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First report of gastrocotylinean post-oncomiracidia (Platyhelminthes: Monogenoidea: Heteronchoinea) on gills of flyingfish (Exocoetidae), snapper (Lutjanidae), dolphinfish (Coryphaenidae), and amberjack (Carangidae) from the Gulf of Mexico: Decoy hosts and the dilution effect

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ABSTRACT

Larvae, identified as post-oncomiracidia of the suborder Gastrocotylinea (Monogenoidea), were collected from formalin-fixed gills excised from six species of marine fishes captured from the Gulf of Mexico off Mississippi and Florida: common dolphinfish, *Coryphaena hippurus* and pompano dolphinfish, *Coryphaena equiselis* (both Perciformes, Coryphaenidae); gray snapper, *Lutjanus griseus* (Perciformes, Lutjanidae); greater amberjack, *Seriola dumerili* (Perciformes, Carangidae); and Atlantic flyingfish, *Cheilopogon melanurus* and sailfin flyingfish, *Parexocoetus hillianus* (both Beloniformes and Exocoetidae). Based on a combination of diagnostic morphological features, the specimens were divided into two basic forms, each of which was further subdivided into two morphotypes. No gastrocotylinean post-oncomiracidium had been reported previously from these hosts. Of the six host species, only *C. hippurus* serves as a host (unconfirmed) for the adult of a gastrocotylinean species, suggesting that the recorded fishes from the Gulf of Mexico comprise dead-end hosts acting as decoys for the oncomiracidia. These comparatively non-susceptible "decoy hosts" apparently dilute the susceptible fish-host population and by intercepting infective larvae (oncomiracidia) decrease the abundance of parasites on their typical hosts.

1. Introduction

1.1. Monogenoidea: host distribution and life cycle

Encompassing 3000–4000 nominal species and perhaps 20,000 extant species [1], the Class Monogenoidea (Platyhelminthes) includes hermaphroditic flatworms that parasitize aquatic and semi-aquatic vertebrates (primarily fishes) and occasionally invertebrates. Despite being generally regarded as having relatively simple life histories, extensive diversification among their life cycles has been reported [2]. Monogenoids are monoxenous, and depending upon the species, transmission is accomplished by either i) transfer of preadult or adult worms through direct or close contact between infected and susceptible hosts [2,3] or, more commonly, ii) as a free-swimming ciliated larva (oncomiracidium) that emerges from an egg and "seeks" a susceptible host in the water column. Once a host is found, the oncomiracidium sheds its cilia and migrates as a post-oncomiracidium to a specific site (microhabitat) on or in the host where it normally develops to maturity. Although some are endoparasitic, the vast majority of monogenoids mature in microhabitats provided by the host's external surfaces, such as, in fish, the gill lamellae, skin, gill arches and capping tissue of gill filaments, eyes, nasal and buccal cavities, fins and lateral-line pits [4].

1.2. Monogenoidean life cycles and larval forms: gaps in our knowledge

Relative to the amount of available information on taxonomic diversity, phylogenetic relationships, hosts, and microhabitats of adult monogenoids, far fewer details are available concerning the morphology, ecology, and general biology of their larvae. While much has been learned about the life cycles of ectoparasitic monogenoids in the context of their serving as pathogens of fishes in aquaculture [4], details of their life histories on wild pelagic and reef-associated fishes are understudied. For example, it is generally unknown what transpires i) in the water column as the oncomiracidium seeks its fish host, ii) on the newly infected host as the post-oncomiracidium seeks

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an optimal microhabitat, and iii) within the optimal microhabitat as the post-oncomiracidium develops to an adult.

1.2.1. In the water column (the oncomiracidium)

For representatives of many of the more than 50 monogenoidean families, oncomiracidial morphology has been characterized using specimens hatched in the laboratory [1,5–10], but virtually nothing is known about their host specificity, physiology, and longevity or the processes by which they find their natural fish hosts in the water column. Moreover, despite published reports of countless marine plankton surveys conducted by fisheries biologists, marine ecologists, limnologists, and oceanographers, no oncomiracidia have been recorded from these surveys. This paucity of information about the oncomiracidium and its interactions with wild fish hosts is possibly the result of logistical difficulties in collecting and identifying them in the water column because of i) their minute size (100–300 μm long), ii) their apparent fragility and short longevity, and iii) possible seasonal and rhythmic hatching.

Under controlled laboratory conditions, however, Kearn [11] has shown that the oncomiracidia of *Entobdella soleae* (van Beneden & Hesse, 1863) Johnston, 1929 (Capsalidae) apparently find their natural demersal host, *Solea solea* (Linnaeus) (Soleidae), by chemoreception, that they attach to the skin of *S. solea* in preference to other soleid, pleuronectid, and elasmobranch flatfishes, and that they did not develop to maturity when attached to other soleid flatfishes. Similar experiments have not been conducted on species representing essentially all remaining families of Monogenoidea, where considerable variation in the results would be expected.

1.2.2. On the newly infected host (the post-oncomiracidium)

Seldom found in the literature are descriptions of the post-oncomiracidium, the non-ciliated larva that is attached to the surface of the host and after having migrated to a suitable microhabitat, normally develops to a mature adult [12–14]. The lack of descriptive work on the post-oncomiracidium is perhaps related to the fact that it does not represent a clearly distinctive life-history stage, i.e., it does not encyst or infect an intermediate host and does not radically metamorphose from the oncomiracidium. The loss or lack of cilia might be used as a biomarker for identification of the post-oncomiracidium, but some monogenoids, i.e., gyrodactylids, udonellids and acanthocotylids, lack surface cilia in all life-history stages [15,16]. Furthermore, post-oncomiracidia are minute relative to their corresponding adults and generally lack species-level diagnostic characters, which renders them interesting but not altogether useful for alpha-taxonomy.

1.2.3. Within the optimal microhabitat (the conspecific adult)

In addition to the daunting tasks of sampling free-swimming oncomiracidia in an oceanic water column and tracking the migration of post-oncomiracidia on fast-swimming pelagic fish, determination of the biology of these life stages is made still more difficult by the scarcity of published records of co-infections of post-oncomiracidia and adult monogenoids. Possible explanations may be i) that the post-oncomiracidium may grow and develop rapidly upon infecting the "normal" host that had harbored its parent(s) or ii) that pelagic marine hosts encounter swarms of infective oncomiracidia that simultaneously infect and transform into post-oncomiracidia at nearly comparable rates. The literature indicates that most adult monogenoids exhibit site specificity [17], suggesting that migrating post-oncomiracidia that fail to reach the hypothetically optimal site or microhabitat on the host eventually die. Alternatively, infections of minute post-oncomiracidia on the gill or in sites outside of the typical microhabitat of the adults are almost always overlooked by investigators during necropsy. In some cases, workers may choose to discard these tiny specimens, which they know lack useful diagnostic characteristics, and focus on the larger adults, which can be identified to species.

1.3. Relevance of the present study

Although the literature on the life cycles of monogenoids suggests that an oncomiracidium would eventually mature, copulate and reproduce once it successfully finds and attaches to a host, few reports suggest a larval monogenoid can attach and apparently persist within a microhabitat on a host without maturing and producing eggs as an adult [18–20]. During surveys of the monogenoidean parasites of fishes from the Gulf of Mexico, several fish species have been found to be parasitized by gastrocotylinean post-oncomiracidia that apparently fail to develop to adulthood. In this paper, these host-parasite records are reported and their potential significance on apparently dead-end hosts is discussed in regard to the life history of the helminths.

2. Materials and methods

Flying fish were opportunely collected from the deck of a research vessel after chance nighttime landings by airborne fish; other hosts were captured with hook-and-line or baited traps from the north-central Gulf of Mexico (29.98°N; 88.49°W) off Mississippi in August 2007 and from the eastern Gulf of Mexico (Florida Middle Grounds, 28.50°N; 84.50°W) off Florida during May through October 2009. Scientific names of fishes are those provided in FishBase [21] and verified using the Catalog of Fishes [22]; common names of fishes are from Nelson et al. [23]. After capture, the gill basket of each fish was excised, placed in a labeled vial or sample bag, doused with hot water (65–70 °C), fixed in 5% phosphate-buffered formalin, and shipped to Idaho State University for study. Monogenoids were subsequently removed from the sediment with a fine probe and either individually mounted unstained in Gray & Wess medium or stained with Gomori's trichrome [24] or Van Cleave's hematoxylin [25] and mounted in Canada balsam on microscope slides. Drawings were made with the aid of a microprojector or camera lucida mounted on a compound microscope. Measurements, all in micrometers (μm), represented the greatest straight-line distances between extreme points and were presented as the average followed by the range and number (n) of specimens measured in parentheses; body length included the length of the haptor. Helminth specimens were deposited in the United States National Parasite Collection (USNPC), Beltsville, Maryland; the University of Nebraska State Museum, Harold W. Manter Laboratory of Parasitology (HWML), Lincoln, Nebraska; and the Invertebrate Specimen Collection (FSBC-I) of the Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute, St. Petersburg, Florida (Table 1).

3. Results

Post-oncomiracidia of the suborder Gastrocotylinea (Figs. 1–18) were collected from formalin-fixed gills excised from six species of marine fishes from the Gulf of Mexico off Mississippi and Florida (Table 1). Two of 2 (100%) common dolphinfish, *Coryphaena hippurus* Linnaeus and 1 of 1 (100%) pompano dolphinfish, *Coryphaena equiselis* Linnaeus (both Perciformes, Coryphaenidae), 1 of 9 (11%) gray snapper, *Lutjanus griseus* (Linnaeus) (Perciformes, Lutjanidae), 1 of 1 (100%) greater amberjack, *Seriola dumerili* (Risso) (Perciformes, Carangidae), and 2 of 2 (100%) Atlantic flyingfish, *Cheilopogon melanurus* (Valenciennes) and 2 of 5 (40%) sailfin flyingfish, *Parexocoetus hillianus* (Gosse) (both Beloniformes, Exocoetidae) were infected. Each of these fish species represents a new host record for gastrocotylinean post-oncomiracidia.

Post-oncomiracidia were identified as members of the Gastrocotylinea by having a haptor armed with i) anterior and posterior pairs of ventral anchors; ii) four bilateral pairs of hooks directed ventrally and positioned along the lateral haptoral margin; and iii) a bilateral pair of usually morphologically distinct hooks situated ventrally near the posterolateral margin of the haptor (Figs. 1, 10). The diagnostic posterior anchor, having a large deep root that is flattened bilaterally