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The Niche of *Salsuginus thalkeni,* a Gill Parasite of *Fundulus zebrinus*

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THE NICHE OF *SALSUGINUS THALKENI,* A GILL PARASITE OF *FUNDULUS ZEBRINUS*

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ABSTRACT: Distribution of a monogenean parasitic helminth *Salsuginus thalkeni* on the gills of the fish *Fundulus zebrinus* is described by calculation of mean positions and niche breadths on the linear spatial resource gradients gill filament length, gill arch length and arch number. All distributions are given for parasites in the presence and absence of various combinations of potential competitors, namely the 6 other parasite species that occupy the same host species. Filament niche breadth was narrowest in the absence of potential competitors; breadth on arch was widest in the presence of potential competitors. Breadth on both resources was correlated positively with mean number of parasites per individual. Arch breadth exhibited cyclic seasonal changes, being lowest in early to mid-summer. Mean position exhibited no repeated pattern of variation on either resource. The results are considered consistent with predictions about the niche structures of species in unsaturated noninteractive specialist communities.

Monogean site specificity has been studied both descriptively and experimentally by numerous workers (e.g., Llewellyn, 1956; Hanek and Fernando, 1978a, 1978b, 1978c; Ramasamy et al., 1985; Cone and Cusack, 1989). The results suggest that monogeneans partition the spatial (and presumably other, related) resources provided by fish gills (Hanek and Fernando, 1978a; Rohde, 1979; Ramasamy et al., 1985).

Although previous investigators have described and quantified the distributions of monogeneans, none has treated the gill spatial resources as niche dimensions in the Hutchinsonian sense (Hutchinson, 1957). That is, none has considered the parasite niche to be a hypervolume that can be quantified by determining the parasites' distribution on several resources, each of which (e.g., temperature) varies linearly. However, Rohde (1979) stated that in monogeneans, fundamental and realized niches were equivalent, basing his assertion largely on qualitative, rather than quantitative, niche determinations.

The ancyrocephalid *Salsuginus thalkeni* Janovy, Ruhnke, and Wheeler, 1989, which occurs on the gills of the plains killifish *Fundulus zebrinus* Garman, 1895, is an ideal organism upon which to apply not only the Hutchinsonian concept, but also the classic test for competitive interaction. Niche breadth can be calculated on 3 linearly measured spatial resources: primary filament length, gill arch length, and gill arch number. In addition, several other gill and body parasites occur, in a variety of combinations (Janovy and Hardin, 1988). This parasite assemblage thus provides an opportunity to determine whether breadth of the *S. thalkeni* niche on spatial resources is altered in the presence of potential competitors.

Finally, the long-term relative stability of the *S. thalkeni* population suggests that it might be determined whether there exists a relationship between abiotic conditions and parasite niche structure (Janovy and Hardin, 1987).

MATERIALS AND METHODS

The killifish, *F. zebrinus,* used in this study were collected from the South Platte River 5 km west of Roscoe, Nebraska. A total of 298 fish were sampled during 1986–1988. Collection dates (number of fish) for the 14 collections of this study are as follows: 21 May 1986 (24), 4 June 1986 (24), 29 June 1986 (24), 16 July 1986 (14), 26 May 1987 (24), 12 June 1987 (20), 30 June 1987 (22), 8 Sept 1987 (24), 11 May 1988 (16), 1 June 1988 (24), 19 June 1988 (24), 10 July 1988 (20), 9 Aug 1988 (20), 11 Oct 1988 (18); these collections are numbered 1–14, respectively, for reference in the Results section below and in the figures. This paper includes observations on all 2,137 *S. thalkeni* collected from these fish. Summer collections were processed at the Cedar Point Biological Station 13 km north of Ogallala, Nebraska; fish from the 2 fall collections were taken to the University of Nebraska in Lincoln for dissection.

Gills were excised and each arch laid anterior (outside) face up in sequence on a microscope slide. A coverslip was added and the fresh preparation examined under 100× magnification for the presence of *S. thalkeni.* The relative filament position of each worm was recorded by measuring the distance of the midhaptor from the gill arch cartilage, then measuring the length of the filament itself. A similar pair of measurements was made for arch position, recording the distance of the worm from the ventral end of the arch, then measuring the length of the arch itself. The gills were then turned over, the posterior (inside) face examined, and worm positions recorded as described above. In addition, all other parasites in and on the fish were identified and counted.

TABLE I.   Relative position and niche breadth of *Salsuginus thalkeni* on gill filaments and gill arches of *Fundulus zebrinus*.*

Circumstance	Filament position (variance)	Breadth on filament	Arch position (variance)	Breadth on arch	n
All worms	4.1 (3.2)	0.57	6.0 (6.3)	0.91	2,137
Front face	4.2 (3.2)	0.57	5.8 (6.3)	0.92	1,057
Rear face	4.1 (3.0)	0.56	6.2 (6.0)	0.88	1,080
First arch	4.2 (3.8)	0.62	6.6 (6.3)	0.84	358
Second arch	4.2 (3.5)	0.59	5.9 (6.3)	0.91	708
Third arch	4.1 (2.8)	0.53	5.9 (6.6)	0.92	622
Fourth arch	4.1 (2.6)	0.53	5.9 (5.5)	0.86	449
With no other parasites	3.7 (3.2)	0.49	5.1 (6.3)	0.81	96
With *Gyrodactylus bulbacanthus* only	One fish, with 1 worm, was present in this circumstance				
With *Trichodina* sp. only	4.3 (2.6)	0.57	6.3 (5.6)	0.82	137
With *Myxosoma funduli* only	3.9 (2.6)	0.51	7.3 (4.8)	0.66	39
With any combination of gill parasites only	4.1 (2.3)	0.50	6.1 (5.9)	0.83	107
With *Neascus* only	4.5 (3.7)	0.55	5.8 (5.3)	0.80	121
With *Gyrodactylus stableri* only	4.5 (5.3)	0.67	6.0 (5.4)	0.81	102
With any combination of other parasites only	4.1 (3.1)	0.56	6.0 (6.5)	0.92	1,534

* Relative position is the mean of the frequency distribution produced when filament or arch lengths are divided into 10ths, then the number of parasites occurring in each of these 10ths is plotted on the vertical axis, the 10ths being the units on the horizontal axis. Breadth entries are niche breadths calculated according to Levins (see Materials and Methods), using the 10ths as units of a resource set.

Computer entries included, in addition to the field data, code numbers for date, individual fish, and specific combinations of other parasites present. Measurement ratios were converted into decimal fractions, multiplied times 10, then rounded to the nearest integer and summed for each unit. Data summary resulted in frequency distributions of worms on the 2 linearly measured resources known as filament length and arch length. Niche breadths on these resources were calculated according to Levins (1968), whose breadth index B takes into account both numbers of units in a resource set and evenness of an organism's distribution among those units. B varies between 1, for maximum evenness, and 1/S, where S is the number of units in the resource; $S = 10$ in the case of filament and arch position, in this study.

Frequency distributions also were compared by means of 1-way single variable analysis of variance, to determine whether mean position on the 2 resources differed depending on collection date, gill face, fish side, arch number, or presence of other parasites. F values corresponding to probabilities of <0.05 were considered statistically significant. A similar ANOVA was used to test for significance of difference between distributions among the 4 arches. A standardized correlation matrix was constructed, comparing niche breadths, mean positions on the filaments and arches, collection months (May = 5, etc.), and *S. thalkeni* infrapopulations.

The other parasite species occupying *F. zebrinus* were *Gyrodactylus bulbacanthus*, a rare gill monogenean; *Gyrodactylus stableri*, a body surface monogenean; *Trichodina* sp., an ectocommensal gill peritrich (ciliate) protozoan; *Myxosoma funduli*, a gill filament tissue, cyst-forming, protozoan; and larval trematodes (larval genus *Neascus*) in the eyes and body cavity. This assemblage was described in detail by Janovy and Hardin (1987, 1988).

If *S. thalkeni* is adapted to a specific area of the gills, then virtually all members of the parasite population should occur within that area, and if interactions between parasite species occur, then those interactions should appear as alterations in the observed distribution of *S. thalkeni* on the spatial resources studied. A corollary to this hypothesis is that the distributions on spatial resources are independent of individual fish, thus data from more than 1 sample could be combined. The null hypothesis tested was therefore: parameters of frequency distributions on spatial resources are independent of fish, sample, and other associated parasite species. Interactions between members of an *S. thalkeni* infrapopulation were not tested by the study design, but they were suggested after the fact by the correlations reported in Table II.

Terminology is consistent with that recommended by Margolis et al. (1982).

RESULTS

Mean positions of *S. thalkeni* on gill arches and filaments, and niche breadths on these resources, are given in Table I. This table includes those values for all *S. thalkeni*, as well as for the following data subsets: those on anterior and posterior gill faces, on each arch, and occurring with various combinations of other parasites. In single species infections, *S. thalkeni* occurred closer to the gill arch cartilage and closer to the ventral end of the arch than did worms on fish infected with various combinations of other parasite species. These differences were statistically significant in all cases except with *M. funduli* only and
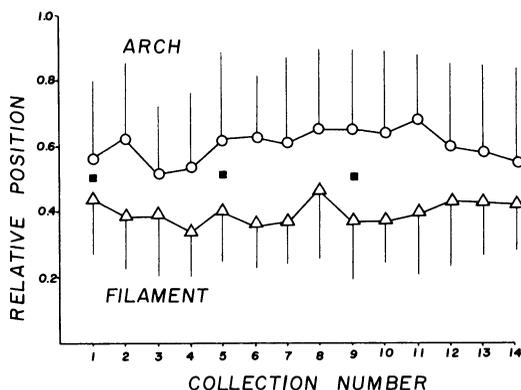
FIGURE 1. Mean relative positions of *Salsuginus thalkeni* on gill arches (circles) and primary filaments (triangles) over time. Vertical lines are variances. Collections 1–4 are from 1986 (21 May, 4 June, 29 June, 16 July); 5–8 from 1987 (26 May, 12 June, 30 June, 8 Sept); 9–14 from 1988 (11 May, 1 June, 19 June, 10 July, 9 Aug, 11 Oct); solid squares are the first collection dates of each of the 3 study years.

TABLE III. Relative position and niche breadth of *Salsuginus thalkeni* on gill filaments and gill arches of *Fundulus zebrinus* not infected with any other species of parasites.*

Circumstance	Filament position (variance)	Breadth on filament	Arch position (variance)	Breadth on arch
Front face	3.4 (2.6)	0.40	4.7 (4.3)	0.69
Rear face	4.0 (3.7)	0.55	5.7 (8.1)	0.80
First arch	3.8 (2.7)	0.56	6.1 (7.5)	0.64
Second arch	4.1 (4.0)	0.41	5.9 (7.7)	0.71
Third arch	3.6 (3.0)	0.49	4.6 (4.1)	0.63
Fourth arch	3.2 (2.6)	0.40	4.1 (5.3)	0.54

* Relative position is the mean of the frequency distribution produced when filament or arch lengths are divided into 10ths, then the number of parasites occurring in each of these 10ths is plotted on the vertical axis, the 10ths being the units on the horizontal axis. Breadth entries are niche breadths calculated according to Levins (see Materials and Methods), using the 10ths as units of a resource set.

other gill parasites only (Table I). There was no statistical difference between the mean filament position of worms on any of the 4 gill arches, or on either face. Arch positions, however, differed significantly, being closer to the ventral end on the anterior face than on the posterior, and furthest from the ventral end on the first gill arch.

Neither filament nor arch positions were significantly different in collections 13 and 14 (see Materials and Methods, above), as shown by *t*-test, indicating transportion of fish had no effect on worm location. Filament position, but not arch position, was significantly higher in collection 8 than in either collection 7 or 9 (Fig. 1). Mean infrapopulations for collections 7, 8, and 9 were, respectively, 2.1, 11.9, and 5.0 worms per fish. Because filament position was correlated positively with infrapopulation (Table II), transportation of sample 8, like that of 13, was judged to have had no effect on the observations.

Mean filament and arch positions, and niche breadths, on both gill faces, and on each of the 4 arches, for only those worms on fish with no other parasite, are given in Table III. There was no statistical difference in mean worm position on filaments, between either the 2 faces or the 4 arches. As in the case with worms from all fish (cf. Tables I, III) mean arch position was closest to the ventral end on the front face and furthest from the ventral end on the first arch. The arch position differences were statistically significant.

All worms were distributed, by percentage, on the gill arches as follows: arch 1, 17%; 2, 33%; 3, 29%; 4, 21% (Table I). This distribution did not vary significantly with any of the tested combinations of associated parasite species, as indicated by ANOVA results. However, distribution on arch varied significantly between anterior and posterior faces under 2 conditions: in the absence of other parasite species, and with any combination of associated gill and body parasites.

TABLE II. Relationships between the various *Salsuginus thalkeni* niche and circumstance descriptors.*

	Collection month	Position on filament	Breadth on filament	Position on arch	Breadth on arch	Mean infrapopulation
Collection month	1.00	0.45	0.29	−0.21	0.40	0.38
Position on filament		1.00	0.73†	0.05	0.47	0.58†
Breadth on filament			1.00	0.12	0.31	0.64†
Position on arch				1.00	−0.32	−0.08
Breadth on arch					1.00	0.61†
Mean infrapopulation						1.00

* Table entries are Pearson's correlation coefficients (*r*); n = 14.
† Probability that *r* = 0 is less than 0.05.

Table II gives correlation coefficients for the pairwise comparison of niche descriptors, mean infrapopulations per sample, and collection month. Both mean filament position and breadth on filament were correlated positively and significantly with mean infrapopulation, as well as with themselves. Niche breadth on arch also was correlated positively and significantly with infrapopulation. However, only in the case of filament position vs. niche breadth on filament was more than 50% of the change in dependent variable explained by changes in dependent variable.

Niche breadths by collection are shown in Figure 2. Niche breadths on the gill arches varied annually, dropping during midsummer of each of the study years. Breadth on the filament also fluctuated over the study period, but there was no repeated annual pattern to these variations. Mean positions of all worms are shown in Figure 1. Although there was no repeated annual pattern to the observed fluctuations, analysis of variance indicated the mean filament and arch positions differed significantly between dates.

DISCUSSION

Previous research has not established for certain whether parasite species assemblages in general are interactive. Those who study rich intestinal faunas tend to interpret their results in terms of interactions described for free-living communities. Thus Stock and Holmes (1987a, 1987b, 1988) and Bush and Holmes (1986a, 1986b) demonstrated abundance hierarchies, reduction of fundamental niches in the presence of presumed competitors, and relatively predictable locations of helminth species within grebe and duck intestines. Those working with species-poor assemblages, however, tend to find little evidence of interactions (Kennedy et al., 1986; Janovy and Hardin, 1988). This difference led Holmes and Price (1986) to predict the occurrence of unsaturated, nonequilibrium, and noninteractive microhabitat specialist, as well as equilibrium interactive communities, the latter with high density populations. Price (1984) and Rohde (1979) extended their discussions of the first to include the idea of vacant niches.

The study of parasite species assemblages has been limited by the relatively few measureable resource gradients that can be studied easily. Intestinal length is 1 obvious such resource, but radial gradients may also exist, and helminths may interact in 1 region of the intestine but not another (Stock and Holmes, 1988). Fish gill par-
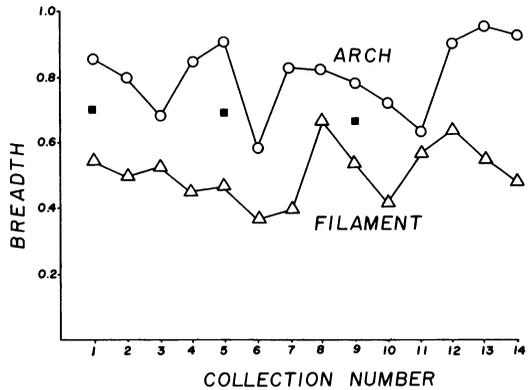

FIGURE 2. Variation in *Salsuginus thalkeni* niche breadths on gill arch (circles) and primary filament (triangles) lengths over time. Collections 1–4 are from 1986 (21 May, 4 June, 29 June, 16 July); 5–8 from 1987 (26 May, 12 June, 30 June, 8 Sept); 9–14 from 1988 (11 May, 1 June, 19 June, 10 July, 9 Aug, 11 Oct). Solid squares are first collection dates of each of the 3 study years.

asites provide an opportunity to begin resolving some of the questions associated with parasite community work, and especially the ones surrounding interactions in species-poor assemblages. If Price's (1984) predictions about specialist assemblages are correct, then little or no evidence for competition between gill monogeneans and other parasites should be seen.

In the present study, *S. thalkeni*'s filament niche breadth was not reduced in the presence of virtually all combinations of potential competitors. In fact, niche breadth was lowest in the absence of other species, suggesting that if present, interactions were of a positive sort, perhaps operating indirectly by reducing the fish's resistance to parasites in general. Niche breadth on the arch was reduced in 1 instance, namely in the presence of only *M. funduli*. But, the observation that arch niche was widest with various combinations of both gill and all parasites, which, on the average, included *M. funduli* more than half the time (Janovy and Hardin, 1987; Knight et al., 1980), suggests that the low niche breadth in the presence of only this species is not a result of direct interactions.

The results also indicate that breadth, as measured in this study, is partially a function of number of worms observed. Thus, in Table III, none of the separate categories has an arch breadth as high as that for the total 96 worms (Table I). However, the mean filament breadth for the 6 categories in Table III is 0.47, whereas that of

the combined sample is 0.49. Biologically, these numbers may reflect the comparatively restricted range of *S. thalkeni* on the filament, as opposed to that on the arch. Thus, the narrower the niche, as on the filament, the more likely a few worms will fall into the full dimension of it. The numbers in Table I also suggest that it is necessary to study about 100 worms to determine the niche breadth on gill arches.

Site specificity in Monogenea has been described in several ways. Llewellyn (1956) analyzed 5 parasite species and found that each occurred most frequently on 1 or 2 gill arches of their respective host species, but he did not quantify the distributions further. Hanek and Fernando (1978a) divided gills into 6 sections and plotted the distribution of 7 monogenean species on the centrarchid fishes *Lepomis gibbosus* and *Ambloplites rupestris*. Most parasites occurred on the anterior gill faces, anterior-medial sections of the gill, and on arches 2 and 3. However, no aspect of the gill was treated as a linear resource gradient.

Rohde (1979, 1981) also addressed the question of whether gill parasite assemblages were interactive. Resources were considered to be host species, geographical range, parts of rivers or areas of reefs, host sex and age, season, and gill arch number and face. Although gill microhabitat was described in a manner similar to that of Hanek and Fernando (1978a) instead of as in the present study, Rohde's (1979) conclusions were that monogeneans exhibited selective site segregation and that fundamental and realized niches were the same.

The prior work most relevant to the present study is that of Ramasamy et al. (1985) involving 4 monogenean species on 4 species of the marine fish genus *Scomberoides*. Gills were divided into regions in a manner similar to that used by Hanek and Fernando (1978a). Instances of actual worm touching, potential touching, and co-occurrence were analyzed using correlations between infrapopulations and the association test of Hurlbert (1969). All 4 parasite species exhibited statistically significant preferences for particular gill regions. Although several species pairs exhibited positive or negative associations, none was statistically significant.

Buchmann (1989) also studied gill monogenea in an attempt to detect interspecies interactions. Although 2 species of *Pseudogyrodactylus* exhibited preferred distributions on gill arches and areas of the gills, those distributions were the same in single species as in mixed species infections. In heavily infected eels, worms of both species were distributed more widely over the gills than in lightly infected fish. However, Buchmann (1989) followed the method of Hanek and Fernando (1978a) in quantifying the distributions.

The present study is the only one to date in which monogenean niche structure is described in a manner consistent with that practiced in the broader field of ecology. The results suggest that the specialist *S. thalkeni* occupies a niche whose dimensions are not reduced in the presence of other assemblage species. This monogenean thus qualifies as a site specialist. However, breadths on arch and filament, and position on filament, all are correlated positively with *S. thalkeni* infrapopulation. Thus niche breadth increases with the number of conspecifics on the host.

ACKNOWLEDGMENTS

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