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FISH PARASITOLOGY - ORIGINAL PAPER

Microhabitat preference, body size, and egg allocation in the gill parasite *Naobranchia lizae* (Copepoda)

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Abstract

The relationships between microhabitat preference, body size, and egg allocation were examined in the copepod *Naobranchia lizae*, which establishes on the gills of striped mullet *Mugil cephalus*. A total of 297 individual *N. lizae* (mean intensity = 5.0 ± 4.8 SD) were recovered from 60 infected hosts collected from the Charleston Harbor Estuarine System, South Carolina USA. For each mullet, we identified 16 microhabitats per gill arch, which yielded 128 microhabitats per host that could potentially be occupied. On average, only 5% of these microhabitats were occupied per host. The distribution pattern of the copepods on the gills revealed that microhabitat preferences occurred both among and within gill arches. For the microhabitats occupied, there was no effect of preference on body size, egg number, or egg size. Similarly, microhabitat sharing, which was more likely to occur at higher infection intensities, was not costly in terms of the copepod body size and egg allocation and there was no detectable trade-off between egg number and egg size. However, results also revealed that about half (48%) of the available microhabitats were never occupied by the copepods. We suggest that the occupancy of these potentially poor quality sites could carry fitness costs not realized in nature since numerous high quality sites are available per host. The findings are consistent with the interpretation that female *N. lizae* occupy a resource-rich habitat on the gill arches of striped mullet that provides conditions for optimal growth and reproduction.

Keywords *Mugil cephalus* · Striped mullet · Copepod · Lernaeopodidae · Reproductive allocation

Introduction

Parasites that inhabit fish gills often exhibit non-random distribution patterns, which likely indicate that microhabitat preferences occur both among and within gill arches (Rohde 1980; Kabata 1981). These preferences have been identified in several gill parasites such as copepods and monogeneans (e.g., Rohde 1980; El Hafidi et al. 1998; Lo and Morand 2001; Siquier 2012; Soler-Jiménez and Fajer-Ávila 2012). Numerous factors associated with properties of the gills have been proposed to influence these preferences, including physical space, water flow, nutrient and mate availability, and competition (e.g., Rohde 1979, 1994; Ramasamy et al. 1985; Gutiérrez and Martorelli 1999; Timi 2003). These types of preferences are expected to be correlated with parasite fitness (e.g., Sukhdeo 1991; Timi et al. 2010) but little is known about the effects of these microhabitat preferences on fitness-related traits in gill parasites.

Members of the genus *Naobranchia* (Lernaeopodidae) are sanguinivorous copepods on the gills of fishes where they exhibit preferences for microhabitats both among and within gill arches (Roubal 1999; Zimmermann et al. 2001; Baker et al. 2005a). Individuals of *N. variabilis* Brian, 1924 prefer anterior gill arches as well as specific regions within gill arches in toadfish (Roubal 1999); individuals of *N. occidentalis* Wilson 1915 prefer middle gill arches and internal hemibranchs in northern rock sole (Zimmermann et al. 2001); and individuals of *N. lizae* (Krøyer, 1863) prefer anterior gill arches in striped mullet (Baker et al. 2005a). We examined the relationship between microhabitat preference and fitness-related traits (body size and egg allocation) in the naobranchiid *N. lizae.*

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In the Charleston Harbor Estuarine System (CHES) in SC, USA, individuals of *N. lizae* are relatively common on the gills of striped mullet *Mugil cephalus* Linnaeus, 1758 (see Baker et al. 2005a; Teemer 2016). In these hosts, juvenile female copepods attach to gill filaments, develop into the adult stage, copulate with "dwarf" males, and deposit fertilized eggs into paired sacs (Wilson 1915; Teemer 2016). To determine the potential importance of microhabitat preference to body size and reproductive allocation, we examined preference-related variation in body size, egg number, and egg size. Using samples of *M. cephalus* from the CHES, we addressed the following specific objectives: (1) acquire a fine resolution of the pattern of microhabitat preference both among and within gill arches; (2) determine the relationships between preferences and fitness-related traits (body size, egg allocation).

Methods

A total of 60 infected individuals of *M. cephalus* were collected from the CHES (2013–2015) by members of the South Carolina Department of Natural Resources (SCDNR, Inshore Fisheries Division). Fish, which had been grouped and stored in bags at − 20 °C, were thawed and measured (mean standard length = 216 ± 18.1 SD mm) prior to examination. For each fish, the left and right opercula were removed, gill arches were dissected individually in distilled water, and the position of each female copepod was recorded at the point of attachment to the gill filament.

To determine the fine pattern of microhabitat preference of the *N. lizae* sample, each of the eight gill arches (four per side) was visually divided into 16 sections, which yielded a total of 128 microhabitats per fish that could potentially be occupied by the parasites (Fig. 1). Microhabitats were assigned codes that identified the following: (1) side of fish (left, right); (2) gill arch (I–IV); (3) gill hemibranch (external, internal); (4) vertical location on gill (proximal to gill bar, distal to gill bar); and (5) anterior-posterior zone of gill (A–D, A being the anterior most). Males were not included in the analysis because they attach to the bodies of females rather than to the gill filaments and are rare in samples from this region (prevalence < 2%, Teemer 2016). Occurrence and location of the monogenean *Metamicrocotyla macracantha* (Alexander 1954) was also recorded. These worms are typically found wrapped around the gill filaments and have been recovered from striped mullet in the CHES (Baker et al. 2005a, b). Additionally, the bodies or body parts (prehensile antennae) of ergasilid copepods were often present but were not attached to specific fish, and hence could not be assigned accurately to a host. Voucher specimens of female *N. lizae* were deposited in the Manter Laboratory of Parasitology, University of Nebraska–Lincoln, USA ($n = 4$, Catalog # HWML-110894).

To determine the relationships between microhabitat preference, body size, and egg allocation, we removed each female *N. lizae* from the gill filaments. To avoid damage during collection, the relevant gill filament was sectioned at its point of connection to the gill bar, and both the filament and the attached parasite were preserved and stored individually in 70% ethanol (EtOH). Each individual was then separated from its gill filament by carefully uncoiling the maxilla. The total number of female *N. lizae* was recorded and mean intensity calculated according to Bush et al. (1997). Developmental stage (juvenile, subadult, adult) was identified for each female according to Roubal (1999) and Teemer (2016), and body size measurements (trunk length, TL; trunk width, TW; maxilla length, ML; neck length, NL; neck width, NW) were recorded for each gravid female (Fig. 2). Egg number was determined by counting the number of eggs present in the egg sacs of gravid females. Egg size was determined by measuring 20 eggs (length, width) from each gravid female then calculating the average. A sub-sample of 20 eggs per female was used rather than all of the eggs because this number was found to be

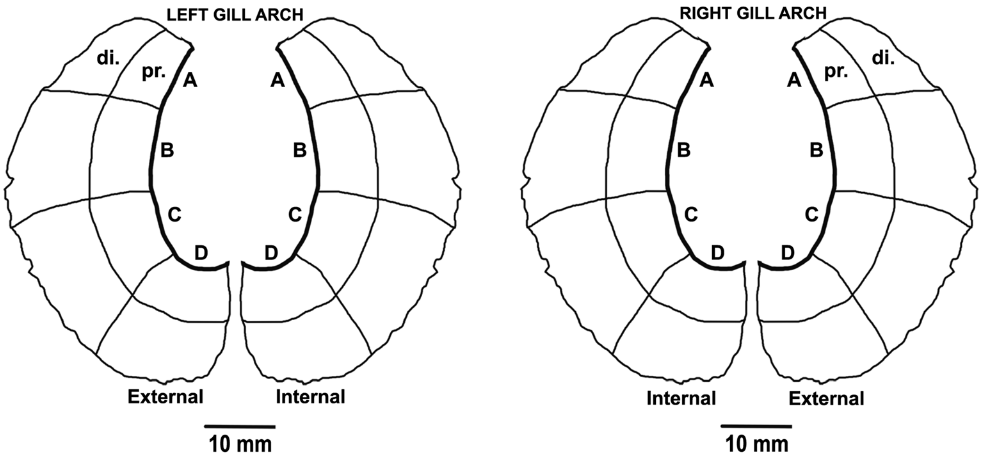

Fig. 1 Gill zoning system used to locate female *Naobranchia lizae* on the eight gill arches of their host, *Mugil cephalus*. Shown are the outer surfaces of a representative gill arch (flattened) to indicate the left and right sides of fish, both hemibranchs (external, internal), zones that are distal (di.) and proximal (pr.) to the gill bar (represented by the bold line), and anterior-posterior zones (A–D), with A being the anterior most zone

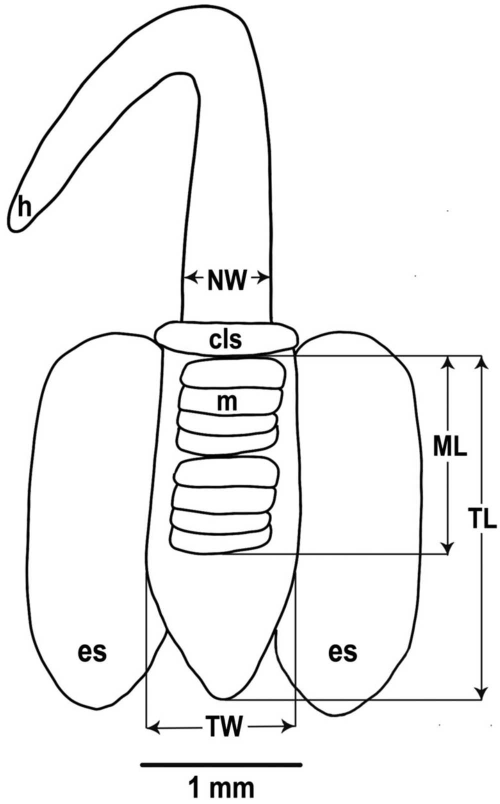

Fig. 2 Body measurements and morphological features of female *N. lizae* (ventral side). m, maxilla; es, egg sac; cls, collar-like swelling; TL, trunk length; TW, trunk width; ML, maxilla length; NW, neck width. Neck length (not shown) was measured between the head (h) and anterior border of the cls

sufficient to estimate mean egg size for the entire clutch (i.e., inclusion of values beyond 20 did not change the estimate, $n = 10$ gravid females).

We used analyses that accounted for the lack of independence between copepods that share a host to determine the patterns of microhabitat preference among and within gill arches. When comparing parasite numbers between two groups (left vs. right side; proximal vs. distal to gill bar; external vs. internal hemibranch), we used a Wilcoxon signed-rank test (Systat 13). When comparing parasite number among four groups (gill arches I, II, III, IV; zones A, B, C, D within a gill arch), we used a Friedman's test with post hoc comparisons (Systat 13).

Correlation analysis (Pearson, Spearman) was used to determine the relationships between the different measures of body size, egg allocation (egg number, egg size), host size, and infection intensity. Only hosts that contained gravid females were included in the analysis ($n = 32$), and the host was used as the unit for analysis to maintain independence among values. Thus, values obtained for each of the measurements (TL, TW, ML, NL, NW, egg number, egg size) were averaged when more than one individual was present on the same host. We used nested ANOVAs (nested by host) for each variable (body size, egg number, egg size) to determine the relationships between microhabitat preference, female body size, and egg allocation. We used paired *t* tests (paired by host) to compare values for body size, egg number, and egg size between females that differed in microhabitat sharing to determine if microhabitat sharing influenced body size and egg allocation. We used logistic regression to determine if infection intensity was a predictor of microhabitat sharing.

Results

A total of 297 female *N. lizae* were recovered from the 60 hosts examined (mean intensity = 5.0, SD = 4.8, range = 1–25). There was no correlation between intensity of female *N. lizae* infection and host size (standard length, $r_s = -0.2$, $p > 0.05$, $n = 60$). There was a small number of monogenean *M. macracantha* present (prevalence = 5%, mean intensity = 1.6, SD = 0.9, range = 1–3). Specimens of *N. lizae* were mostly adult females (adult = 64%, subadult = 29%, juvenile = 7%, $n = 297$), and the proportional distribution (6:3:1) of the different developmental stages was generally consistent among gill arches. On average, only 5% of the 128 microhabitats available per host were occupied by female *N. lizae* (SD = 5%, range = 1–13%, $n = 60$).

Table 1 summarizes the distribution patterns of female *N. lizae* both among and within the gill arches. There was no detectable preference for the right or left side of the fish (Wilcoxon test $Z = 0.8, p > 0.05$). There was a significant preference among gill arches (Friedman test $\chi^2_3 = 61.9, p < 0.001$) and pairwise comparisons revealed that gill arches I, II, and II were preferred over gill arch IV. There was a significant preference for the external hemibranch (Wilcoxon test $Z = 5.9$, $p < 0.001$) and locations proximal to the gill bar within the gill arch (Wilcoxon test $Z = 2.4, p < 0.05$). There was also a preference among zones within the gill arch (Friedman test $\chi^2_3 = 17.7$, $p < 0.001$), and pairwise comparisons that revealed the middle zones (B and C) in the anterior to posterior zoning system were preferred over the other zones (A, D).

Gravid female *N. lizae* were present on the gills of 32 hosts examined. For these females ($n = 144$), four of the five measurements used to assess body size were correlated with each other (TL, TW, ML, NW, $r_p > 0.5, p < 0.001$) but not with host size. Neck length (NL) was not correlated with any of these measures but was correlated positively with host size (standard length, $r_p = 0.32, p < 0.05$). Trunk length (TL) yielded the strongest correlation with egg number ($r_p = 0.6$, $p < 0.001$) and was used to represent body size in subsequent analysis. There was no correlation between TL and egg size ($r_p = 0.05$, $p > 0.05$). Infection intensity was not correlated with TL ($r_s = 0.02$, $p > 0.05$), egg size ($r_s = 0.01$, $p > 0.05$), or egg number ($r_s = 0.1, p > 0.05$). There was also no correlation between egg

Table 1 Microhabitat preference of female *Naobranchia lizae* on the gills of striped mullet *Mugil cephalus*

Location	n	%	Median no. per host	Range	Preference
Left side	144	48	2	0–16	–
Right side	153	52	2	0–12	–
Gill arch I	119	40	1	0–10	P
Gill arch II	82	28	1	0–14	P
Gill arch III	90	30	1	0–8	P
Gill arch IV	6	2	0	0–1	NP
External hemibranch	224	75	2.5	1–22	P
Internal hemibranch	73	25	0	0–8	NP
Proximal to gill bar	180	60	2	0–17	P
Distal to gill bar	117	40	1.5	0–9	NP
Zone A	55	18	0	0–5	NP
Zone B	89	30	1	0–6	P
Zone C	103	35	1	0–12	P
Zone D	50	17	0	0–5	NP

There was no preference for the side of the fish

N. lizae, $n = 297$; *M. cephalus*, $n = 60$; *P*, preferred microhabitats; *NP*, non-preferred microhabitats

number and egg size ($r_p = -0.07$, $p > 0.05$) or relative egg number (adjusted for female TL using residuals) and relative egg size ($r_p = -0.1$, $p > 0.05$).

Table 2 summarizes the relationships between microhabitat preference, body size, and egg allocation for gravid females ($n = 144$). None of the microhabitat preferences described above was associated with variation in body size, egg number, or egg size (nested ANOVA, $p > 0.05$ in all cases). Analysis was not performed on the preference for gill arch (I, II, III, vs. IV) due to the low sample size in the non-preferred group ($n = 2$, Table 2). The mean proportion of gravid/non-gravid adult females was similar between preferred and non-preferred sites (preferred microhabitats = 0.76; non-preferred microhabitats = 0.82).

There were 26 cases of microhabitat sharing, which occurred when two or more females occupied the same zone. Sharing occurred in 14 hosts (mean intensity = 10.1, SD = 6.9, range = 2–25), involved 56 of the 297 females (19%), and was more likely to occur at higher infection intensities (logistic regression, $G_1 = 17.1$, $p < 0.001$, $\rho^2 = 0.3$, $n = 50$). In seven cases, the host harbored both sharing and non-sharing gravid females. For these individuals, there was no detectable effect of microhabitat sharing on TL ($t_6 = 0.7$, $p > 0.05$), egg number ($t_6 = 0.5$, $p > 0.05$), or egg size ($t_6 = 0.6$, $p > 0.05$).

Table 2 Microhabitat preference, body size, and egg allocation for gravid female *Naobranchia lizae* on gills of striped mullet *Mugil cephalus*

	Body size (mm)		Egg number		Egg size (μm)	
Preference	P	NP	P	NP	P	NP
Gill arches I, II, or III [142, 2]	1.85	1.95	382	564	130	134
	(0.28)	(0.69)	(126)	(291)	(7.5)	(1.4)
External hemibranch [102, 42]	1.85	1.85	383	396	131	130
	(0.26)	(0.32)	(138)	(192)	(7.3)	(7.5)
Middle zones [97, 47]	1.87	1.81	372	394	131	130
	(0.29)	(0.27)	(127)	(132)	(7.3)	(7.6)
Proximal to gill bar [80, 64]	1.87	1.83	378	398	131	130
	(0.26)	(0.31)	(131)	(127)	(7.7)	(7.2)
All preferences [56, 88]	1.88	1.83	385	388	132	130
	(0.25)	(0.30)	(132)	(131)	(7.6)	(7.2)

Mean values with one unit of standard deviation in parentheses are provided ($n = 144$). Trunk length represents body size (see text for details). Sample sizes for each preference are in brackets [preferred, non-preferred]. Values for “all preferences” are from individuals that were located in all preferred microhabitats, i.e., proximal to the gill bar in the middle zones of the external hemibranchs of gill arches I, II, or III

P, preferred microhabitat; *NP*, non-preferred microhabitat

Discussion

Previous research on the distribution patterns of female *N. lizae* on striped mullet showed that the anterior gill arches are preferred with gill arch I having the highest level of infection (Baker et al. 2005a). The results obtained here were generally consistent with this pattern in that gill arch I had the highest level of infection although the preference among gill arches in the current sample included arches I, II, and III. The results also extended the previous findings by showing that preferences occurred for sites within the gill arches (external hemibranch, middle regions of the gill, proximal to the gill bar). In addition, the results showed that there were numerous microhabitats that remained vacant in all of the hosts examined, which is a pattern that has been documented for several other gill parasites (Rohde 1980). Preferences similar to those shown in female *N. lizae*, although in different combinations, have been reported for individuals of *N. variabilis* on toadfish (anterior gill arches, external hemibranchs, distal to the gill bar; Roubal 1999) and for individuals of *N. occidentalis* on northern rock sole (middle gill arches, internal hemibranchs; Zimmermann et al. 2001). Physical and biological properties such as space availability, water flow, nutrient availability, mate availability, and competition have been proposed as potential explanatory variables for microhabitat preference in gill parasites (Rohde 1979, 1994; Ramasamy et al. 1985; Gutiérrez and Martorelli 1999; Timi 2003). Several of these factors could potentially play a role in the *N. lizae*–*M. cephalus* system, except for space availability, which appears to be plentiful in this system. However, the lack of consistency in microhabitat preference by congeneric female *Naobranchia* does not provide insights into the specific factors of importance for individuals of this taxon. Instead, microhabitat preferences are likely associated with host physiology and ecology.

Timi et al. (2010) showed that microhabitat preferences were associated with reproductive payoffs in the copepod *Parabrachiella spinicephala* Ringuelet, 1945 (as *Neobrachiella spinicephala*), which attaches to the fins, gills, and operculum of sandperch. In this system, host size acts as a constraint on attachment in preferred microhabitats (fins). In large hosts, females attach to suboptimal sites (lips, operculum) and pay a cost in terms of body size and egg production. Contrary to this pattern, female *N. lizae* did not appear to be constrained in their ability to occupy a small number of preferred microhabitats, and females that occupied either non-preferred or shared microhabitats did not appear to pay costs in terms of body size or egg allocation. Thus, based on the females included in the analysis, there was no association between microhabitat preference and expression of these particular fitness-related traits. It should also be noted that numerous microhabitats were never occupied in any of the fish examined (48%). These microhabitats may represent the true low quality zones, which were not included in the analysis because of their lack of occupancy by female *N. lizae*. It may be the case that these microhabitats carry fitness costs that are not realized in nature because of the abundance of high quality alternatives. It is also possible that fitness-related traits that were not examined here carry fitness costs (e.g., energy content of eggs). A third possibility is that female *N. lizae* do not express preferences among microhabitats and that their distribution is due instead to non-random patterns of water flow over the gills, which deposit the parasites in a non-random manner (e.g., Paling 1968). Regardless of these alternatives, results indicated that the microhabitats occupied by female *N. lizae* on the gills of striped mullet appeared to provide optimal conditions for adult growth, and allocation to both egg size and egg number.

Additional evidence to support the interpretation that female *N. lizae* have access to nutrients in amounts that exceed their needs is provided by the pattern of energy allocation between egg number and egg size that showed no correlation. In free-living freshwater or marine copepods, a trade-off often occurs between egg size and egg number because the energy needed to allocate to both traits simultaneously may be in short supply (e.g., Cooney and Gehrs 1980; Guisande et al. 1996). Parasites that live at low densities with access to high levels of nutrients do not typically experience such a trade-off (e.g., nematodes (Rossin et al. 2005; Herreras et al. 2007), copepods (Timi et al. 2005)), but there are exceptions (Herreras et al. 2007; Cavaleiro and Santos 2014). In female *N. lizae*, no trade-off between egg number and egg size occurred, indicating that egg allocation is unconstrained likely because nutrient availability is high. In addition, while larger eggs in general have the potential to increase body size in later stages, decrease mortality rates, and increase transmission success (Jennings and Calow 1975; Cooney and Gehrs 1980), egg size was not correlated with female body size in *N. lizae*. This likely indicates that females are able to produce eggs of an optimal size regardless of their own body sizes.

In conclusion, while female *N. lizae* do show preferences for particular microhabitats on the gills of the striped mullet *M. cephalus*, occupation of microhabitats that were categorized as non-preferred is not associated with saturation of preferred zones, and there is no indication that females in non-preferred zones or shared preferred habitats pay cost in terms of body size or egg allocation. The lack of trade-offs along with the non-saturation of these parasites' niche reflects the presence of a resource-rich environment that provides optimal conditions for living, typical of low-density populations.

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Compliance with ethical standards

Ethical statement The research presented here is in compliance with national laws and regulations.

Conflict of interest The authors declare that they have no conflict of interest.

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