

## ISOPODS ASSOCIATED WITH FISHES: A SYNOPSIS AND CORRECTIONS

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Isopods associated with fishes are biologically and economically important. Unfortunately, little more than basic taxonomic studies have been conducted, with both isopod specialists and fish parasitologists largely ignoring their biology. This lack of knowledge has resulted in incomplete and erroneous portrayals of the group. To allay confusion concerning this important group, we first provide an overview and synoptic information and, second, directly address some of the published misconceptions.

Essentially any isopod collected with a fish is suspected of having been associated with that fish. We refer to isopods on fishes as an "association" rather than "parasitism" because the exact relationship between host and isopod has not been established in all cases. A gradation from casually associated micropredation to parasitism occurs between flabelliferan isopod families, i.e., cirrolanids to corallanids to aegids to cymothoids (Tables I, II). Sometimes this gradient can even occur within isopod genera. We define association as being in, or attached on, the host fish longer than is necessary to simply feed and drop off, as does a micropredator. Our definition allows this rather diverse, but related group, to be considered cohesively without dwelling on the sometimes sterile, and always complex, problem of defining parasitism, predation, and other relationships. We are not belittling the importance of establishing the exact relationships between isopods and fishes, just ignoring it for the sake of expediency.

Isopods associate with fishes from Himalayan Mountain streams to abyssal depths of the sea, although most species are marine, shallow-water, and coastal. Some 500 species are known in 5 families (Tables I, II). Cymothoids and aegids are among the largest parasites of fishes, but other taxa, for example most gnathiids, are difficult to see without the aid of a dissecting microscope (Table II). Isopods attach to all external, branchial, and buccal surfaces of fishes, especially the gills, mouth, and anterior body. Some cymothoids also form pouches in the lateral musculature of a few freshwater and marine fishes. One cirrolanid even burrows into the flesh of sharks (Bird, 1981). Most cymothoids are highly host and site specific. A few corallanids seem to have some host specificity, but other isopods apparently have none. Some prefer fishes from particular habitats or with certain behaviors. Species vary in biogeographic range from a short section of coast or single freshwater lake to those occurring worldwide. Gnathiids have been relatively successful in the greater depths. A few cymothoids occur in the inland fresh waters of South America, Asia, and Africa; a freshwater aegid occurs in Asia and Australia, freshwater corallanids in Asia, Java, Sulawesi, and Sumatra, and some marine or brackish water cymothoids invade coastal freshwaters. Many species occur in the tropics, but more numbers of individuals

occur in the temperate zones. A few species are found in the Arctic and Antarctic.

Many cymothoids and aegids inflict large wounds, often stunt the growth of, and occasionally kill, fishes. Gnathiids sometimes cause tissue damage (Honma et al., 1991) and have caused losses of cage-held fishes. Other isopods cause little physical damage. Superinfections by any isopods (Williams and Bunkley-Williams, 1996) can kill fishes (Williams and Bunkley-Williams, 1994b), with confined fishes being particularly vulnerable. Juvenile isopods kill or damage the young of many commercially and recreationally important fishes. These potentially great losses are largely undocumented but may be more important than the obvious damage to adult hosts by adult isopods. Each female isopod produces multiple broods of dozens to hundreds of juveniles. Each juvenile has the potential of killing several young fishes.

Cymothoids are protandrous hermaphrodites (developing into males and then females), whereas other fish-associated isopods have separate sexes. Female cymothoids often inhibit the sexual transformation of their associated males and thus maintain a stable female-male pair. These isopods develop from egg to juveniles in brood pouches of the female. Cymothoids and gnathiids lose their swimming ability after the juvenile stages, but the other isopods remain active swimmers. Because of their size, survivability, ease of manipulation, range of association, and ubiquity, fish-associated isopods provide excellent experimental and observational research opportunities that are unavailable in other parasite groups.

Although some fish isopods detrimentally affect some of the most commercially important fish resources (Williams and Bunkley-Williams, 1996), they have received only modest attention in modern texts on isopods (see Schultz, 1969; Kensley and Schotte, 1989) and fish parasitology (see Kabata, 1970; Post, 1987; Roberts, 1989; Sindermann, 1990; Schaperclaus, 1991; Stoskopf 1992). These and other sources on occasion provide inadequate and often erroneous depictions of this important group. These inaccuracies were not created by the above authors but have accumulated from the older literature, from mistaken translations, or from the best efforts of authors to extrapolate from inadequate information. Correcting these errors is important because these and other references are repeatedly cited and quoted. Some excellent synopses of different isopod groups have appeared in the modern scientific literature (Brusca, 1981, 1983; Bruce, 1983, 1986, 1987a, 1987b, 1987c, 1990; Delaney, 1984, 1989; Delaney and Brusca, 1985; Williams and Williams, 1985a; Camp, 1988; Bruce and Bowman, 1989; Trilles, 1991; Brusca and France, 1992; Williams and Bunkley-Williams, 1992, 1994a), but this information has not been properly utilized in most modern volumes.

Some texts consider all isopods associated with fishes as parasitic (Schultz, 1969; Stoskopf, 1992), whereas others ignore all that are not permanent parasites (Provenzano, 1983; Sindermann, 1990). These discrepancies occurred largely because the

Received 29 September 1997; revised 17 March 1998; accepted 17 March 1998.

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TABLE I. Classification of isopods associated with fishes.\*

Subphylum Crustacea Pennant, 1777—crustaceans
Class Malacostraca Latreille, 1806
Order Isopoda Latreille, 1817—isopods
Suborder Gnathiidea Hansen, 1916
Family Gnathiidae Harger, 1880
Suborder Flabellifera Sars, 1882
Family Aegidae Leach, 1815
Family Cirolanidae Dana, 1852
Family Corallanidae Hansen, 1890
Family Cymothoidae Leach, 1818

\* The sphaeromatid (Flabellifera) and bopyrid (Epicaridea) records from fishes were apparently based on misidentifications, and the fossil flabelliferan from a fish remains unclassified at the family level (Bowman, 1971).

authors defined parasitism differently or were not critical in their use of terminology. We regard cymothoids and gnathiids as permanent parasites; and aegids, corallanids, and, possibly, cirolanids as temporary parasites. Permanent parasites do not change hosts or leave hosts during a single life-cycle stage. For example, adult cymothoids never leave their hosts; juvenile gnathiids only leave a host between juvenile stages or to become adults (Wägele, 1988). Temporary parasites may change hosts, live away from hosts, but must stay associated with a host for a longer period of time than simply to feed. This has been called predation (Brusca, 1983; Kensley and Schotte, 1989) but, due to the association, seems more like parasitism than predation. In contrast, the various forms of predation would allow no association with the host other than feeding. Most aegids and many corallanids associated with fishes are temporary parasites. Most cirolanids, however, are actually predators on restrained fishes or scavengers on dead ones. Unfortunately, we do not know enough about the biology of many isopods found on fishes to characterize adequately their exact relationship with the host.

A variety of old and new families have been listed as fish parasites by modern references, whereas a few obvious ones have been omitted. Provenzano (1983) and Sindermann (1990) mention only 2 families, Schaperclaus (1991) 4, whereas we recognize 5 (Table I). Schultz (1969) and Kensley and Schotte (1989) identify 6, whereas Stoskopf (1992) recognizes different

numbers of families in different parts of the same reference. Anilocridae, as used by Stoskopf (1992) and others, is a subfamily of Cymothoidae as redefined by Bruce (1987a). Excorallanidae (used by Schultz, 1969) and Tridentellidae (used by Kensley and Schotte, 1989) were based on single genera in the family Corallanidae. Excorallanidae was synonymized with Corallanidae by Bruce et al. (1982). Delaney and Brusca (1985) did not formally synonymize Tridentellidae but refuted most of the characters separating it from Corallanidae.

Schultz (1969) stated that most cymothoids are parasites of fishes. We believe all cymothoids are permanent parasites on fishes and that the rare reports of cymothoids from squid, gastropods, or free-living were dislodged from fishes as also suggested by Brusca (1981) and Kensley and Schotte (1989).

Brusca (1981) suggested that females of some species of cymothoids apparently do not feed. This has been distorted in the popular literature to suggest that cymothoids are not parasitic as adults, whereas Provenzano (1983) suggested that they were only parasitic as adults. Both views have been repeated elsewhere (Stoskopf, 1992; Kensley and Schotte, 1989; Sindermann, 1990), and both are incorrect. Males of protandrous hermaphrodites are merely a transitional stage and the maturity of nonovigerous females can only be determined histologically. The reproductive products of the brood pouch occupy most of the space in the female cymothoid's body and the oostegites cover the mouthparts so that they cannot feed. Thus, if the gravid female is assumed to be the only adult form in cymothoids and if it is assumed they can only harm the host by feeding, then they cannot be a parasite. However, nongravid females are adults and feed, and gravid females harm their hosts. Moreover, female cymothoids alternate between ovigerous (reproductive) and vegetative stages where feeding and growth occur (Williams and Williams, 1982; Bunkley-Williams, 1984). These stages may repeat several times, with molting occurring after both reproduction and growth. Evidence for this life-cycle alteration is based on nonovigerous females that are larger than some ovigerous females of the same species and spent ovigerous females observed in the process of molting into nonovigerous females (Williams and Williams, 1982; Bunkley-Williams, 1984). Cymothoids thus associate as parasites for long periods of time with their hosts. The size of female cy-

TABLE II. Characteristics of isopods associated with fishes.

Family of isopods	Type of association	Species % (n = 500)	General abundance* on fishes	Average % of fish infested*	Sexual dimorphism	Adult size ♀ (mm)	Modifications for parasitism
Cymothoids	Permanent	62	Common	1	Usually pronounced	10–100	Mouthparts Dactyls
Gnathiids	Permanent (juvenile)	14	Abundant	10	Extreme#	1–8¶	Mouthparts
Aegids	Temporary†	14	Common	1	Slight	7–60	Mouthparts
Corallanids	Temporary or accidental‡	6	Rare	0.01	Moderate	7–26	Mouthparts
Cirolanids	Accidentally associated?§	3	Extremely rare	0	Slight	5–38	None

\* Our generalizations, averages may not apply to exact localities, hosts, or species.

† Some aegids may be free living.

‡ Most corallanids are free living.

§ Most, possibly all, cirolanids are predaceous and are serious pests destroying fishes in nets and cages.

|| The female is always, sometimes drastically, larger than the male, and slight morphological differences usually occur.

# Males and females are so morphologically different that they were originally named in different genera.

¶ Juveniles (found on fishes), adults are free living and larger.

mothoids often appears closely related to the sizes of their hosts, which also suggests a long host-association and multiple broods (Williams and Williams, 1982; Bunkley-Williams, 1984).

What Schultz (1969) and Provenzano (1983) refer to as a free-living form of immature cymothoids is actually the free-swimming juvenile stage. Almost all aquatic parasites have free-swimming infective stages. Many workers have reported juvenile cymothoids on various hosts (as summarized by Bunkley-Williams, 1984). We have shown that juvenile cymothoids will attach to definitive hosts as soon as they leave the brood pouch (Bunkley-Williams, 1984; Williams and Williams, 1985b) and may attach for a short period of time to paratenic hosts until a definitive host can be located. Once a juvenile attaches to its definitive host, it loses its swimming setae and begins to develop into a male. Cymothoids thus are completely parasitic.

Gnathiids feed on fishes and then drop off to reproduce, transforming into nonswimming and nonfeeding benthic adults that never return to a host (Wägele, 1988). The life cycles of most corallanids are unknown, but the suggestions that they are similar to gnathiids (Kabata, 1970; Stoskopf, 1992) are incorrect. Most corallanids seem to be free living and a few temporarily associate with fishes, but those species occupying the narrows of marine fishes and those on freshwater fishes apparently have longer periods of association with their hosts and are at least temporary parasites.

Provenzano (1983) stated that cymothoids feed on blood or other tissues, or both. Some cymothoids feed on whole blood, whereas others feed on oozings of plasma in wounds (Bunkley-Williams and Williams, unpubl. obs.). The tissue damage to hosts by cymothoids is often impressive, but this damage is caused by crypting (a necrotic eroding reaction of host tissues pressed against the parasite) or deformation (host growing around the parasite). Cymothoid piercing-sucking mouth parts seem more suited to body fluids. Aegids and gnathiids feed on whole blood, the food of corallanids on fishes is not known, and cirolanids probably feed on fish tissue.

Stoskopf (1992) stated that the mouthparts of fish-associated isopods are highly modified for parasitic feeding. This is true in cymothoids, gnathiids, and aegids but not in corallanids or cirolanids (Table II). This assertion is also misleading as fish isopods are the least modified from their free-living relatives of any parasitic group.

Schaperclaus (1991) began 1 paragraph by referring to cirolanids as predators but ended the same paragraph calling a cirolanid a parasite! He also stated that some aegids are "stationary (=permanent?) blood-suckers." We are not aware of any evidence suggesting that aegids are permanent parasites.

Post (1987) stated that the sexes of all crustacean parasites of fishes are separate but considered Cymothoidae as the model for other isopod parasites. Cymothoids, however, are protandrous hermaphrodites, becoming males first and then transforming into females.

Stoskopf (1992) illustrated a female isopod with a cymothoid body shape, 1 pair of pereopods (legs) terminated with curved hooks, and 5 pairs of pereopods terminated with setae. No fish-associated isopods have pereopods that terminate in setae. Moreover no female isopod has 6 pairs of pereopods. Gnathiids have 5 pairs of pereopods, whereas the other fish-associated

isopods have 7 pairs. Cymothoid legs all terminate in large hooks (except genera *Artystone* and *Riggia*), and aegids have large hooks on the first 3 pair and single acute dactylopods on the last 4. Corallanids and cirolanids reported from fishes have single, acute dactylopods on all pereopods (Williams and Bunkley-Williams, 1995).

Schultz (1969) suggested that more than 1 species of cymothoid rarely occurs on the same host specimen. We have found 2 sets of Caribbean cymothoid species commonly inhabiting the same fish (*Anilocra acanthuri* and *Agarna cumulus* parasitizing *Acanthurus chirurgus*; and *Anilocra abudefdufi* and *Kuna insularis* parasitizing *Abudefduf saxatilis*). The occurrence of 1 of the species was apparently facilitated by the presence of the other species (Williams and Williams, 1985a).

Stoskopf (1992) noted that Moser et al. (1986) found that a praziquantel bath killed larval forms of *Lironeca* (= *Vanamea*) *symmetrica*. However, Moser et al. (1986) did not mention isopods nor has Moser ever treated isopods with praziquantel (M. Moser, pers. comm.). The only published treatment for fish isopods was the use of formalin to control *Livoneca ovalis* (Williams, 1974) as noted by Brusca (1981) but missed by Provenzano (1983), Schaperclaus (1991), and Stoskopf (1992). As mentioned above, cymothoids develop directly and have no larval stages. The forms leaving the brood pouch are juveniles. The larval forms referred to by Stoskopf (1992) were probably juveniles.

Woodlice are terrestrial isopods (suborder Oniscidea). None of these forms is parasitic. The term "parasitic woodlice" used by Schaperclaus (1991) is most unfortunate and confusing. We sympathize with his attempt to create a common name for fish-associated isopods. A variety of authors have used "fish louse" or "fish lice" for isopods, but these terms have also been applied to branchiurans, larger copepods, or a mixture of all fish-associated crustaceans. The great variety of isopod morphologies and the superficial similarity of other fish-associated crustaceans make a single common name other than isopods impractical.

We hope our synopsis and corrections will make this important group of fish associates better recognized as a potential problem for fishes and will encourage more attention and research on these organisms. We conclude that the detrimental aspects of fish-associated isopods have been underestimated and that their potential to provide valuable information about their hosts has been underutilized.

#### ACKNOWLEDGMENTS

We thank Thomas E. Bowman (deceased) and Brian Kensley, Smithsonian Institution, and Thomas G. Rand, St. Mary's University, Halifax, Nova Scotia, Canada for reviewing the manuscript.

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