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Host-Parasite Relationships between the Copepod *Naobranchia lizae* and its Host (Striped Mullet, *Mugil cephalus*): A Description of Morphological Development

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**ABSTRACT** The parasitic copepod, *Naobranchia lizae*, is often found within the gill arches of the striped mullet, *Mugil cephalus*, in the Charleston Harbor Estuarine System of South Carolina. The parasite is relatively common, but little is known about its early stages of development. In order to describe the developmental stages and pattern of morphological development, 221 female *N. lizae* that were collected between February 2002 and May 2003 were used. Using variation in morphological characters (maxilla, trunk), these parasites were assigned to developmental stages (juvenile, subadult, adult). A small number of the males (three ‘dwarf’ males) were also found attached to the females. In females, size measurements revealed that the maxilla, which plays a role in initial attachment to the gill, was generally larger than the trunk in the juvenile stage. In contrast, the trunk, which is associated with egg production, was larger than the maxilla in the adult stage. This is the first study to describe the pattern of growth of *N. lizae* in nature and this description should provide useful information for future studies on this common host-parasite relationship.

**INTRODUCTION**

Parasitism is a symbiotic ecological interaction between two organisms, where one organism (the parasite) lives on or in another organism and benefits from the association, while the other is negatively impacted (the host). Parasite infection has been shown to influence individuals, populations, communities, and ecosystems, thus emphasizing the importance of parasites to ecological and evolutionary relationships (Moore, 2002; Poulin, 2011). Although numerous studies document the occurrence of host-parasite relationships in nature, the pattern of growth and development of the parasites is often not described (e.g., El...
Hafidi et al., 1997; Baker et al., 2005). This type of description is critical because it provides the foundation upon which ecological and evolutionary questions can be addressed. The study presented here provides a detailed analysis of the pattern of development of a copepod parasite that is commonly found on the gills of its fish host (Figure 1).

Figure 1. Naobranchia lizae on the gills of Mugil cephalus; dorsal; scale bar = 0.5 mm

The crustacean copepod Naobranchia lizae (Krøyer, 1863) is a hematophagic (blood-feeding) parasite found on the gills of fishes in the Southeast region of the United States and the Gulf of Mexico (Wilson, 1915). In this genus, there is considerable size dimorphism between the sexes, with males (categorized as ‘dwarves’) being significantly smaller than females (Bush et al., 2001; Hamza et al., 2015). Striped mullet Mugil cephalus is a common host of N. lizae (Baker et al., 2005) and distribution patterns of N. lizae on the gills appear to be influenced by competitive interactions between female N. lizae (Baker et al., 2005). Roubl (1999) documented the morphological development of females in a related species, Naobranchia variabilis, but there has not been a study detailing the development of N. lizae. The study describes the pattern of development of female N. lizae using morphological characters. These descriptions are based on 221 females recovered from the gills of M. cephalus. Three male N. lizae were also recovered attached to females but they were not described in detail because of both their small size and low level of occurrence in the sample.

The morphological features examined in this study were the maxilla, trunk, and egg sacs (Figure 2a). Although varying in relative size with N. lizae development, maxilla and trunk are present in all three stages. The parasite has been found positioned on the gill arch with the dorsal portion exposed along the external surface of the gill filaments, while the ventral side, containing the maxilla, is closest to the surface of the gill (Figure 1). The maxilla is paired and ribbon-like (Figure 2a), and encloses around the gill filaments of the host for temporary attachment during feeding, and categorizes the genus Naobranchia (Hamza et al., 2015). The maxillae of N. lizae also possess three muscle strands, and the maxilla is connected medially and anteriorly on the ventral surface of the trunk, possessing a claw-like hook at the distal end that is visible when extended (Nigrelli, 1935; Wilson, 1915). At maturity, the trunk is longer than wide with rounded edges, and flattened dorso-ventrally (Wilson, 1915). Egg sacs are evident as membranous pouches in the subadult and adult stage. The cephalothorax consists of the head and neck of the parasite, beginning from the most anterior tip of the head, and ending posteriorly at the most anterior edge of the collar-like swelling (Figure 2a). It is usually found curved in a hook-like position, with the most curved part of the cephalothorax nearest to the gill arch, but it is known to be flexible for feeding (Bush et al., 2001), and thus found in many other positions.

Even though these characters are present at almost all stages (juvenile, subadult, adult), little is known about how they compare in both relative and absolute size across each stage of development. The goals of this study were to document the pattern of morphological development of N. lizae, provide a description of the major developmental stages, and to include relevant measures of growth. This information will be used in future studies examining the physiological and reproductive costs of competitive interactions.
METHODS

A sample of 221 female intact *N. lizae*, recovered from the gills of *M. cephalus* obtained from the Charleston Harbor Estuarine System between 2002-2003, was used for the analysis. These samples were originally collected as part of a larger study on competitive interactions among gill parasites (Baker et al., 2005). All of these samples were preserved in 70% ethanol at the time of collection and stored until use in this study. The identification of parasites to species-level was confirmed using Wilson (1915) and Nigrelli (1935).

Female *N. lizae* were assigned to developmental stages (juvenile, subadult, adult) based on the relative size of morphological features (maxilla, trunk, Figure 2a) following Roubal (1999). Size measurements of each morphological feature were then obtained to describe the stages (see Figure 2b). Measurements were made using a stereoscopic dissecting microscope (Leica MZ12). Specifically, maxilla length (ML) was measured parallel to the long axis of the gill filament. Trunk length (TL) was measured from the anterior end of the trunk underneath the collar-like swelling, to the posterior end of the fused abdomen. Trunk width (TW) was measured directly between the two maxillae, parallel to the muscle strands.

RESULTS

JUVENILES

There were four *N. lizae* categorized as juveniles (Figure 3a). Juveniles were generally small in size (TL < 0.5 mm). At this stage, maxilla length was larger than trunk length ($t_3 = 4.0, p < 0.05$) and there were no egg sacs present. The mean sizes of maxilla and trunk were: TL = 0.35 mm (SD = 0.15, range = 0.18-0.49), TW = 0.29 mm (SD = 0.14, range = 0.18-0.49), ML = 0.47 mm (SD = 0.12, range = 0.34-0.61).
SUBADULTS

There were 99 *N. lizae* categorized as subadult females (Figure 3b). Subadult females were generally larger than juveniles (TL, \( t_{100} = 5.4, p < 0.001 \)). In the subadult stage, maxilla length and trunk length were similar in size (\( t_{97} = 1.1, p > 0.05 \)). Egg sacs were present but did not contain eggs and the membranous tissue of the sac was wrinkled and shrunken medially toward the body. The mean sizes of maxilla and trunk were: TL = 1.4 mm (SD = 0.39, range = 0.37-2.1), TW = 0.44 mm (SD = 0.13, range = 0.18-0.79), ML = 0.1.4 mm (SD = 0.38, range = 0.58-2.1).

ADULTS

There were 118 *N. lizae* categorized as adult females (Figures 3c, 3d). Adult females were generally larger than subadult females (TL, \( t_{211} = 7.2, p < 0.001 \)). In the adult stage, maxilla length was smaller than trunk length (\( t_{114} = 7.0, p < 0.001 \)). Egg sacs were present, or lacked eggs but were swollen in appearance and had a smooth surface. Females that contained eggs in their sacs were categorized as gravid (gravid, \( n = 82 \); non-gravid, \( n = 36 \)). The mean sizes of maxilla and trunk were: TL = 1.7 mm (SD = 0.27, range = 0.97-2.3), TW = 0.57 mm (SD = 0.21, range = 0.21-1.8), ML = 1.6 mm (SD = 0.30, range = 0.67-2.2).

PATTERN OF GROWTH AND DEVELOPMENT

The relationship between growth and development for female *N. lizae* is summarized in Figure 4. Most of the body size growth occurred between the juvenile and subadult stage during which time TL increased by 300%, ML increased by 189% and TW increased by 52%. Some additional growth occurred between the subadult and adult stages during which time TL increased by 23%, ML increased by 14% and TW increased by 30%.
DISCUSSION
The general body plan of *N. lizae* is similar to the other members of the *Naobranchia* genus, in that they possess ribbon-like maxillae for attachment on to gill filaments, an elongated neck and head for feeding, as well as the presence of a trunk and egg sacs at maturity (Nigrelli, 1935). Detailed information about developmental stages has been provided for one member of this genus, where growth of the parasite has been related to growth of the trunk and maxilla (*N. variabilis*, Roubal, 1999). Overall, these species are similar in appearance, but differences occur in the morphology of the maxillae and egg sacs, and relative width of the trunk (Nigrelli, 1935; Roubal, 1999). Maxillae differ between species in that *N. variabilis* have four muscle strands and are relatively short (0.87 mm). In contrast, *N. lizae* have three muscle strands and are relatively long (1.6 mm) (Nigrelli, 1935). Average trunk width in adult *N. variabilis* is relatively wide (2.0 mm, Roubal, 1999) compared to *N. lizae* (0.6 mm). These differences emphasize the importance of providing a detailed description of the pattern of growth and development of *N. lizae*.

Comparison of the relative sizes of trunk and maxilla during different developmental stages revealed that maxilla size was larger than trunk size in the juvenile stage, and that this relationship was reversed in the adult stage. This pattern differs to the pattern in *N. variabilis* (Roubal, 1999). One hypothesis to explain this pattern is associated with the role of the maxilla during attachment of *N. lizae* to gill filaments. A juvenile *N. lizae* wraps the maxilla around a gill filament to secure a position on the gill during the early stages of development. The longer maxilla may result in a more secure attachment to the gill filament. Following attachment, the parasite could allocate more energy to trunk
growth, resulting in an increase in relative size of trunk to the maxilla during the adult stage.

An additional observation was made concerning the occurrence of male *N. lizae* in the sample, which was that there were relatively few males compared to females (3 males, 221 females ≈ 1% males). Each of the three males was found attached to females from each developmental stage, which is consistent with previous observations of *N. variabilis* (Roubal and Graham, 1999). This observed pattern may indicate that males in this species exhibit precopulatory mate guarding, where the male attaches to the female prior to copulation. The male then inseminates the female during the short time period that the female is receptive to copulate (Roubal and Graham, 1999). It has also been proposed that females store sperm for later use and that males are motile (Roubal and Graham, 1999). This pattern is somewhat consistent with a study of *N. variabilis*, in which males were less common than females (males ≈ 16%, n = 1233, Roubal and Graham, 1999). However, the percentage of males to females in *N. lizae* was only 1%, indicating that male *N. lizae* were less common than male *N. variabilis*. Future studies are required to determine the potential biological significance of this difference.

In summary, the results provide the first description of the pattern of growth and development of female *N. lizae* on the gills of *M. cephalus*. This pattern is relatively consistent with patterns described in other members of the genus *Naobranchia*, but appears to differ in terms of the relative growth of maxilla and trunk during development. More studies are required to determine the potential biological significance of this difference. Future research will use this descriptive information to examine seasonal development of *N. lizae* and the potential for competition, both within and between developmental stages, to influence site preference among gills.

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**AUTHOR CONTRIBUTIONS**

All authors contributed extensively to this project. ST collected the data, wrote the paper, and captured all photographs and images. TS designed the study and analyzed the data. ID provided samples and provided preliminary information about the parasites.
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