ORIGINAL ARTICLE

Infection prevalence and pathology of the cymothoid parasite *Olencira praegustator* in Atlantic menhaden

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Abstract

Isopod parasites in the family Cymothoidae can cause reduced growth, castration, or even mortality in their hosts. *Olencira praegustator* is a cymothoid that parasitizes the mouth and gill chamber of *Brevoortia tyrannus* (Atlantic menhaden), which is the basis for the largest fishery along the eastern coast of the USA and an important link within estuarine food webs. To better characterize interactions between *O. praegustator* and *B. tyrannus*, including parasite-induced pathology, we sampled hosts and parasites from three estuarine sites on Kiawah Island, South Carolina. Over 5 weeks, we collected, measured, and weighed 169 juvenile menhaden; remarkably, 96% of these fish were infected with *O. praegustator*, typically with one isopod found in the mouth of each host. Based on the external morphologies of 163 examined isopods, 58 were female (35.6%), 9 of which were gravid, and 105 were male (64.4%). Although fish size was unrelated to isopod length or mass, isopod length was a direct predictor of the amount of damage observed on the host operculum, which in severe cases involved tissue atrophy and hemorrhage. Considering the high infection prevalence, significant damage associated with infections, as well as the impairing effects of other cymothoids on their hosts, the consequences of interactions between *B. tyrannus* and *O. praegustator* warrant additional investigation for understanding the management and ecology of Atlantic menhaden.

KEYWORDS
Brevoortia tyrannus, Cymothoidae, disease pathology, isopod, parasite ecology

1 | INTRODUCTION

Cymothoidae (Crustacea, Isopoda) is a family of obligate ectoparasites that infect boney and cartilaginous fishes in aquatic environments worldwide, excluding the Arctic (Smit et al., 2014). Most cymothoids are found in shallow tropical waters, and the central Indo-Pacific supports the highest cymothoid diversity, with 79 of the estimated 365 species worldwide (Smit et al., 2014). While 310 species representing 32 genera of Cymothoidae are found on or in marine fishes, several genera have adapted to freshwater systems, notably within the Amazon Basin and Rift Valley Lakes in eastern Africa (Hata et al., 2017; Smit et al., 2014). As true ectoparasites, cymothoids attach exteriorly to the scales of fish, burrow inside hosts' body cavities, or infest the buccal and branchial cavities, where they consume host tissue and blood (Sikkel & Welicky, 2019; Smit et al., 2014). Although many species are relative generalists able to infect multiple species (Bruce, 1986; Smit et al., 2014), others have been documented on only a single fish species. For instance, *Anilocra chaetodontis* Bunkley Williams & Williams 1981 can infect four species in the genus *Chaetodon* (Welicky et al., 2017), but *Mothocya bermudensis* Bruce, 1986 is highly host specific and has only been reported from one species, the common halfbeak (*Hyporhamphus unifasciatus* Ranzani 1841) (Bruce, 1986).

All species in Cymothoidae exhibit protandrous hermaphroditism in which individuals hatch sexually undifferentiated, initially develop male reproductive organs, and eventually undergo a transformation into a sexually mature female (Cook & Munguia, 2015; Jones et al., 2008). After they are released from the marsupium of a gravid female, sexually undifferentiated juvenile isopods (mancae; Adlard & Lester, 1995) are free living in freshwater and marine environments. Mancae seek out and attach to hosts on which they feed and grow in size (Cook & Munguia, 2015; Fogelman & Grutter, 2008). If this host is a suitable definitive host and is uninhabited by conspecifics, the mancae may persist and develop into sexually mature females (Fogelman & Grutter, 2008; Jones et al., 2008) which are no longer capable of moving between hosts. If a mature female is already present, males will mate before seeking out a new host on which to begin the hermaphroditic transition into a female (Fogelman et al., 2009; Mladineo, 2003; Trilles, 2007). There is also substantial variation in reproductive output among cymothoid taxa; gravid females of *Anilocra apogonae* BRUCE 1987 produce as few as 53–178 mancae per brood (Fogelman & Grutter, 2008), whereas females of *Ichthyoxenos fushanensis* TSAI & DAI 1999 produce between 107 and 820 mancae per brood (Tsai et al., 1999). Although some cymothoid life cycles have been well documented (Adlard & Lester, 1995; Jones et al., 2008; Tsai et al., 1999), there is broad heterogeneity among species in both host use and specific attributes of the life cycle, with many species remaining under studied.

Cymothoids can impair growth and cause physical damage to their hosts during all life stages (Fogelman et al., 2009; Kroger & Guthrie, 1972; Mladineo, 2003; Rameshkumar et al., 2013; Sikkel & Welicky, 2019; Smit et al., 2014). Immediately after release from the marsupium, mancae of *A. apogonae* are capable of attaching and taking a blood meal from a host (Fogelman & Grutter, 2008). The aggressive feeding behaviors documented in all life stages of cymothoids can lead to localized hemorrhaging, lesions, and atrophy of gill filaments of hosts (Adlard & Lester, 1995; Guthrie & Kroger, 1974; Stephenson, 1976), and pathology associated with

infection can negatively impact host individuals and even populations when the prevalence is high (Horton & Okamura, 2001; Papapanagiotou & Trilles, 2001; Parker & Booth, 2013). For example, Čolak et al., (2018) reported that commercially raised meagre (*Argyrosomus regius* ASSO 1801) were, on average, 33% shorter in length and 74% lower in mass when infected with *Ceratothoa oestroides* (RISSO 1816), relative to uninfected individuals. Others have demonstrated experimentally that cymothoid infection of juvenile cardinal fish results in undeveloped gonads and decreased sex hormone concentrations, in some cases leading to castration (Da Silva et al., 2005; Fogelman et al., 2009). Host mortality can also occur when cymothoids infect juvenile fish, particularly if the duration of infection is prolonged (Adlard & Lester, 1995; Fogelman & Grutter, 2008). Lastly, cymothoid isopods can negatively affect host behavior by impairing locomotion (Binning et al., 2013), altering daily migration patterns (Welicky & Sikkel, 2015), and increasing agonistic interactions with conspecifics (Meadows & Meadows, 2003).

In the western Atlantic Ocean, juveniles of the Atlantic menhaden, *Brevoortia tyrannus* (LATROBE 1802), can become infected with the cymothoid parasite *Olencira praegustator* (LATROBE 1802), which typically attaches underneath the operculum or in the upper palate of the buccal cavity (Figure 1; Trilles, 2007). Although first observed in the early 1800s, interactions between *O. praegustator* and *B. tyrannus* remained relatively unexplored until Kroger and Guthrie (1972) surveyed 19 estuaries from Massachusetts to Florida to better understand infection prevalence and distribution of *O. praegustator*. Prevalence was highest in Nansemond River, Virginia, where 46% of *B. tyrannus* were infected (range 0%–46%). They also documented visible pathology linked to infection: infected individuals exhibited destroyed rakers, damaged or missing gill filaments, and hemorrhaging from the eyes and snout (Kroger & Guthrie, 1972). In a subsequent study to determine whether *O. praegustator* infects *B. tyrannus* outside of their estuarine nurseries, Guthrie and Kroger (1974) assessed infection prevalence within ~ 100,000 adults of *B. tyrannus* collected offshore by commercial fishing boats and found

FIGURE 1 Infection by the isopod *Olencira praegustator*. **A.** Juvenile Atlantic menhaden (*Brevoortia tyrannus*) infected with female of *Olencira praegustator*, prior to removal of the isopod. The fork length of captured individuals of *B. tyrannus* was 168.8 ± 0.03 mm (mean ± *SE*; range 146.4–196.5 mm; *n* = 169). **B.** Ventral view of gravid female of *O. praegustator* following removal. The average length of gravid female isopods was 27.96 ± 0.43 mm (range 26.41–30.33 mm; *n* = 9)

that few were infected. Based on results from both studies (~50% prevalence in juvenile populations in estuaries and ~ 0% infection in adult populations offshore), the authors suggested that *O. praegustator* infects only juveniles of *B. tyrannus* within estuarine ecosystems and that infected individuals of *B. tyrannus* also have difficulty avoiding capture. More than 30 years later, Trilles (2007) published detailed morphological drawings and descriptions of each life stage of *O. praegustator* based on previously deposited specimens. However, no other published research has assessed the patterns of infection in fish hosts or considered the pathological impacts of infection.

Understanding the prevalence and pathology of *O. praegustator* is further relevant for managing the commercial fishery for *B. tyrannus*, which represents the largest fishery on the U.S. Atlantic coast, and supports a multimillion-dollar industry with thousands of jobs across the mid-Atlantic states (Franklin, 2007). Alongside its economic importance, *B. tyrannus* also plays an influential role in marine food webs by providing predatory species such as bluefish, striped bass, mackerel, and bottlenose dolphins with a major prey resource (Franklin, 2007; SEDAR, 2020). By converting planktonic biomass into resources accessible by higher trophic levels, *B. tyrannus* is considered a critical link in the flow of energy within coastal ecosystems (Ahrenholz, 1991; Buchheister et al., 2017; Franklin, 2007). A more complete understanding of the relationship between *O. praegustator* and its primary fish host could thus provide valuable information as to the consequences of infection for juvenile menhaden growth or recruitment.

In the present study, we examined interactions between the cymothoid parasite *O. praegustator* and juveniles of *B. tyrannus* to characterize the patterns of infection and evaluate the signs of infection-associated pathology. Within three estuarine nurseries on Kiawah Island, South Carolina, we assessed how infection prevalence varied among sites and with host demographic information such as sex, size, and weight. By creating a novel metric to record standardized operculum damage in fish hosts, we quantified the relationship between isopod size, life stage, and the amount of pathology in menhaden. Our goal is that this additional information will enhance not only our understanding of how parasitism by *O. praegustator* affects its host *B. tyrannus*, but also contribute information relevant for future ecological and economic management efforts.

2 | METHODS

2.1 | Study sites

Sampling sites were located on Kiawah Island, SC, a barrier island 40 km southwest of Charleston, SC (Figure 2). The Kiawah River extends westward from the Atlantic Ocean and eventually moves southwest, separating Kiawah Island from the mainland. The eastern end of the island supports ~ 13 km^2 of salt marsh habitat with a network of tidal creeks that flood at high tide twice daily (Ward, 981). We selected three sampling sites (Figure 2) located at the terminal end of the tidal creeks and within 10 m of Governor's Drive, Kiawah Island: Bass Creek (latitude and longitude in decimal degrees 32.6126, −80.0459), Fire Site (32.6139, −80.0514), and Governor's Drive (32.6161, −80.0496). The pools that form at the end of these creeks are similar in size but vary in distance from the Kiawah River. These salt creeks support breeding and nursery grounds for not only *B. tyrannus*, but also striped mullet, *Mugil cephalus* LINNAEUS 1758; red drum, *Sciaenops ocellatus* (LINNAEUS 1766); black drum, *Pogonias cromis* (LINNAEUS 1766); mummichog, *Fundulus heteroclitus* (LINNAEUS 1766); and spotted sea trout, *Cynoscion nebulosus* (CUVIER 1,830) (Shenker & Dean, 1979). Other common species present
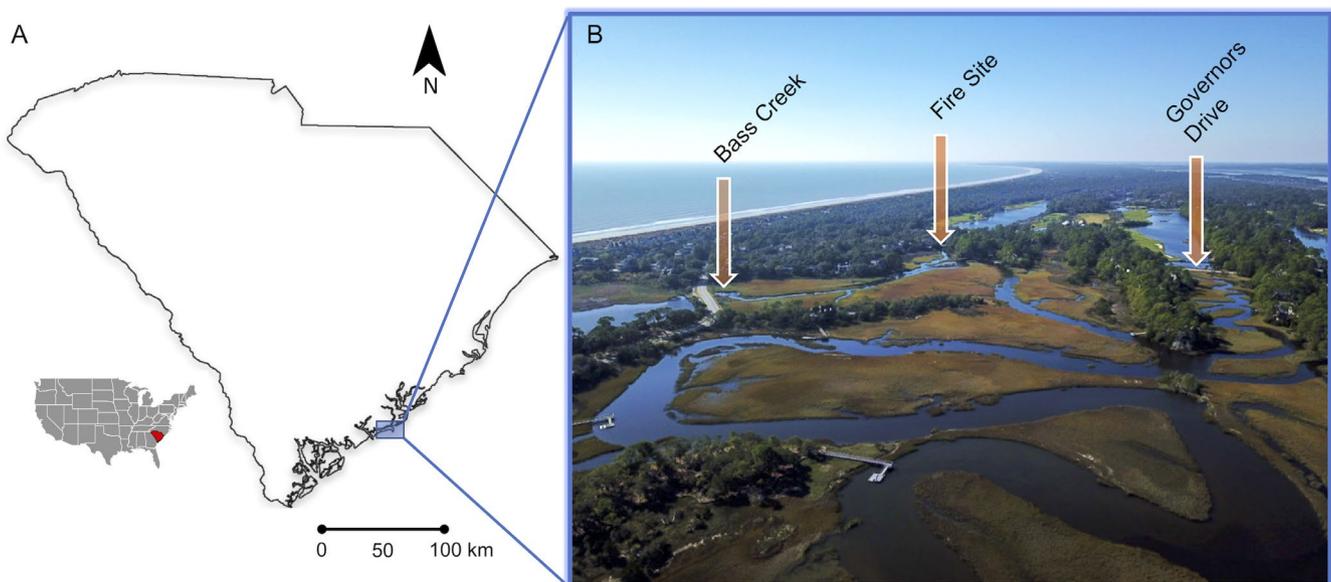
FIGURE 2 **A.** Atlantic menhaden (*Brevoortia tyrannus*) were collected from three locations at the terminal ends of Bass Creek, which is fed by the Kiawah River system of South Carolina. **B.** The three marked locations denote Bass Creek (BC; latitude and longitude in decimal degrees 32.6126, −80.0459, Fire Site (FS; 32.6139, −80.0514), and Governor's Drive (GD; 32.6161, −80.0496). The linear distance between BS and FS is 0.4 km, and that between FS and GD is 0.37 km
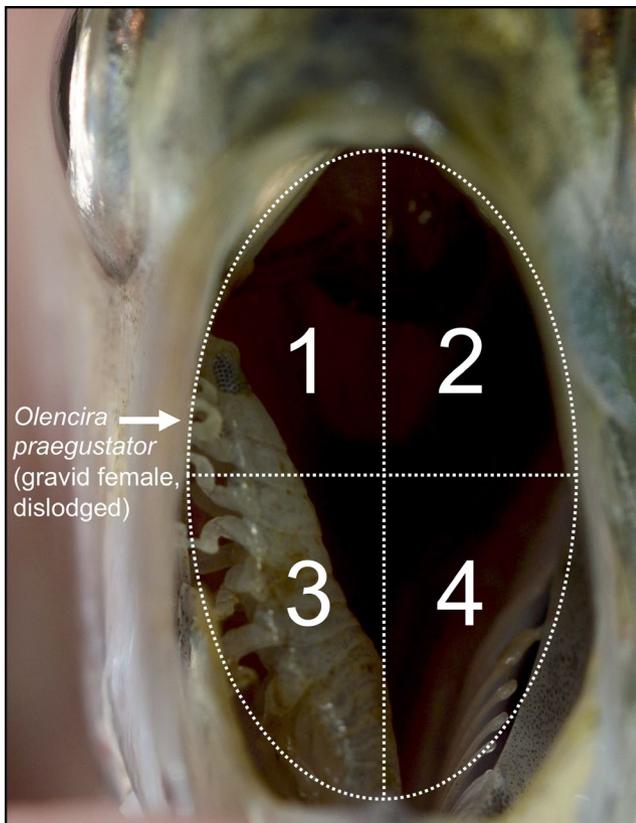
in these creeks include southern flounder, *Paralichthys lethostigma* JORDAN & GILBERT 1884; sheepshead, *Archosargus probatocephalus* (WALBAUM 1792), and the introduced blue tilapia, *Oreochromis aureus* (STEINDACHNER 1864) (Canonico et al., 2005; Shenker & Dean, 1979).

2.2 | Field surveys

To determine infection prevalence by *O. praegustator*, we sampled *B. tyrannus* in July and August of 2017 using a 1.2-m cast net with 16-mm mesh. Sampling was conducted during low tide to facilitate catching success. When casting efforts were successful, we first released any nontarget fish species after checking them for infection by examining their mouth and gills. Captured individuals of *B. tyrannus* were briefly held in a 20-L bucket with aerated seawater. If an isopod was observed, we documented the location of the parasite and its orientation within the buccal cavity. Because there is differential use in microhabitat between life stages of *O. praegustator* (Trilles, 2007), the exact locations of each isopod were recorded as a quadrant of the buccal cavity (1 = top left, 2 = top right, 3 = bottom left, 4 = bottom right). We also designated whether the isopod was facing anteriorly or posteriorly (i.e., rear facing or front facing, respectively; see Figure 3). Isopods were then carefully extracted

FIGURE 3 Classification system for recording the position and orientation of isopod parasites, *Olencira praegustator*, when examining field-caught individuals of *Brevoortia tyrannus*. For each infected host, the location and position of parasites were noted using a quadrant system numbered one through four

from fish hosts by use of forceps (Figure 1), identified as *O. praegustator* based on the descriptions provided by Trilles (2007), placed into sterile 20-mL vials, and stored on ice for further analysis. We used digital calipers to measure fork length (mm) of each fish, which is the distance from the tip of the snout to the end of the middle caudal rays. A subset of infected fishes was photographed to assess the exterior damage to the operculum (see below).

Specimens of *O. praegustator* were massed (g), measured (mm), sexed, and classified by life stage using the illustrations and descriptions provided by Trilles (2007). To determine sex, the seventh set of pereopods was compared to sets 1 through 6. In mature females, the seventh set of pereopods is significantly longer than that in males to anchor the marsupium while brooding young (Trilles, 2007). The absence of setae on the uropods (or swimming appendages) is another indicator that the specimen is a mature female. Once transformed into females, individuals of *O. praegustator* no longer have the need to swim and these body parts are lost (Trilles, 2007). Although we recognized that some male individuals could have been transitioning to females, the use of discrete and external morphological characteristics did not allow identification of such individuals. Specimens were thawed for 20 min at room temperature and blotted dry to remove excess water prior to measurement on a microscale with a precision of 0.001 g.

2.3 | Statistical analysis and rating of infection-associated pathology

We used generalized linear models (GLMs) to evaluate whether attributes of the host (length) influenced attributes of the parasites (mass, length, or sex). Because nearly all sampled hosts were infected, regardless of site, we were unable to evaluate host or environmental factors that influenced the likelihood of infection. In addition, we characterized the allometric relationship between parasite length and mass using a GLM after natural log transformation. To predict the body size inflection point for hermaphroditic sex change in *O. praegustator*, we used a binomial GLM with a logit link function, with parasite body length as a fixed effect predictor and parasite sex (male or female) as the response. This analysis specifically examines the degree to which parasite body size reliably predicts parasite sex, as classified based on external morphology. Finally, we assessed whether the number of *O. praegustator* per host deviated from random (i.e., expected values following a Poisson distribution) using a chi-square goodness-of-fit test. Models were implemented using the lm and glm functions in R (R Core Team, 2019).

We assessed infection-associated damage in hosts from photographs of infected individuals. Using the freely available software program ImageJ (Schneider et al., 2012), we used the trace function to calculate the area of damaged tissue (in pixels) present on the opercula of infected fish. Cymothoid species, including *O. praegustator*, cause damage to host branchial chambers, gill filaments, and gill arches (Trilles, 2007); this damage associated with buccal and branchial parasites is attributed to both consumption of host tissue

and the abrasive nature of a large parasite occupying such a tight space (Stephenson, 1976). When severe enough, operculum damage can even become evident externally on a fish. Because the distance between the camera and the host in each photo varied, we standardized values by dividing the area of damaged operculum by the area of the pupil of the eye (black circle in the center of the iris). Because the pupil can be consistently measured with the oval tool in ImageJ, this approach facilitated uniform damage calculations among images even for instances when we did not have direct measurements of fish body length. We used a GLM with a Gaussian distribution to test the influence of parasite body length on the standardized amount of operculum damage.

3 | RESULTS

We sampled 169 individuals of *B. tyrannus* from three sites on Kiawah Island, SC, and of these samples 163 were infected (96%). At Bass Creek, 98% of individuals (n = 49) were infected, 88.7% (n = 47) were infected at Fire Site, and 100% (n = 66) were infected at Governor's Drive (Figure 2). Of the six uninfected individuals of *B.*

TABLE 1 Life stages and size attributes from a sample population (n = 163) of *Olencira praegustator* in Kiawah Island, South Carolina. Determination of isopods as male or female was based on external morphology only and descriptions provided by Trilles (2007)

|	Number	Proportion	Average mass (g)	Average length (mm)	Gravid
Male	105	0.64	0.09	15.88	–
Female	58	0.36	0.217	22.21	9
Total	163	1.00	0.135	18.41	9

tyrannus, five exhibited possible signs of previous infection (i.e., scarring in the mouth or branchial cavities), leaving only one individual with no visible signs of current or previous infection. All but one of the infected hosts supported a single individual of *O. praegustator*. One specimen of *B. tyrannus* contained an adult female of *O. praegustator* and a small manca, which escaped from the gill chamber as it was collected. Based on the goodness-of-fit test, the distribution of parasites on hosts was nonrandom, such that more hosts than expected supported exactly one isopod (164 observed, 62.14 expected), whereas fewer than expected hosted two or more isopods (1 observed, 30.15 expected; $\chi^2 = 253.82$; $df = 3$; $p < .0001$). The average length of *B. tyrannus* was 168.8 ± 0.03 (mean ± SE; range 146.4–196.5 mm), suggesting that most individuals were young of the year (yearlings) or approaching sexual maturity (Ahrenholz, 1991; Guthrie & Kroger, 1974).

All detected individuals of *O. praegustator* were in one of the two locations: on the roof of the buccal cavity facing anteriorly (quadrants 1 and 2; n = 58; Figure 1A), or in the gill chambers facing posteriorly (quadrants 3 and 4; n = 105; Figure 3). Of the specimens collected, 58 were female (35.6%) and 105 were male (64.4%; Table 1). The average length and mass of examined isopods were 18.41 ± 0.29 mm and 0.135 ± 0.007 g (mean ± SE), respectively. On average, female isopods were 37.1% longer and 128.4% heavier than males (length, $t = 12.98$, $df = 70.29$, $p < .0001$; mass, $t = 8.51$, $df = 61.77$, $p < .00001$). Of the 58 females, nine were gravid (Figure 1B). The smallest specimen was a male with a length of 12.32 mm and a mass of 0.035 g, whereas the largest individual was a gravid female with a length of 28.57 mm and a mass of 0.472 g, which was nearly 13.5× heavier than the smallest specimen. While there was no relationship between host and parasite length (GLM, $R^2 = 0.001$, $p > .1$), isopod length and mass exhibited a strongly allometric relationship, as expected ($df = 160$, $R^2 = .88$, $p < .0001$; Figure 4). Parasite size and sex were also strongly related; because *O. praegustator* is a protandrous

FIGURE 4 Mass (g) as a function of length (mm) in the parasitic isopod *Olencira praegustator*, after natural log transformation. Males are indicated as green triangles and females as orange circles. Isopod length and sex together accounted for ~ 88% of the variation in isopod mass, illustrating the allometric relationship between growth and sexual dimorphism (ln[mass] = −9.276 + 2.460*ln[isopod length]; $R^2 = .88$; $p < .0001$). The best-fit line, with 95% confidence interval, is depicted
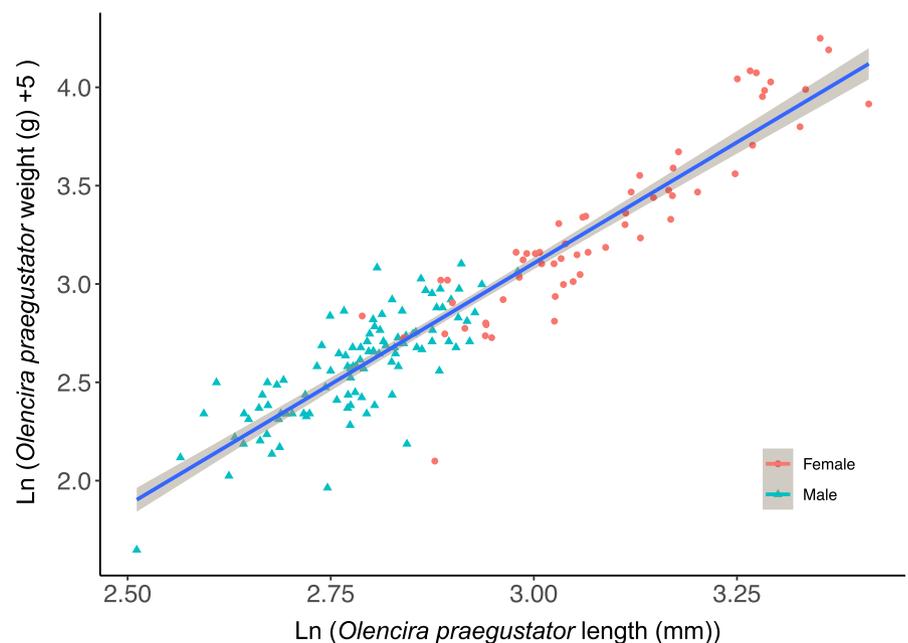
hermaphrodite, individuals begin the reproductive cycle as males and eventually transform into females. Based on a logistic regression to predict sex, this transition occurs at ~18 mm in length (Binomial GLM, effect of length $\pm SE = -1.764 \pm 0.342$, $z = -5.15$, $p < .0001$; see Figure 5).
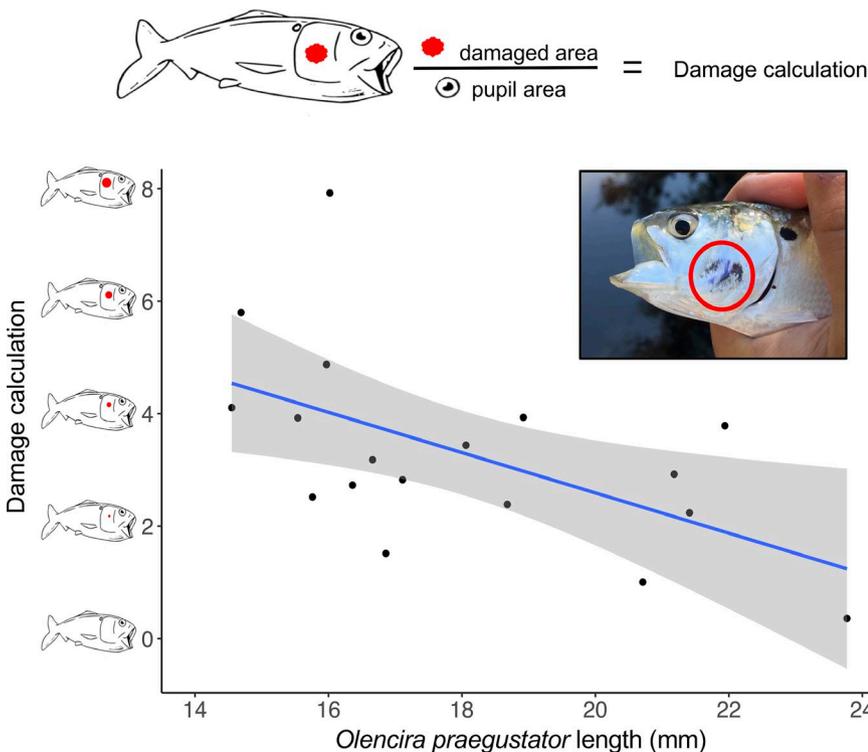
A subset of infected individuals of *B. tyrannus* ($n = 18$) were photographed to assess the degree of external pathology or damaged tissue (Figure 6). Damaged tissue on the operculum and hemorrhaging from the eyes and buccal cavity were recorded; in extreme cases, we observed a large portion of the operculum atrophy from the host, leaving gill filaments exposed underneath. Based on the ImageJ analysis, estimated values for damaged tissue on the operculum

(calculated as a pixel ratio of the damaged area relative to fish pupil size) ranged 0–7.93 (mean, 2.91 ± 0.42; Figure 6). Among fish with evident damage, smaller isopods were associated with greater external pathology (GLM, effect of parasite length $\pm SE = -0.361 \pm 0.099$, $t = -3.64$, $R^2 = .42$, $p < .005$). This finding likely owed to the strong relationship between parasite length and sex: smaller parasites were more likely to be male (see Figure 4), and males more often infected the operculum and gill chamber. Mature females were found almost exclusively in the buccal cavity, where any incurred damage was less visible externally.

None of the other fish species examined exhibited any signs of infection by *O. praegustator*. In total, we collected six additional fish
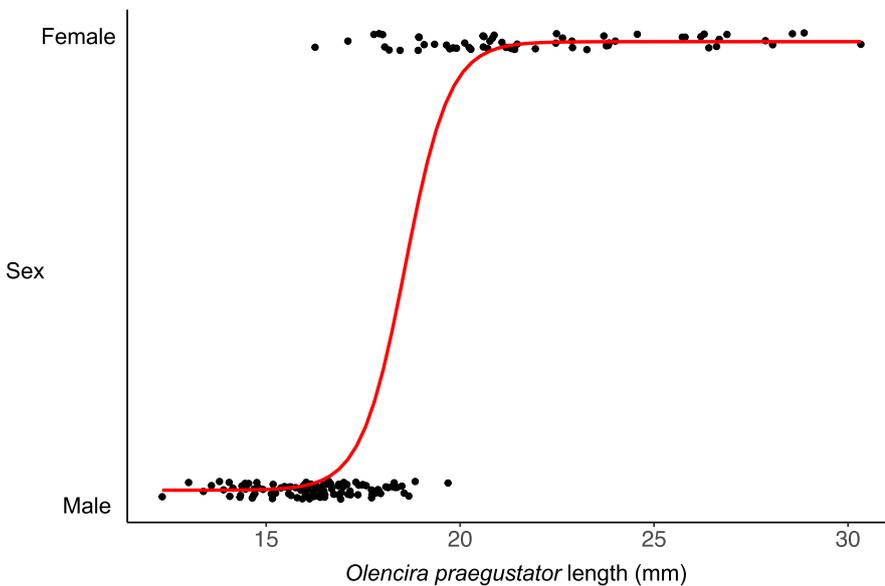
FIGURE 5 Binomial logistic regression plot illustrating the relationship between isopod length and the presence of sex-specific morphological characteristics in the parasitic isopod *Olencira praegustator*. The red line reflects the best-fit line from the generalized linear model with a logit link function and binomial distribution (logit[p] = −1.764*[isopod length] +0.342)

FIGURE 6 Relationship between infection by the isopod *Olencira praegustator* and pathology in the fish host, *Brevoortia tyrannus* (Atlantic menhaden). Visible damage on the operculum of individuals of *B. tyrannus* as a function of infecting isopod length ($R^2 = .28$, $p < .005$, $n = 18$). The damage calculation is the ratio of the pixel size of external lesions or damage relative to the pixel size of the fish pupil as the method of standardization. The ratio, which ranges 0.146–7.93 among fish with detected pathology, correlated negatively with parasite length (mm), suggesting that smaller isopods are associated with more visible operculum damage in the host. Blue line represents with the best-fit line from the regression analysis, with the 95% confidence interval indicated with gray shading

species, including ~250 striped mullet, *M. cephalus*, 12 tilapia, *O. aureus*, 1 red fish, *S. ocellatus*, 4 mummichog, *F. heteroclitus*, 1 black drum, *P. cromis*, and 37 pinfish, *Lagodon rhomboids* (Linnaeus 1766). Although mummichogs and drums were reported as hosts for *O. praegustator* by Trilles (2007), we detected evidence of infection only among individuals of *B. tyrannus*.

4 | DISCUSSION

Cymothoid parasites are a highly pathogenic group of crustacean ectoparasites that frequently specialize on fish hosts. Particular species or environmental conditions have been associated with negative effects on host growth (Roche et al., 2013), reproduction (Fogelman et al., 2009), behavior, and energetics (Binning et al., 2013), especially when prevalence is high (Rameshkumar et al., 2012). Despite the ecological and economic importance of Atlantic menhaden (Buchheister et al., 2017; Franklin, 2007; SEDAR, 2020), surprisingly little is known about interactions in this species with the cymothoid *O. praegustator*. Sampling from the current study of juveniles of *B. tyrannus* in estuaries from South Carolina yielded a remarkably high infection prevalence of 96.4%. This is considerably higher than previous values for infection prevalence reported by Kroger and Guthrie (1972), which ranged 0%–46% among sites. To the best of our knowledge, it is also among the highest prevalence of cymothoid parasites reported in wild fish populations (Panakkool-Thamban et al., 2016; Parker & Booth, 2013; Ravichandran et al., 2016; Roche et al., 2013; Welicky & Sikkel, 2014). Indeed, the high prevalence values among sites (88%–100%) precluded us from testing for correlations between site-level characteristics (e.g., temperature, salinity, or pH) and infection by *O. praegustator*. Why prevalence was so high remains an open question; the locations of our sampling sites are at the terminal end of tidal creeks, which could facilitate transmission by pushing hosts through narrow passageways or confining them into lower volume channels, particularly at low tide. Additional, comparative sampling throughout different portions of tidal creeks would be informative to understand whether it was these specific sites or this entire marsh that support such elevated infection. It is noteworthy that Kroger and Guthrie (1972) sampled 19 different marshes distributed across 11 states in the eastern USA, for which the average prevalence was 7.2%.

Beyond the high prevalence values, our results reinforce and extend the findings of the few previous studies on this host–parasite interaction. Kroger and Guthrie (1972) noted severe damage to the operculum, gills, and rakers of juvenile menhaden, as also observed here. Our results helped to quantify the link between infection and damage to the host operculum. The damage analysis based on ImageJ provided a novel method for assessing the atrophied or damaged tissue associated with infection of the gills, standardized for the size of the host (and more specifically, relative to its pupil). This assumes that the growth of the host is at least allometrically related to the growth of its eye, which requires further validation in the

future. Interestingly, operculum damage correlated negatively with the body length of *O. praegustator*. While superficially surprising, the likely explanation for this trend has to do with differential use of host resources across each life stage of the parasite (Trilles, 2007). In *O. praegustator*, juvenile and male life stages inhabit the branchial cavity of Atlantic menhaden and eventually move to the buccal cavity following the sexual transformation (Trilles, 2007). Feeding during these initial stages causes damage to gills, gill rakers, and operculum through direct consumption of tissue or blood (Trilles, 2007). It is likely that the tissues around the operculum start to regenerate (Stephenson, 1976) by the time a parasite reaches sexual maturity and assumes a front-facing position in the mouth of its hosts, thereby explaining why less damage was detected among hosts with larger (female) parasites. This analysis lends support to the hypothesis of Kroger and Guthrie (1972) that damage to the gills, rakers, and opercula is repaired with time. Although we did not have enough uninfected fishes to quantitatively demonstrate the link between isopod presence and operculum damage, it is unlikely that the observed trauma was due to causes other than infection.

One important question is whether infections by *O. praegustator* and the visible damage associated with them incur fitness costs to menhaden hosts. Several lines of evidence suggest that infections could be costly. First, the amount of damage detected in this study was considerable, often leaving exposed underlying skin and blood vessels (see Figure 6). Such significant injuries have the potential to incur metabolic costs with respect to tissue repair that delay growth or limit energy storage. Concurrently, damage could subsequently lead to secondary infection or increased risk of predation. Other cymothoid parasites are known to cause decreases in fish host fitness following infection (Čolak et al., 2018; Fogelman et al., 2009; Mladineo, 2003; Parker & Booth, 2013). For instance, Fogelman et al. (2009) found that infection by *Anilocra apogonae* castrates its host, *Cheilodipterus quinquelineatus* Cuvier 1828, by decreasing the number and size of ova in females and preventing males from mouth-brooding their young. Similarly, individuals of *Cyphocharax gilbert* (Quoy & Gaimard 1824) exhibit undeveloped gonads and lowered concentrations of sex steroids when parasitized by the cymothoid *Riggia paranensis* Szidat 1948 (Lima et al., 2007).

In addition to fitness costs, other cymothoid hosts have also been documented to swim slower and travel less distance than uninfected conspecifics (Binning et al., 2013; Welicky & Sikkel, 2015). In the Caribbean, cymothoid-infected French grunts, *Haemulon flavolineatum* (Desmarest 1823) were less likely to complete their daily migration to and from their nightly feeding grounds (Welicky & Sikkel, 2015). While behavioral impacts of infection vary by both host and parasite species, these findings support the anecdotal observations by Guthrie and Kroger (1974) that cymothoid-infected individuals of *B. tyrannus* exhibit impaired movement and are more likely to remain in estuaries with juveniles and other injured adults. During daytime trawling efforts, they captured 11 fish in the genus *Brevoortia*, all of which harbored individuals of *O. praegustator*; conversely, during similar nighttime trawling efforts, only 0.5% of 4,000 captured fish were infected. Guthrie and Kroger inferred that infected individuals were less able

to avoid daytime capture in comparison to uninfected conspecifics. Because reproduction of *B. tyrannus* depends on successful migration to pelagic spawning grounds (Ahrenholz, 1991), future studies need to address whether populations of infected *B. tyrannus* can reliably reach their spawning grounds.

We observed exceptionally high parasite prevalence, including scarring, among the few uninfected hosts, and nonrandom parasite distribution (i.e., overrepresentation of hosts with exactly one parasite). To better understand how such exposure affects juvenile fish growth, survival, and reproduction, we highlight the value of combining both experimental infection studies in a controlled environment, as well as field-based studies involving the removal of infections from tagged menhaden. One interesting question is whether aspects of the pathology induced by individuals of *O. praegustator* in fish hosts are a function of attachment site or morphology of the parasite. In contrast to many other buccal cymothoids that attach to the tongue or the buccal floor, *O. praegustator* attaches upside down to the upper palate of its host (Trilles, 2007; Welicky et al., 2019). One other example of a palate-infesting isopod is *Cinusa tetrodontis* Schioedte & Meinart 1884, which parasitizes fishes in South Africa (Welicky et al., 2019). Further comparisons between these and similar cymothoids with respect to morphology and host damage would be valuable. For instance, while both of these cymothoids are similar in length, individuals of *O. praegustator* are much narrower than *C. tetrodontis*: a gravid female of *O. praegustator* is 3.7 times as long as wide (Trilles, 2007), whereas a female of *C. tetrodontis* is 1.3–1.5 times as long as wide (Hadfield et al., 2010). These discrepancies may be associated with differences in host ecology; because menhaden are filter feeders with large gaping mouths and are constantly processing water for microorganisms, individuals of *O. praegustator* likely experience greater hydrodynamic forces than most other buccal-dwelling isopods.

Understanding the consequences of infections by *O. praegustator* for *B. tyrannus* can also inform management. Every year, the Atlantic States Marine Fisheries Committee publishes a stock assessment update, yet so far parasitic infections are not a factor considered in the assessment. The 2020 *B. tyrannus* assessment reads, "no information is available concerning the extent of parasitism or its possible effect on survival [of *B. tyrannus*]" (SEDAR, 2020). Even relatively small effects on host growth and survival could manifest to substantial differences in yield when considered at the scale of commercial operations, which harvest over 100,000 metric tons (mt) of *B. tyrannus* annually (Franklin, 2007; SEDAR, 2020). Populations with high parasite prevalence, such as those on Kiawah Island, have the potential to operate as population or biomass sinks for Atlantic menhaden, particularly if infected individuals have a lower likelihood of reaching sexual maturity. It will thus be important to determine whether the localized hotspots of infection detected here are anomalous or part of a larger spatial or temporal trend, for which the current data shortage limits our knowledge. Considering the high prevalence cited in this study, and the possibility of other ecosystems along the Atlantic coast exhibiting similar infection rates, understanding large-scale patterns of infection by *O. praegustator*, as well as its effects on *B.* *tyrannus* populations, will be valuable for informing future management decisions and characterizing parasite effects on the food web.

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