occurred down

to the myomeres, and occasionally nearly an entire fin was eroded or eaten away. It is of interest to note that the host fishes of this isopod are entirely unrelated phylogenetically, although they are related behaviorly. This and other aspects of cymothoid host-parasite relationships will be the topic of a future paper.

Zoogeographic considerations. — There are two known species of the genus Nerocila in the eastern Pacific, N. californica and N. excisa (Richardson 1901). Until 1972 Nerocila excisa was known from a single specimen only, reported by Richardson (1914) from the stomach of Coryphaena sp. (probably Coryphaena hippurus L., the dolphinfish), collected in the mid-Pacific Ocean about midway between the Galapagos and Hawaiian Islands. The single specimen upon which Richardson based her description was lacking the uropoda and had a damaged pleotelson. In 1972 Trilles synonymized this species with its juvenile form, Aegathoa excisa Richardson, 1901, establishing this species as a nearly trans-Pacific form, known from New Caledonia to Cocos Island, off Costa Rica. I have specimens of what is probably a third species of Nerocila, at present known only from the Gulf of California. All three species are very similar to the species of this genus occurring in the Caribbean region, and the two Gulf of California forms no doubt represent one facet of the generalized transisthmian tract (as described by Croizat, Nelson & Rosen, 1974), which dates back to the pre-Pliocene, prior to the formation of the Panama isthmus. Nerocila californica is very similar to N. acuminata Schioedte & Meinert, 1881. The latter species ranges from Virginia south, into the Gulf of Mexico, and Nerocila acuminata may be considered an Atlantic analog, or geminate species to N. californica and these two species probably stem from a common ancestor. Nerocila excisa, on the other hand, appears to be of Indo-Pacific origin. The genus Nerocila is represented by numerous species in the Indian Ocean and Mediterranean regions and no doubt the early distribution of this genus (and the very similar genus Anilocra) was part of a global Tethian/transatlantic tract. There are no amphi-American species of Nerocila known and it is probable that species differentiation in N. californica occurred subsequent to the Pliocene. This vicariance may therefore be assumed to be a direct result of the formation of the Panama land bridge.

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RESUME

Description et figuration du cymothoadien ectoparasite de poissons Nerocila californica (Isopoda: Flabellifera). Le développement et le cycle évolutif sont discutés et les stades de développement figurés. Le travail porte également sur la zoogéographie et l'association hôte/parasite, ainsi que sur les différents hôtes possibles pour la famille.

LITERATURE CITED

- 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.
- BRUSCA, R. C., in press. Range extensions and new host records of cymothoid isopods (Isopoda: Cymothoidae) in the east Pacific.
- —, in preparation. Studies on the cymothoid fish symbionts of the eastern Pacific (Crustacea: Isopoda: Cymothoidae). II. Biology of Lironeca panamensis.
- Burbanck, M. P. & W. D. Burbank, 1974. Sex reversal of female Cyathura polita (Stimpson 1855) (Isopoda, Anthuridae). Crustaceana, 26 (1): 110-113.
- CROIZAT, L., G. NELSON & D. E. ROSEN, 1974. Centers of origin and related concepts. Syst. Zool., 23 (2): 265-287.
- HALE, H. M., 1926. Review of Australian isopods of the cymothoid group. Part II. Trans. Royal Soc. South Australia, 50: 201-234.
- Howes, N. H., 1939. Observations on the biology and postembryonic development of Idotea viridis (Slabber) (Isopoda, Valvifera) from New England Creek, south-east Essex. Jour. Mar. Biol. Assoc., 23: 279-310.
- KJENNERUD, J., 1950. Ecological observations on Idothea neglecta G. O. Sars. Univ. Bergen Arbok, (naturvidensk. ser.) 7: 1-47.
- MAYR, E., 1969. Principles of systematic zoology: 1-428. (New York).
- MENZIES, R. J., T. E. BOWMAN & F. G. ALVERSON, 1955. Studies on the biology of the fish parasite Livoneca convexa Richardson (Crustacea, Isopoda, Cymothoidae). Wasmann Journ. Biol., 13 (2): 277-295.
- MENZIES, R. J. & R. J. WAIDZUNAS, 1948. Postembryonic growth changes in the isopod Pentidotea resecata (Stimpson) with remarks on their taxonomic significance. Biol. Bull., 95: 107-113.
- Montalenti, G., 1941. Studi sull'ermafroditismo dei Cimotoide. I. Emetha audouinii (M. Edw.) e Anilocra physodes (L.). Pubb. Stazione Zool. Napoli, 18 (2): 337-394.
- NAYLOR, E., 1955. The life cycle of the isopod Idotea emarginata (Fabricius). Jour. Animal Ecology, 24: 270-281.
- NIERSTRASZ, H. F., 1915. Die Isopoden-Sammlung im Naturhistorischen Reichs-Museum zu Leiden. I. Cymothoidae. Zool. Meded. Leiden, 1 (1): 71-108.
- —, 1931. Die Isopoden der Siboga-Expedition. III. Isopoda Genuina. II. Flabellifera. Siboga Exped. Monogr., **32**(c): 123-233. (E. J. Brill, Leiden).
- RICHARDSON, H. R., 1899a. Key to the isopods of the Pacific coast of North America, with descriptions of twenty-two new species. Proc. U.S. Nat. Mus., 21: 815-869.
- —, 1899b. 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.
- —, 1900. Synopses of North American invertebrates. VIII. The Isopoda. Amer. Natur., 34: 207-320.
- —, 1901. Papers from the Hopkins-Stanford Galapagos Expedition, 1898-1899. VI. The Isopods. Proc. Washington Acad. Sci., 3: 565-568.
- ----, 1905. A monograph on the isopods of North America. Bull. U.S. Nat. Mus., 54: 1-727.
- —, 1914. Reports on the scientific results of the expedition to the tropical Pacific in charge of Alexander Agassiz, on the U.S. Fish Commission Steamer "Albatross", from August 1899 to March 1900, Commander Jefferson F. Moser, U.S.N. commanding. XVII and XXVIII. Isopoda. Bull. Mus. Comp. Zool., **58** (8): 363-372.
- ROMESTAND, M. B., 1971. Etude électrophorétique des protéines de l'hémolymphe, chez l'Isopode Cymothoidae Meinertia oestroides (Risso), à rapport avec les différentes phases de l'évolution sexuelle. C.R. Acad. Sci. Paris, 272: 2342-2345.

- Schioedte, J. C. & F. Meinert, 1881. Symbolae at monographiam cymothoarum, crustaceorum isopodum familiae. II. Anilocridae. Naturhistorisk Tidsskift, (3) 13: 1-166.
- SCHULTZ, G. A., 1969. How to know the marine isopod crustaceans: 1-359. (Wm. C. Brown Co., Dubuque, Iowa).
- TRILLES, J. P., 1964. Sur la présence et l'évolution regressive de l'appendix masculina chez les Isopodes Cymothoidae. C.R. Acad. Sci. Paris, 258: 5739-5741.
- , 1968. Recherches sur les isopodes Cymothoidae des côtes françaises. Part 1. Systématique et faunistique; Vol. I. Bionomie et parasitisme; Vol. II. Biologie générale et sexualité. Ph.D. Thesis, Univ. Montpellier, France.
- —, 1969. Recherches sur les Isopodes "Cymothoidae" des côtes françaises. Aperçu général et comparatif sur la bionomie et la sexualité de ces Crustacés. Bull. Soc. Zool. France, 94 (3):
- —, 1972. Sur quatre isopodes cymothoides du Pacifique (Nouvelle Calédonie). Cahiers O.R.S.T.O.M., (sér. Oceanogr.) 10 (1): 3-17.
- UNWIN, E. E., 1920. Notes upon the reproduction of Asellus aquaticus. Jour. Linn. Soc. Zool. London, 34: 335-343.