Four Cases of Unusual Crustacean–Fish Associations and Comments on Parasitic Processes

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Abstract.—Unusual short-term associations provide insight into the long-term development or modification of parasitism. A superinfestation of a trap-held crevalle jack Caranx hippos by juvenile cymothoid isopods Cymothoa oestrum suggested loss of the mechanism controlling numbers of isopods on a host, and overcrowding on the host overcame this isopod's strict site specificity. Crabs (Decapoda) have not been reported as parasites of fishes, but unidentified crab zoeae superinfested the gills of a trap-held gray angelfish Pomacanthus arcuatus. Adult burrowing crabs Raninoides lamarckii invaded the gills of trap-held gray snapper Lutjanus griseus; this suggested how a relatively large crustacean could become an opercular chamber parasite and how wound feeding could occur. An apparent prey-to-predator transfer of the cymothoid isopod Anilocra acuta to a free-swimming king mackerel Scomberomorus cavalla also represented a move from an external to a pharyngeal-attachment position in this site-specific isopod. Trap confinement may have protected the infestations of juvenile C. oestrum and crab zoeae from organisms that serve as cleaners. New associations are usually begun by immature stages, but may also be initiated by adult crustaceans, as in the cases of A. acuta and R. lamarckii. The ability of crustaceans to survive, adapt, and be observed makes them excellent subjects for use in discerning complex parasitological processes.

How parasitic modes of life develop, how the abundance of a parasite on a host is controlled, and how site specificity on a host is maintained are fundamental questions in parasitology. Direct observations of the long-term development of these processes are wanting. Most information concerning the evolution of parasitism has been extrapolated from existing associations. Little hard evidence exists and most speculations are impossible to test (Whitfield 1979). Recognizing the initiation of a parasitic process would be extremely difficult. Any phenomena even vaguely resembling the beginning of or early changes in parasitism may be worthy of close scrutiny. Short-term observations may provide some insight into the evolutionary processes of parasitism. We describe four cases of unusual crustacean–fish associations that may offer such insight.

Methods
We examined four unusual crustacean–fish associations. Crustaceans were preserved in 70% ethanol. Larval or juvenile crustaceans were measured to the nearest 0.1 mm, and adult crustaceans were measured to the nearest millimeter. Specimens deposited in the U.S. National Museum of Natural History (USNM) Crustacean Collection are indicated in the text by USNM numbers. Fish were identified in the field and not preserved.

Superinfestation of cymothoid isopods on a crevalle jack.—On 16 May 1975, we examined an 81-cm (fork length) crevalle jack Caranx hippos (Perciformes: Carangidae) that had been confined for an unknown period of time in a fish trap in 3 m of water off a dock on Magueyes Island, Puerto Rico. The fish trap was an arrowhead-shaped, mangrove-wood frame (0.3 \( \times \) 1.0 \( \times \) 1.5 m) covered with chicken wire. We recovered it by scuba diving.

We experimentally exposed juvenile cymothoid isopods Cymothoa oestrum, which normally parasitize jacks (Carangidae) and a few other Caribbean fishes, to 55 specimens (total) of 27 species of acanthurids, grammids, holocentrids, labrids, lutjanids, pomacentrids, pomadasyids, sciaenids, serranids, and sparids. We collected these isopods from off La Parguera, Puerto Rico, with a plankton net towed by a small boat. We sorted juvenile Cymothoa oestrum from live plankton and measured them with the aid of a dissection microscope. We placed one to five juvenile isopods in 40-L aquaria with one small fish each. Isopods lengths were 7.0–7.9 mm.

Crab larvae inhabiting the gills of a fish.—We collected a 35.6-cm (standard length, SL) gray angelfish Pomacanthus arcuatus (Perciformes: Pomacanthidae) from a fish trap in 9 m of water off Mona Island on 23 April 1976. This trap was sim-
ilar to the one described from Puerto Rico. We
examined three gray angelfish collected from near
the trap on 23 April 1976, and 22 specimens of
17 species of fishes in 11 families during this cruise
to Mona Island (19–23 April 1976). Fishes col-
clected at Mona Island were examined immediate-
ly for metazoan parasites in the laboratory of the
RV Crawford, which was anchored above the dive
sites.

We also examined 25 other specimens of gray
angelfish from Mona Island and Puerto Rico dur-
ing 1974–1992. We placed gray angelfish in cages
for 3–17 d in Puerto Rico and Mona Island in
attempts to duplicate the superinfestation.

Adult crabs infesting the opercular chambers
of gray snappers.—We examined three gray snappers
Lutjanus griseus (Perciformes: Lutjanidae), 25–30
cm SL, taken from a fish trap set for 4 d in 30 m
of water off Santa Marta, Colombia, 10 May 1977.
The trap was rectangular (about 1 m³ volume) and
was constructed of a steel frame with wire mesh.

Transfer of a cymothoid isopod from prey to
predator.—An 11.3-kg king mackerel Scomber-
emorus cavalla (Perciformes: Scombridae) was
cought with sport-trolling gear 27 km off the shore
of Southport, North Carolina, on 4 October 1986.
Parasites from this host were removed, preserved,
and sent to us (I. Clavijo, University of North
Carolina, personal communication).

We examined 55 specimens of four species of
mackerel Scomberomorus spp. for parasites. These
hosts from the Caribbean were collected by hook
and line, spearing, or Gill nets.

Results

Superinfestation of Cymothoid Isopods on a
Crevalle Jack

The crevalle jack was infested with 260 juvenile
Cymothoa oestrum in the gills, mouth, opercular
chamber, and head. In a subsample, juvenile iso-
pods preserved from this host were 6.5–9.7 mm
long ($N = 56$; USNM). Isopod lengths were clus-
tered into three groups: 11 of the isopods were
7.2–7.6 mm, 24 were 7.8–8.6 mm, and 17 were
9.0–9.7 mm (Figure 1). Four juveniles, 6.5, 7.2,
8.1, and 9.0 mm long, were partially molted.
The amount of time the host had been confined in the
trap could not be determined.

All fishes exposed to juvenile Cymothoa oes-
trum in aquaria were infested with one of these
isopods in the mouth within 24 h. The isopod
invariably attached on the host’s tongue, facing
out of the mouth.

Crab Larvae Inhabiting the Gills of a Fish

We found more than 350 live unidentified crab
zoae (USNM), 2.0 mm long, attached to the
branchial filaments of the gray angelfish from the
trap at Mona Island. Other parasites present in-
cluded two Hatschekia albirubia (Copepoda) on
the gills, 37 Theletrum justiforme (Digenea) in
the pyloric ceaces, and 26 Cotylogaster basiri (Asphi-
dogastrea) in the stomach. The amount of time
the host had been confined in the trap could not
be determined.

Other gray angelfish and several additional spe-
cies of fish examined from Mona Island during
April 1976 yielded no more zoae. Examinations of
45 gray angelfish from Mona Island and Puerto
Rico over a 19-year-period failed to reveal any

Adult Crabs Infesting the Opercular Chambers
of Gray Snappers

Two of the gray snappers from the Colombian
traps each had one burrowing crab, Raninoides
lamarcki (Decapoda: Raninidae), in one opercular
chamber. The crabs were 18 and 27 mm long. The
third gray snapper was infested with a 15-mm-
long monogram isopod, Rocinela signata (Isopo-
da: Aegidae), in an opercular chamber. The isopod
caused little recognizable damage to the branchial
filaments, but in the opercular chambers contain-
ing a crab, the branchial filaments had been com-
pletely destroyed except for remnants of the basal
portions.

This burrowing crab species was not found in
gray snappers or other fish species from traps set
under similar conditions around Puerto Rico. We
checked hundreds of traps set off the west and
southwest coasts of Puerto Rico and Mona Island.
These traps were of a variety of sizes and had
metal frames. Because samples of this crab have
been unobtainable, we have not been able to at-
tempt to duplicate this association experimentally.

Transfer of a Cymothoid Isopod from Prey
to Predator

The king mackerel caught off North Carolina
had a live 35-mm-long female Anilocra acuta
(Isopoda: Cymothoidae) attached in the extreme
posterior part of its pharynx. The isopod had the
asymmetrical body shape characteristic of externally developing cymothoid isopods.

The only isopod found during examinations of mackerels was *Lironeca redmanii* (Isopoda: Cymothoidae). We have received reports of the isopods found in thousands of other specimens of mackerels taken in experimental gill nets set for a tagging program off the Caribbean coast of Mexico (K. Burns, Mote Marine Laboratory, personal communication). This isopod occurs in the opercular chambers of mackerels. We have not found any cymothoids in the pharynx of these fishes.

Discussion

*Parasites Overcoming Mechanisms That Control Intensity*

All of the fish experimentally exposed to juvenile *Cymothoa oestrum* became infested. The juvenile isopods were attached on top of the tongue of the host; the head of the isopod was oriented toward the mouth of the host. Each fish was infested within 24 h by one juvenile isopod whether exposed to one or more (two to five) isopods.

*Cymothoa oestrum* typically have attachment-site specificity, an infestation level of two parasites per host, and a lack of juveniles on adult hosts (our unpublished data). An exception to these characteristics occurred in the crevalle jack that was infested with 260 juvenile *C. oestrum*. This superinfestation was not the result of a burst release (Williams and Williams 1985) from a female isopod in the mouth of this host, because no female nor the characteristic permanent damage caused by the presence of a female isopod was present. The three size-groups of isopods and the 3.2-mm size range between smallest and largest isopod (Figure 1) suggest multiple infestation of this host by planktonic juveniles from broods of different *C. oestrum* over a period of several days and development of these juveniles on the host over a period of at least several days. Size differences were not due to differences in the quality of attachment sites, because isopods of various sizes occurred at the different sites with no apparent size-site discrimination. Juveniles within the brood pouch of a cymothoid isopod vary no more than 0.1 or 0.2 mm in length (our unpublished data). Sizes of isopods from the crevalle jack were comparable to those of isopods used in our exposure experiments (7.0–7.9 mm) and comparable to sizes of juvenile *C. oestrum* collected from naturally infested young crevalle jacks (7.6–9.3 mm; our unpublished data). If the juvenile isopods on the crevalle jack were recruited from the plankton, then this superinfestation demonstrates the high availability of *C. oestrum* juveniles in a small area over a relatively short period of time.

Overstreet (1978) reported what may have been a superinfestation of juvenile isopods on the skin of a groupper *Epinephelus* sp. (Perciformes: Serranidae) in the Bahamas, but he did not provide sufficient details to allow comparison with the present case. Harassing a host infested with a female *Anilocra* sp. can induce a burst release of juvenile isopods (Williams and Williams 1985), and some of the juveniles may attach to the original host (our unpublished data). We have observed gnathiids isopods swarming over the bodies of many species of Caribbean reef fishes at night. During the day, most of these gnathiids have either dropped off or have been removed by cleaners. Stepień and Brusca (1985) documented mass attacks by predacious ostracods and cirrolanid isopods on fishes held in traps and discussed similar reports from the literature. Apparently mass at-
tacks by predacious crustaceans are not uncommon, but mass infestation by parasitic cymothoid isopods is unusual.

Cleaner organisms remove juvenile cymothoid isopods attached to coral reef fishes (L. Williams 1984). Confinement of the crevalle jack in a trap may have protected the juvenile *C. oestrum* from being removed by cleaners.

**Changes in Attachment Site Because of Overcrowding**

The superinfestation of *Cymothoa oestrum* discussed above caused these isopods to attach in unusual positions. As stated before, all other *C. oestrum* have been found as single juveniles or as female–male pairs attached on the top of the tongue of the host. In the case of the crevalle jack in the trap, not only was the tongue of the host densely covered with juvenile isopods, but also isopods were attached elsewhere in the mouth, in the opercular chamber, on the gills, and even on the external surfaces of the fish, near the mouth and opercular openings. Overcrowding seems to have forced these isopods, which are highly site-specific (even as juveniles), to new locations on the host. These tongue-dwelling isopods attached in sites where other species of cymothoid isopods are known to mature. However, the survival of these normally tongue-dwelling isopods to adult stage seems unlikely. We have never seen *C. oestrum* develop on the external surfaces of a host. We have collected two Japanese fish on which normally opercular chamber-dwelling isopods were overcrowded out of the opercular chamber and on to the surface of the host near the opercular opening. These isopods developed into adult females and caused well-formed attachment depressions (indicating long-term attachment at these sites) on the external surface of the fish, near the opercular opening (our unpublished data). The genera *Anilocra* and *Nerocila* contain numerous species that externally attach to fishes. One species in each genus has been found to attach in the opercular cavity and not externally on its host (Bruce 1987a, 1987b). These two species very likely shifted site specificity from external attachment to gill-dwelling.

A similar shift of attachment sites also occurs in normally site-specific Caribbean *Anilocra*. When the normal sites for *Anilocra haemulii* beneath the host's eyes are occupied by females, a third female can become established on the dorsal midline of the head of the same host (Williams and Williams 1981). We have also observed *Anilocra chaeto-

dontis* and *Anilocra chromis* to have similar rare shifts caused by overcrowding. The dorsal surface of the head is the normal attachment position for *Anilocra holocentri* and *Anilocra myripristis* (Williams and Williams 1981).

Brusca (1981) suggested that the ancestral cymothoid isopods became established on the outside of fishes and more advanced species moved to the mouth and opercular cavity. The shift of attachment sites from the opercular chambers or mouth to the exterior of the host because of overcrowding does not contradict his suggestion, but rather suggests that overcrowding can cause a change in attachment site.

**Change in Attachment Site Associated with Change of Host**

One explanation for the adult *Anilocra acuta* attached in the pharynx of a king mackerel is the transfer of an externally attached, and thus easily detached, isopod of prey to a new attachment site in predator (the king mackerel). Such a transfer would have involved a shift in host species as well as attachment site. The more likely scenario for prey–predator shifts of cymothoids would involve a burst release of juveniles from a female in the mouth of the predator (Williams and Williams 1985). An infestation in the mouth of the predator by released juvenile isopods from a prey-derived, mouth-dwelling isopod could occur without an adult isopod changing attachment site. The combination of a successful site shift and a successful adult transfer seems most unlikely, but it appears to have been the case in the king mackerel we described. That a juvenile of *A. acuta* would have been able to infest this host and subsequently develop into an adult is unlikely, as is discussed below.

**Parasite Transfer from Prey to Predator Species**

Read (1970) suggested that most parasites are introduced into a new host species by being swallowed by the host. In the process of attacking and eating prey, predators are exposed to a wide array of adult parasites of their prey. The more similar the prey and predator species, the more likely repeated exposure may allow parasitization of the predator by prey-specific adult parasites. But such transfers of parasites have seldom been documented. Bychowsky and Nagibina (1967) suggested that species in two genera of monogeneans are transmitted to mackerels (Perciformes: Cybiidae) from prey fishes. We described a different
transfer method above involving a scrombrid mackerel.

The attachment of an adult *Anilocra acuta* in the pharynx is puzzling for a number of reasons. Species of *Anilocra* are not known to occur in the pharynx or mouth of fishes. *Anilocra acuta* has never been reported from a host in full-salinity coastal marine waters (Bowman et al. 1977; Williams and Bunkley-Williams, in press), much less 27 km into the Atlantic Ocean.

Infestation of this king mackerel by a juvenile *A. acuta* while the host was near shore is unlikely, because these juvenile isopods are probably even less tolerant of high salinity levels than adults. If juveniles and developmental stages of this isopod infest king mackerels, records of its occurrence would exist in this highly examined and commercially important species.

The bodies of *Anilocra* spp. are thought to become asymmetrical due to their positions on their hosts, because those on the right-hand side of a host turn slightly one way, and those on the left-hand side turn the opposite way. Species of isopods from the pharynx or mouths of fishes are symmetrical. The specimen of *A. acuta* from the king mackerel was asymmetrical and therefore most likely developed on the outside of a fish.

The case in question probably resulted from the king mackerel consuming a host with a natural infestation of *A. acuta* while inshore and dislodging the isopod during the attack. This parasite could then have attached in the pharynx of the king mackerel as the original host was swallowed. The isopod might then have survived in this position long enough to be transported offshore by the king mackerel. The survival of an externally attaching cymothoid in a habitat similar to that occupied by gill- or mouth-dwelling isopods is very interesting. If the transfer occurred inshore, as we assume, then the *A. acuta* may have survived in an abnormal position for a considerable period of time (even if only the time for the unlikely straight-line distance swim of 27 km is considered). This case provides insight into how adult parasites of prey could become parasites of predators and how external parasites could become internal parasites. The occurrence of many large cymothoid isopods in the mouths of predators (jacks, barracuda, and snappers in the Caribbean, for example; our unpublished data) makes this suggestion all the more intriguing.

Williams and Williams (1982) found that the female and male of *Mothocya bohlkeorum* were too large to fit together in one opercular chamber of their cardinalfish (*Apogon* spp.) hosts; therefore, the parasite may have originated in a larger host species. Prey-predator shifts of cymothoids would be simpler, because they would be shifts from a smaller prey to a larger predator host.

**Free-Living Larvae Invading Gills of a Fish**

Young (3-mm) spider crabs of the genus *Libinia* (Brachyura: Majidae) are known to associate with medusae (Cnidaria: Scyphoza) (A. Williams 1984). Some species of crabs (including species of anomurans, brachyurans, and carideans) have adults that are parasites or commensals of benthic invertebrates (Schmidt and Roberts 1977). One crab has been reported as an inadvertent parasite of a turtle (Clark 1965), but we are not aware of any crab parasites or commensals that attach to fishes.

The movement intensity, physical condition, and health of the gray angelfish may have been lowered by extended confinement in the fish trap. This combination of factors could have encouraged infestation of the gills with crab zoae. However, this host was not emaciated and showed no signs of disease. Crab zoal stages are usually found free-living in the plankton. They are not known to attach to or feed on any host, but the massive infestation of zoae on the gills of the gray angelfish cannot be explained by accidental contact. Gray angelfish do not feed on plankton (Randall 1967). The absence of zoae in adjacent free-swimming gray angelfish suggests that the impairment of the host by the trap led to the superinfestation.

Cleaner organisms remove parasites (cymothoid and gnathiid isopods, copepods, and monocoeans) from coral reef fishes. Confinement of the gray angelfish in a trap may have protected the crab zoae from removal by cleaners.

Some otherwise free-living mollusks have a parasitic larval stage on the gills of fishes (Hoffman 1967), although most mollusks are free-living at this larval stage. First contact must occur in any new parasitic process but could very likely never be recognized. Any process that places living organisms in contact with a potential host is worthy of close examination.

**Free-Living Adult Crabs Associating with a Host**

Clark (1965) observed a small stone crab, *Menippe mercenaria* (Decapoda: Xanthidae), on a wound under the deformed shell of an Atlantic hawksbill turtle *Eretmochelys imbricata* (Cheloniidae). The adult burrowing crab inhabiting the gill chambers of gray snappers seems to constitute a
similar association. Five similar cases involving the same species of crab and host had been noted by the staff of the Instituto de Investigaciones Marinas de Punta de Betín (IMPB), Santa Marta, Colombia (I. Velez, IMPB, personal communication). Randall (1967) and Starck (1971) did not list the family of this crab species in the diet of the gray snapper.

The amount of time the burrowing crabs remained in the opercular chamber could not be determined. A crab did not leave its new abode created by the removal of the host's branchial filaments, even when this presumed food source was depleted. Possibly the crab could feed on clotted blood and fluids from the wounds (as some gill-dwelling parasitic isopods do). The desirability of this new "niche" was further demonstrated by the reluctance of the crabs to abandon the opercular chamber after the trap was hauled from the bottom, through 30 m of water, while being held out of the water, and even after transport to the lab. The long-term stability of this particular association might be in doubt, but the situation does demonstrate how a relatively large, adult, free-living crustacean might take the role of a opercular chamber parasite. This physical association is not so different from that of some cymothoid isopods that more completely fill the opercular chambers of their hosts. Some of these, such as Lironeca redmanii, commonly destroy up to 50–60% of the branchial filaments in the chamber they occupy (our unpublished data).

Invasion of New Hosts by Adult Organisms

Transfer of parasites to new hosts typically occurs only in larval or developing forms, which are the normal infective stages. In two of the cases described above, adult stages were involved. Williams et al. (1982) and L. Williams (1984) successfully transferred adult female cymothoid isopods to new hosts that had not previously been infested. Adult transfers should also be considered as possible routes in establishing new host-parasite relationships.

Adult crustacean parasites from prey species do not die immediately when swallowed and must occasionally survive for short periods in predators. The Anilocra acuta in the pharynx of a king mackerel is of interest because the isopod survived for at least several, and perhaps many days in this new host. Potentially, this parasite could have survived for years, if the host had not been captured. The completion of the life cycle on this new host and any reorientation of the infective stages to seek this new host seems unlikely, but successful transfer and survival of an adult parasite did occur.

Parasites have long been theorized to be modified predators, but examples of transitional stages have never been found. If the burrowing crab Raninoides lamarki has not yet become an associate or parasite of the gray snapper, it is at least predisposed to do so.

Early Portion of the Cymothoid Life Cycle

Portions of the life cycle of many cymothoids (e.g., attached juveniles, maturing adults, and adult females with developing broods) are well known largely because such samples may be found in fish markets or museums. However, the portion of the cymothoid life cycle after the escape from the brood pouch and before attachment to a host is virtually unstudied. Attached juvenile isopods rarely occur on fishes, and the few that do are almost always lost when fishes are captured and processed. This is probably true of most parasites with a lengthy free-swimming infective stage. The Cymothoa oestrum from the crevalle jack were juveniles of different ages. Only 4 of the 56 specimens (lengths: 6.5, 7.2, 8.1, and 9.0 mm) were partially molted. These lengths represented four almost evenly spaced stages. Because they fell in the beginning of the three length clusters, these sizes may represent the first four molts in the post-brood-pouch phase of this isopod's life cycle.

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